

An Individual-based Model for Smallmouth Bass Reproduction and Young-of-year Dynamics in Streams

Henriette I. Jager
Donald L. DeAngelis
Michael J. Sale
Webb Van Winkle
Denise D. Schmoyer
*Environmental Sciences Division
Oak Ridge National Laboratory
Oak Ridge, Tennessee 37831-6036*

Matthew J. Sabo
Donald J. Orth
Joseph A. Lukas
*Virginia Polytechnic Institute and State University
Blacksburg, Virginia 24061-0321*

ABSTRACT: We summarize the first step in the development of a new tool to evaluate the influence of alternative flow regimes on smallmouth bass recruitment in streams. Our objectives are to describe and demonstrate a mechanistic model that simulates the relationship between streamflow and smallmouth bass recruitment and to present the results of the first round in an ongoing process of model validation. The model couples the hydraulic simulation method of the Physical Habitat Simulation (PHABSIM) system directly with an individual-based model for smallmouth bass reproduction and young-of-year (YOY) dynamics, thereby eliminating reliance on the habitat-based component of the PHABSIM. We compare simulated reproductive success and first year growth with field observations from the North Anna River in Virginia. Although the model predictions compare favorably with empirical data in many respects, there is room for improvement. For example, our comparisons of reproduction and larval growth suggest that improvements are needed to understand the nesting behavior and re-nesting capabilities of individual spawners in streams and the bioenergetics of larval smallmouth bass. We conclude that research in these two areas, followed by model improvement and a second round of model validation, is needed. Because it is mechanistic and amenable to iterative refinement, the model's potential value as a tool for evaluating the effects of alternative flow regimes on smallmouth bass recruitment is high.

KEY WORDS: Instream flow, *Micropterus dolomieu*, North Anna River, Physical Habitat Simulation, spatial model.

INTRODUCTION

A prominent issue related to stream ecosystems is flow regulation associated with new hydropower development and the relicensing of existing facilities (Sale et al. 1991). Rapidly fluctuating flows, periodic dewatering, low flows, and reduced quality and quantity of habitat are considered to be the most significant con-

cerns for fish populations and stream communities (Bain and Boltz 1989). In the next few decades, the pressures faced by natural resource agencies to recommend instream flows for streams will increase as many hydropower projects undergo federal relicensing and competition for limited water resources increases. Better tools to predict the biological response to alternative instream flow recommendations are needed to improve the scientific basis for these decisions.

Instream flow decisions are usually based on habitat-based models that relate weighted usable area (WUA) available for fish habitat to flow (Reiser et al. 1989). Simplicity and minimal data needs are advantages of these habitat-based models. Unfortunately, there is little correlation between WUA and population status (Orth and Maughan 1982; Mathur et al. 1985) and, perhaps, none should be expected (Gore and Nestler 1988). Uncertainties in the hydraulic simulation techniques used (Osborne et al. 1988), inadequacies in the stream sampling design (Morhardt et al. 1983), and problems in the application of habitat suitability index (HSI) functions undermine the predictive value of WUA. Habitat-based models rely on HSI curves that are purely descriptive and provide no explanations of why fish were observed in different habitats or how habitat use would respond to changes in site, flow, season, fish activity (e.g., foraging), the density of conspecifics, or other factors.

A more fundamental problem is that WUA predicts the elusive and unknowable "carrying capacity" (see Peters 1991) rather than population status itself. This leaves the nontrivial problem of bridging the gap from a lifestage-specific carrying capacity to population status. Models that combine WUA with a stage-based population model have attempted to bridge this gap (Williams 1984; Cheslak and Jacobson 1990; Williamson et al. 1993). We question the ability of these models to translate a carrying capacity into population status without understanding the linkages between habitat and processes that control population dynamics (e.g., reproduction, energetics, mortality). We contend that, in the long run, the best approach to gaining an understanding of, and therefore the ability

to predict, fish response to flow is to study the mechanisms involved.

We developed a mechanistic model that links flow to stream habitat and biological response (i.e., recruitment of smallmouth bass [*Micropterus dolomieu*]), by superimposing the daily activities of individual fish on a heterogeneous stream habitat. It draws on the strengths of two areas: the Physical Habitat Simulation (PHABSIM) system provides the capability for predicting the spatiotemporal distribution of depth and velocity under different flows, and the individual-based modeling approach provides a tool for predicting population dynamics. We use only the hydraulic simulation component of the PHABSIM (Milhous et al. 1989) and replace the usual output, weighted usable area (WUA), with a mechanistic population model of fish response to habitat. To model the reproduction and young-of-year (YOY) dynamics of smallmouth bass we used an individual-based approach (Huston et al. 1988; DeAngelis and Gross 1992; Van Winkle et al. 1993) that simulates individual fish in a representative reach of stream (Morhardt et al. 1983) in a spatially explicit fashion. This modeling approach enables population attributes to depend on relevant attributes of individual fish, which respond, in turn, to a dynamic and heterogeneous stream habitat. The linkages between the physical stream habitat and the life cycle of smallmouth bass are shown in Figure 1.

The spatially explicit nature of the model permits us to include behavioral responses that allow fish to mitigate temporary setbacks in habitat quality. These behaviors, such as reneating after flood events and movement to avoid dewatered stream margins, may have important implications for population persistence. The vulnerability of early less-mobile life stages to local habitat degradation is also represented in a more realistic manner here than is possible using WUA predictions.

The most important advantage of our model is that it lends itself to a process of iterative testing and improvement. Whereas it is unclear what measurable attribute of stream populations WUA predicts, our model provides testable predictions of reproductive success (including the number, timing, and fate of nests) and YOY dynam-

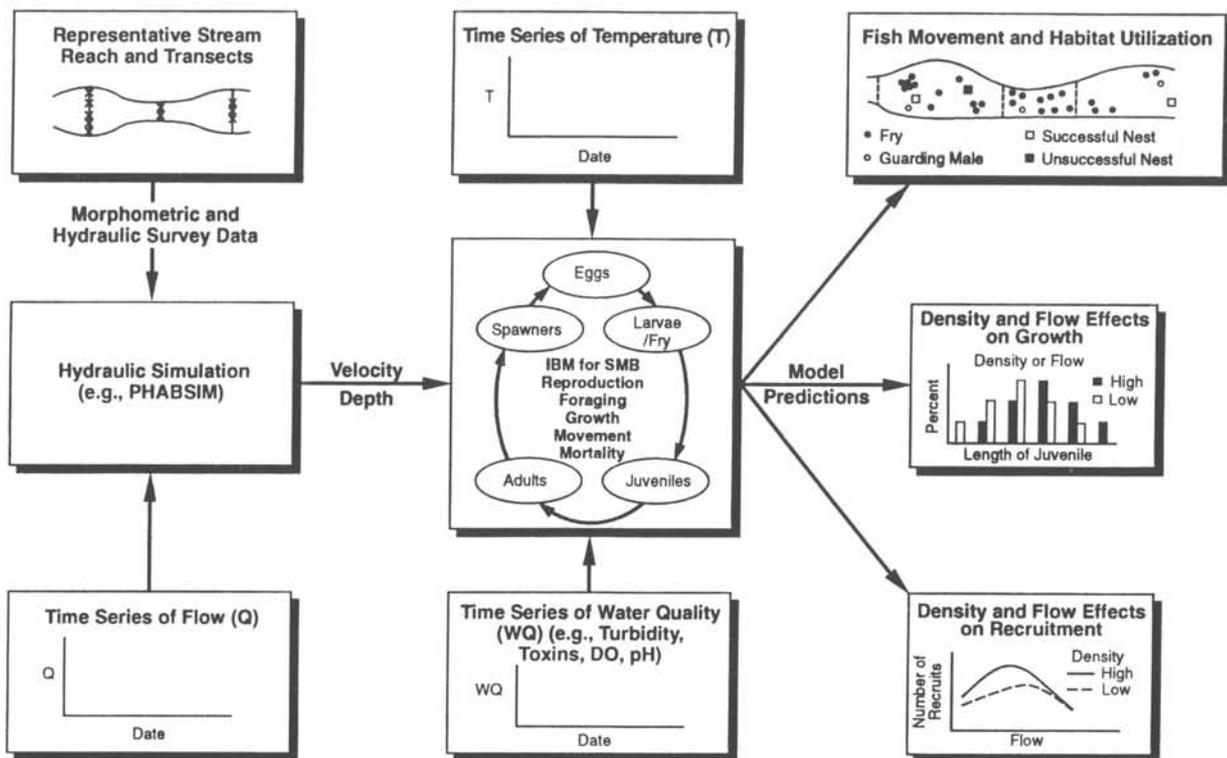


FIGURE 1. Schematic of a model for stream populations of smallmouth bass illustrating linkages between a Physical Habitat Simulation (PHABSIM) as a function of flow and an individual-based model (IBM) of processes (reproduction, growth, movement, and mortality) that regulate each life stage of smallmouth bass (SMB).

ics (including fish numbers, sizes, locations, foraging success, habitat use, and survival). In addition to average population properties, we generate predictions that depend on the attributes of individual fish such as the timing of events during the spawning season, habitat preferences, and fish growth.

This paper describes and demonstrates the model and presents the results of our first round of model validation. We present

baseline simulations for the 1990 and 1991 growing seasons for a representative reach in the North Anna River, Virginia. Field data collected during these two years in this reach are compared with simulation results for smallmouth bass reproduction and YOY dynamics. More detailed information regarding replication or extension of our results can be obtained by contacting the principal author.

MODEL OF STREAM HABITAT

The purpose of our habitat simulation is to predict the spatial distribution of depth and velocity as a function of daily flow. The resulting "streamscape" provides the environmental background on which we simulate the daily activities of smallmouth bass.

The model requires records of streamflow (m^3/sec) and water temperature ($^{\circ}C$) for the period of the simulation (Figure 1). Both records can be provided as input from historical daily measurements, or they can be generated by the model. Currently, we

assume that temperature on a given day is the same for all stream cells. A PHABSIM survey of the representative reach is also needed to simulate the stream habitat. The survey provides measurements of water surface elevation, depth, and velocity at stations spanning cross-sectional transects for a range of streamflows. Substrate is also characterized at these stations.

We partition a representative stream reach into spatial cells such that each cell contains one or more measurement stations used in a PHABSIM survey of the

reach. These cells provide a fixed spatial reference system for the duration of the simulation. Spatial cells are constructed by combining a specified number (aggregation factor) of measurement stations across each transect. Each cell is centered over the measurement stations used to characterize it. Aggregation allows us to translate from the microhabitat scale of the PHABSIM survey to a mesohabitat scale appropriate for the activities of YOY fish on a daily timestep. Adjacent measurement stations that are combined are not required to be similar in depth, velocity, or substrate. Longitudinal cell boundaries extend between transects according to a weighting factor assigned during the survey that indicates the distance upstream represented by conditions at the transect. Average ve-

locity and depth for the aggregated cells are area-weighted averages of station velocities and depths.

The model requires daily predictions of average depth and velocity for each station in the representative reach. Although it is possible to use standard PHABSIM output data as the input to this model, the size of the file necessary to characterize depths and velocities in each cell on each day is prohibitive. A more efficient approach uses the hydraulic component of PHABSIM to estimate hydraulic variables for each measurement station based on the data collected in the PHABSIM survey. These variables are provided to the model as input and are used to predict the depth and velocity of each cell as a function of daily average flow.

MODEL OF REPRODUCTION AND YOUNG-OF-YEAR DYNAMICS

The biological model starts with the spawning of individual adults in spring and follows the progeny until the following spring. The three YOY life stages defined in the model have different characteristics that are important in predicting responses to flow and density (Table 1). The first life stage starts with newly fertilized eggs and ends with the rise of swim-up larvae from the nest when they are between 8.0 and 8.8 mm total length. For this

life stage, the model tracks the characteristics of each brood collectively, rather than as individuals. After swim-up, the larvae are no longer sustained by the yolk sac and rely on foraging for growth. The model tracks fish as individuals from this point of development. Larvae in the brood forage by day under the supervision of the male parent and settle in the vicinity of the nest in the evening. During the gradual transition to the juvenile life stage (13-19 mm), the swimming ability of the larvae improves, enabling individuals in the brood to spread out over a larger and larger area. We terminate the second life stage in the model when the guarding male parent leaves the brood. The third life stage starts with juveniles dispersing from the area of the nest and ends at the formation of the first annulus.

The model cycles over simulated days. Habitat conditions and prey densities in each cell are revised daily in response to flow and the previous day's foraging. During the spawning season, the model evaluates spawning events such as spawning, nest abandonment, and egg mortality. The model evaluates foraging, growth, movement, and mortality for each individual fish in the larval and older life stages on a daily basis. In the following subsections we describe our model formulations for repro-

TABLE 1

Relative importance of various processes on each of three model life stages (L = low, M = medium, H = high, and X = unknown).

Process	Life stage		
	Egg	Larval	Juvenile
Movement			X
Foraging intake			
Temperature-dependent		H	H
Flow-dependent		M	M
Energetic costs			
Temperature-dependent		X	X
Flow-dependent		X	X
Mortality factor			
Temperature-induced	X		
Flow-induced	H	M	L
Starvation		H	M
Size-dependent			H

duction, foraging, growth, movement, and mortality.

Reproduction

The reproductive season in late spring-early summer is a period when smallmouth bass nests are vulnerable to environmental extremes of temperature and flow. These risks are mitigated by the behavioral adaptability of individual spawners. Our model simulates the selection of a nest site by males, spawning of eggs by females, nest desertion and possible re-nesting by the guarding male, and the development of eggs into swim-up larvae. The initial population of yearling and older smallmouth bass in the model has a specified size distribution and density. The spawning season begins after stream temperatures reach 15°C and ends when they reach 25°C (Carlander 1985; Graham and Orth 1986). Within that period, a male may establish a nest at any time after reaching spawning condition based on a relation derived by Ridgway et al. (1991) between male size and the number of accumulated degree-days. In general, larger males are prepared to nest before smaller males, and in migratory populations, the larger males return to spawning reaches before the smaller ones (Robbins and MacCrimmon 1977). Conditions on a given day are considered unacceptable for nest building activity when water temperatures fall outside of the range 15–25°C, when the flow exceeds bankful flow, or when the increase in flow from the previous day exceeds a threshold value. The thresholds for flow are specific to the stream being modeled (10 m³/sec in the North Anna River).

Selection of Nest Site by Males. As the spawning season progresses, each adult male is allowed to select the best available nesting site in the representative reach. Because gonad development is completed earlier for larger fish, males in the model tend to select nests in order of size (DeAngelis et al. 1991). For a given fish, nesting can be prevented by a lack of unoccupied suitable spawning habitat. This can be a short-term situation caused by high or low flows, or it can be caused by overcrowding.

Individual males select spawning sites

on the day that they reach spawning condition using one of two model options. Both options assume that spawners have access to the whole reach for the purpose of spawning. The first model option draws nest cells sequentially from a ranked list of cells in the representative reach in the order that they were used in the field and assigns them to model males as they reach spawning condition. Alternatively, the model can rank cells in the reach based on habitat suitability criteria and the number of nests already in the cell.

Spawning by Females. Spawning can be modeled with the female producing one or more clutches of eggs. Winemiller and Taylor (1982) reported observations of repeated spawning by females and multiple females providing eggs to the nest of one male in an Ohio stream. Other researchers have concluded that mating is, for the most part, monogamous (Wiegmann 1990). The capability of producing multiple clutches is potentially important in a variable stream environment because females with viable eggs are needed to supply re-nesting efforts following a flood event.

The potential fecundity of each female (F_{max}) of weight W_q (g) is calculated as:

$$F_{max} = -1214.77 + 10.85W_q, \quad (1)$$

based on data from Hubert (1976). The number of eggs provided to a given nest in the model by a sexually mature female can be determined by assuming either that it deposits all of the eggs (single-clutch spawning) or a fraction of the eggs (multiple-clutch spawning). The model selects an adult female at the time that each nest is built by identifying the female in the representative reach with the greatest number of mature eggs. We assume that males become preoccupied with guarding the nest after receiving eggs from one female and that other females are not courted.

If single-clutch spawning is selected, the largest female that has not yet spawned provides all of her eggs to the current nest. If multiple-clutch spawning is selected, the number of eggs provided by the selected female must be estimated, and currently, very little empirical data are available to suggest a reasonable allocation scheme. There is some evidence that egg develop-

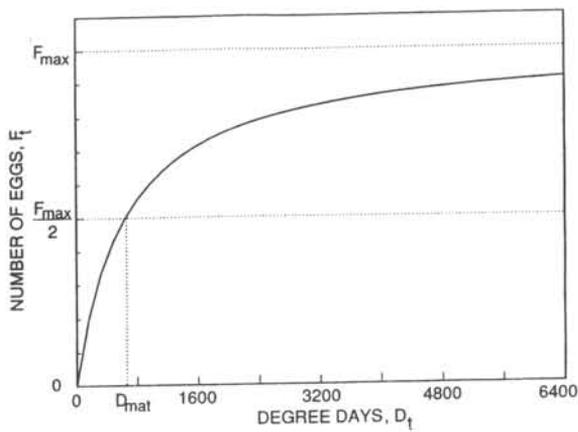


FIGURE 2. The degree-day relationship (Equation 2) used to model the number of large eggs at time t (F_t). F_{max} is the total number of eggs in the ovary at the start of the spawning season and D_{mat} is the number of degree-days that we specify are needed for half of the total eggs to reach maturity.

ment is an ongoing process during the spawning season that provides a mechanism for repeat spawning (Inslee 1975; Hubert and Mitchell 1979). We hypothesize that the number of viable eggs at any one time F_t is described by a Michaelis-Menton-type function (Equation 2) between the total number of viable eggs (F_{max}) present in the ovaries and accumulated degree-days D_t as shown in Figure 2:

$$F_t = \frac{F_{max} D_t}{D_{mat} + D_t} \quad (2)$$

Half of the total eggs present in the ovaries are considered viable when the female fish has accumulated a threshold number of degree-days. This threshold is taken to be the number of degree-days required for male smallmouth bass to spawn (D_{mat} ; Ridgway et al. 1991).

Nest Desertion. Males in the model may leave the nest that they are guarding for a number of reasons. If eggs are not provided to a nest within a specified waiting period, then the nest is abandoned. Pflieger (1966) reported an average time of 3 days for a male to wait to receive eggs before abandoning the nest. Model fish remain in the nest cell and do not feed during this waiting period.

Model nests that do receive eggs may be abandoned prematurely as a result of either of two environmental factors: extreme water temperatures (Latta 1963; Wrenn 1984) or extreme flows (Winemiller and Taylor 1982). The loss of nests because of

extreme temperatures after egg-laying and before swim-up is modeled in a stochastic fashion following Shuter et al. (1980). Nest desertion is certain for stream temperatures above 30°C or below 10°C. For temperatures in the range 15 to 25°C, the probability of nest desertion is nil. Between 10 and 15°C and between 25 and 30°C, the probability of nest desertion is modeled as a straight-line function between 0 and 1.

Males may also abandon model nests as a result of nest-site degradation following episodes of high or low flow (Reynolds and O'Bara 1991). On any day in the interval between egg-laying and swim-up, the nest is lost if the mean column velocity exceeds a critical threshold ($V_{max} = 0.2$ m/sec; Lukas 1993) or if stream depth falls below a threshold depth ($D_{min} = 0.2$ m).

If all goes well (the male receives eggs and the nest is not abandoned prematurely), males in the model discontinue nest-guarding behavior when the average length of fry in the brood exceeds 16 mm.

Nest desertion by the guarding male at any time after egg fertilization and before the larvae become free-feeding is assumed to result in mortality for all individuals from that nest. We do not assume 100% mortality for larvae abandoned after swim-up, but as a consequence of being small, they are exposed to high levels of size-dependent mortality once the male leaves (see "Mortality" section for details).

Renesting. Renesting is a common occurrence in natural streams (Pflieger 1975; Winemiller and Taylor 1982). In the model, males have the opportunity to attempt to reneest if nest disruption occurs before the end of the spawning period. Male condition is probably an important factor in determining the ability of a male to reneest, but currently all males are assumed to be capable of reneesting following nest failure. The male however, may find that there are no females left (in single-clutch spawning) or no eggs left (in multiple-clutch spawning).

Growth and Development. The duration of the first life stage (the time between egg-laying and the rise of swim-up larvae from the nest) is related to the average temperature after egg-laying for each individual nest (Shuter et al. 1980; DeAngelis et al. 1991) and is usually between 1 and 2 wk

TABLE 2

Parameters and sources of data for prey fed on by YOY smallmouth bass in the model.

Prey taxon	Allometric parameters		Parameter source	Size range (mm)	Habitat suitability curve source
	<i>a</i>	<i>b^a</i>			
Mayflies, stoneflies, and hemipterans	-2.18	2.88	Smock 1980	0-15	Peters et al. 1988
Microcrustaceans	-2.16	3.25	Spitze 1985	0-5	Peters et al. 1988
Ichthyoplankton	-6.10	3.15	North Anna River	0-25	Herricks et al. 1980
Simuliids	-2.27	2.43	Smock 1980	0-5	Peters et al. 1988
Chironomids	-2.29	2.32	Smock 1980	0-10	Minshall ^b
Caddisflies	-2.72	3.12	Smock 1980	0-50	Gore and Judy 1981
Odonates	-1.85	2.78	Smock 1980	10-75	Minshall ^b
Megaloptera	-2.54	2.75	Smock 1980	20-75	Minshall ^b

^a $\log_{10}(W) = a + b \log_{10}(L)$, where *W* is wet weight (mg) and *L* is length (mm).

^b Unpublished data from the Snake River, Idaho, 1984.

(Graham and Orth 1986). Each swim-up larva is assigned a length at random from a uniform distribution between 8.0 and 8.8 mm.

Foraging

The purpose of the foraging module is to simulate the daily intake of prey by each individual smallmouth bass. The smallmouth are assumed to start foraging on the day that they swim up from the nest as larvae. There are four distinct components of the algorithm for simulating the prey intake of individual fish. First, the availability of prey is determined for each prey type for each cell of the representative reach on a daily basis. Second, a mean daily encounter rate with each prey type is determined for each fish. Third, an optimal foraging algorithm is used to predict the diet and the amount of time spent feeding on each prey type. Finally, a realization of this diet is simulated for each individual fish to introduce stochasticity caused by prey patchiness.

Availability of Prey. A number of prey taxa can be specified, depending on the forage available to local smallmouth bass in the stream of interest. Each prey taxon represents a collection of prey species that share a common allometric length-weight relationship and similar habitat preferences. Information needed for each prey taxon (Table 2) includes the parameters of the allometric relationship and HSI relation-

ships for depth and velocity (Figure 3). The main use of HSI curves in the model is to simulate prey dynamics.

A spectrum of prey size classes is defined and tracked within each prey taxon. The median length and initial densities (number per square meter) are specified for each taxon-size class. The initial prey densities are multiplied by a factor ($cc = 3.0$) to obtain a carrying capacity *K* for each taxon-size class that would exist under optimal flow conditions and in the absence of predation. The model is calibrated to prey levels available to smallmouth bass in a given stream system using an availability factor that represents the probability of detection and capture by smallmouth bass, given that a prey individual is in the search volume or area of the predator. The calibration pro-

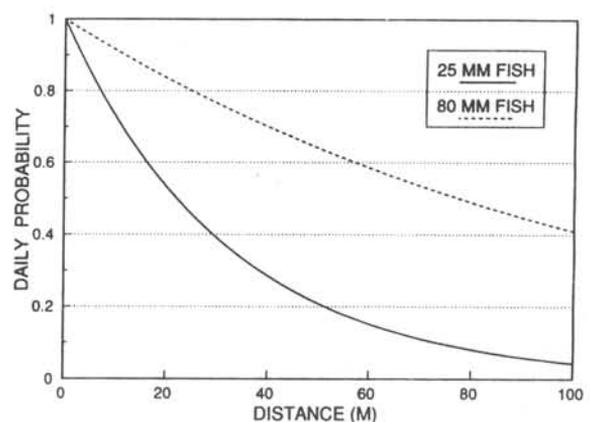


FIGURE 3. The probability that a smallmouth bass will move to a new location at distance *D* for fish of different sizes (Equation 12).

cess depends on the type of information available for the system of interest. Availability factors can be adjusted to match field observations of the proportion of the day spent foraging, the proportion of maximum daily ration received, shifts in diet composition, and the sizes of fish at different times in the growing season.

The prey dynamics in the model are cell-specific, following the assumptions that support the use of habitat suitability criteria (e.g., that local prey densities can be predicted from empirical relations with local habitat variables). The number of prey of each type is calculated for each cell i on each day t as:

$$N_{i,t+1} = N_{i,t} \left[1 + r_i \left(\frac{K_{i,t} - N_{i,t}}{K_{i,t}} \right) \right] - E_{i,t} \quad (3)$$

where $N_{i,t}$ is the number of prey of a given type in cell i on day t , r_i is the turnover rate for that prey taxon-size class at the temperature occurring on day t (Morin and Bourassa 1992), and $E_{i,t}$ is the number of prey of that class eaten by smallmouth bass in cell i on day t . We simulate the dynamics of each taxon-size class of a taxon independently by using Equation 3 and do not grow prey from one size class to the next.

The variable $K_{i,t}$ in Equation 3 is a cell-specific and time-varying carrying capacity. It depends on the daily habitat quality of the cell and is calculated for each prey type as:

$$K_{i,t} = \begin{cases} H_{i,t} \cdot K, & \text{if } H_{i,t} > H_{min} \\ H_{min} \cdot K, & \text{if } H_{i,t} \leq H_{min} \end{cases} \quad (4)$$

$H_{i,t}$ is the joint (depth and velocity) habitat suitability index for this prey taxon-size class in cell i on day t and is calculated as the geometric mean of the habitat suitability indices for depth and velocity. K is the maximum cell-independent carrying capacity as defined previously. A minimum suitability H_{min} is specified to represent the presence of prey refuges in the cell. If $N_{i,t} > K_{i,t+1}$, then the new density on day $t + 1$ is set to $K_{i,t+1}$.

Encounters with Prey. We calculate an expected rate of prey encounters for each prey taxon-size class in the model. The actual number encountered will be drawn from a Poisson distribution with this rate as its parameter.

We model the expected encounter rate as a product of the density of prey and the daily volume (or area for benthic feeding) searched by the foraging fish. The search area or volume is estimated as a product of the distance searched (either by swimming or holding position in the current) and the width of stream bottom or cross-sectional area of the water column within reach of the predator (reactive distance). The reactive distance of model fish increases with the size of the prey and the size of the predator (Breck and Gitter 1983). We calculate the search area when foraging in the benthos by assuming that the fish swims at a constant rate. The area or volume searched daily is limited to that searched by a fish moving at a sustained swimming speed of five body lengths per second.

For fish foraging on the stream bottom, the area of the bottom searched per unit time (SA) is calculated as:

$$SA = \begin{cases} 2S\sqrt{RD^2 - H^2}, & \text{if } H \leq RD \\ 0, & \text{if } H > RD. \end{cases} \quad (5)$$

S is the average swimming speed of the fish, RD is the reactive distance, and H is the fish's height above the stream bottom (Dunbrack and Dill 1983). We specify the fish's distance from the stream bottom as 5% of the fish's length. The volume of water searched per unit time (SV) is calculated for fish feeding in the water column as:

$$SV = \begin{cases} \pi S \cdot RD^2 - (RD^2 - H^2) \cdot \cos^{-1} \left(\frac{H}{RD} \right), & \text{if } H \leq RD \\ \pi S \cdot RD^2, & \text{if } H > RD. \end{cases} \quad (6)$$

The second term removes the portion of the search volume truncated by the stream bottom when reactive distance exceeds fish height, which is set to 20% of the distance to the surface. Reactive distance is calculated as a function of angle of acuity, which in turn decreases as the length of the smallmouth bass increases and as prey size increases (DeAngelis et al. 1991).

Selection of Diet. The diet selection algorithm determines which prey taxon-size classes are to be included in the diet of a model fish on a particular day. The variety of prey classes included in the optimal diet is restricted when the cost of increased

handling outweighs the benefit of including less valuable prey classes. The diet selection algorithm allows the composition of the diet to change in response to temporal and spatial variation in prey densities (e.g., high prey densities allow a more specialized diet). The algorithm estimates the time spent feeding each day, which we use to model the energetic effects of foraging in different habitats (i.e., model cells with different velocities).

The diet selection algorithm starts by filtering the spectrum of available prey taxon-size classes to exclude those too large for the fish to eat because of gape limitation or too small for the fish because of a reduced probability of detection or gill raker spacing. We exclude prey classes from the diet by imposing a lower limit of 0.05 (Dunsmoor et al. 1991) and an upper limit of 0.4 (Livingstone and Rabeni 1991) on the ratio of prey to predator size.

Within this size-restricted menu of prey, the algorithm sequentially adds those prey items that increase the expected rate of energy intake ($\Delta C/t_f$) until the rate reaches a maximum. The daily intake is ΔC (g) and t_f (hr) is the total time spent foraging (handling + search time). The two constraints on the solution are that the total intake may not exceed a maximum daily intake C_{max} and that the total time spent foraging may not exceed the number of daylight hours.

Variability among Fish. We begin with the average encounter rate with each prey taxon-size class that will be included in the optimal diet of a particular bass. On each day and for each taxon-size class, one realization is drawn from a Poisson distribution with that encounter rate as its parameter. This adds stochasticity to the number of prey of each taxon-size class that are captured on any given day by different fish.

We assume that autocorrelation in prey encounters is an important source of variability in the daily prey consumption among individual fish. Both the patchy spatial distribution of prey and the tendency of fish predators to form a search image and preference for certain prey or the habitats in which they are found contribute to this autocorrelation. To simulate autocorrelation we assume that once a fish has encountered a particular prey type, it

will encounter prey of the same taxon-size class in the subsequent G time encounters. G can be estimated from field data that describe the variation in stomach fullness among individual fish. We used a G value of 15 based on a comparison between the distributions of the proportion of maximum daily ration estimated from video data in the field site in late summer and that predicted by the model.

Growth

The bioenergetic model that describes the daily growth of individual fish is:

$$W(t + 1) = W(t) + [(1 - \beta)\Delta C - (\rho R_{s+a})], \quad (7)$$

where W is wet weight of the fish (g), ΔC is the daily intake (wet weight [g]), R_{s+a} is the rate of respiration (ash-free dry weight [g]/day), β combines the loss factors of egestion, excretion, and specific dynamic action, and ρ converts units of ash-free dry weight to wet weight, W . With the exception of total respiration costs (standard plus active; R_{s+a}) the components of Equation 7 are defined as in DeAngelis et al. (1991).

The standard rate of respiration (ash-free dry weight [g]/day) is modeled as a function of temperature T ($^{\circ}\text{C}$) and total fish length L (mm) (Shuter et al. 1993):

$$R_s = \alpha L^{\beta} T^{\gamma}, \quad (8)$$

where the variables used are $\alpha = 3.18 \times 10^{-7}$, $\beta = 1.93$, $\gamma = 1.08$.

Total respiration includes the costs of three types of daily activities: foraging, between-cell movement, and resting (Equation 9). For all fish except males guarding nests, the model assumes that fish partition the day into time (hr) spent foraging (t_f), time spent on nonforaging movement (t_m), and time spent resting (t_r):

$$R_{s+a} = R_s \left(\frac{t_f \cdot e^{\mu F} + t_m \cdot e^{\mu S} + t_r \cdot e^{\mu V_{rest}}}{24} \right). \quad (9)$$

Variable μ is a coefficient for swimming speed dependence of respiration (=1.96 sec/m from Rice et al. 1983), F is the effort expended foraging, S is the average swimming speed (m/sec), and V_{rest} is the velocity (m/sec) near the bottom. V_{rest} is calculated from a logarithmic relation that describes velocity at a specified position in the water

column (z in m) as a function of water depth (D in m), critical shear velocity V^* , a constant related to density k_0 , and average velocity V (Gray and Wigham 1973):

$$V_{rest} = V + \frac{V^*}{k_0} \left[1 + \ln \left(\frac{z}{D} \right) \right]. \quad (10)$$

The daily time spent in each of the activities in Equation 9 is determined as follows: The diet selection algorithm calculates an expected time t_f required to obtain the maximum ration C_{max} up to the number of daylight hours. The amount of time spent in movement t_m is calculated from the average swimming speed and the distance between the current cell and the fish's cell on the previous day. For the remainder of the day t_r , it is assumed that the fish is able to rest in a velocity-sheltered location.

The metabolic cost associated with each of the three activities in Equation 9 involves consideration of water velocity and/or swimming speed. For the time spent foraging, the swimming effort required to maintain an average swimming speed of one body length per second is calculated as a function of both water velocity and average swimming speed. For the between-cell-movement term in Equation 9, we assume that the average swimming speed is maintained, but current velocity is not considered because we are not modeling the fish's path between its location on one day and the next. During time spent resting, fish are assumed to inhabit locations with reduced water velocity (e.g., behind boulders or near the bottom of a pool).

Movement

An important assumption of this model is that emigration to and immigration from the representative reach balance each other. This assumption is more likely to be met by YOY smallmouth bass than by older life stages.

There are two steps to modeling fish movement within the representative reach: the decision to move (departure rules) and the selection of a new location. Departure is not allowed when water temperatures are less than 10°C. In the model, each fish tries to leave its current location (1) if the HSI of the cell for smallmouth bass of its life stage falls below a threshold value (0.0)

or (2) if the growth of the fish in the current cell is lower than its expected growth based on past experience.

At the start of each simulated day, a fish may depart the current cell if the flow for that day is such that the joint depth and velocity HSI for that life stage indicates a lack of suitability ($HSI = 0$), for example if the cell becomes dewatered. The sole purpose of this rule is to prevent model fish from spending an entire day in a location that is clearly unsuitable as an artifact of the daily timestep of the model.

The representative reach can be viewed as a two-dimensional surface of growth potential that changes over time in response to changes in flow and prey density. We assume that each fish moves with the goal of maximizing its growth rate but that it is constrained by the amount of information that it has about the surrounding environment. We assume that the fish has a sense of its energetic status; in the model, daily growth is used as an integrated measure of energy intake and metabolic cost. We also assume that fish form an expectation for energetic status; in the model, each fish has its own estimate of ΔW^* , (Equation 11), an individual expectation of potential growth that is simulated as a running average of its unique growth history (Bernstein et al. 1988, 1991) with a memory factor (δ) of 0.5:

$$\Delta W^*_t = \delta \cdot \Delta W^*_{t-1} + (1 - \delta) \cdot \Delta W_{t-1}. \quad (11)$$

Our growth-based departure rule allows fish to move when conditions for growth in the current location are below expectation. At the end of each simulation day, a model fish departs its current cell if its growth in the cell during day t (ΔW_t) is lower than expected from past experience (ΔW^*_t) (Charnov 1976).

Once a fish has decided to move, a new cell is selected from a probability distribution that gives higher weight to those cells close to the current cell and that increases the likelihood of selecting a more-distant cell for larger fish. Let P_i be the probability of moving to cell i from the current cell. P_i is a function of both fish length L and the distance between cells D_i , as shown in Equation 12 and Figure 3. For a given fish length, P_i is an exponentially decaying function of D_i . For a fixed prob-

ability, such as $P_i = 0.5$, we relate the (median) daily distance moved by a fish to its size and allow D_i to increase to an asymptote for large fish:

$$P_i = e^{-\left\{\frac{L^* + b_r}{a_r L^*} D_i\right\}}. \quad (12)$$

Coefficients a_r and b_r scale the results to observed movement patterns. We selected the maximum median between-day movement a_r to be 500 m and the length of the fish when it has half the maximum mobility b_r as 250 mm. In Equation 12, L^* is fish length L (mm) minus minimum length (8.0 mm).

To move a fish to a new location, the model selects an alternative cell at random from the representative reach, calculates P_i , and draws a random number R from a uniform distribution on the interval [0,1]. If $R \leq P_i$, the cell is accepted; otherwise an alternative cell is drawn. This process is repeated until an acceptable new cell is found based on the distance criterion. At this point, we may require that other criteria be satisfied by the new cell before allowing the fish to relocate. For example, we can require that at least one neighboring cell has suitable habitat to ensure that the fish is not trapped in its current cell. We limit the number of cells that can be considered on any attempt to move to the number of cells in the system. If a suitable cell is not identified before reaching this limit, then the fish remains in the current cell.

Mortality

On each simulated day, model fish are exposed to a variety of mortality risks that depend on individual attributes such as size, life stage, and local habitat conditions. Sources of mortality are modeled mechanistically whenever possible. Causes of mortality in stream habitats that we represent mechanistically include extreme habitat degradation, displacement of larvae by current, and starvation. Habitat degradation can cause direct mortality for all model life stages. Prior to swim-up, entire broods can be lost if the guarding male abandons the nest due to extremes in water temperature or streamflow, as described in the section "Reproduction." During the larval life stage, nest abandonment resulting from temperature or flow extremes ex-

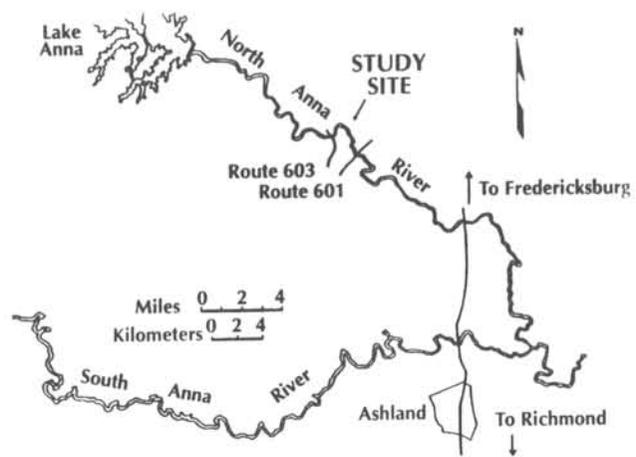


FIGURE 4. The location of the representative reach used as our study site on the North Anna River.

poses larvae to high predation risk. For juveniles, each fish in the model has an opportunity to change location when conditions are perceived as poor (see "Movement" section). Individuals with lower mobility have a higher risk exposure to extreme local habitat degradation (e.g., dewatering). More often, the combination of poor habitat and low mobility will contribute indirectly to mortality. For example, the current cell may continue to provide inadequate levels of prey or high energetic costs that eventually lead to starvation.

Larvae and juveniles less than 25 mm long are at risk of being swept away by the current (Harvey 1987). We assume that when faced with a risk of being swept downstream, the fish will orient toward the bottom where velocities are lower. We describe the probability that a fish will resist entrainment by the current P_{sweep} as a function of bottom velocity V_{bott} , fish swimming speed (related linearly to fish length), and turbidity T_b :

$$P_{sweep} = e^{-\left\{\frac{V_{bott}(\alpha + \beta T_b)}{L}\right\}}. \quad (13)$$

Variables obtained by fitting to data from Larimore (1975) are: $\alpha = -72.68$, $\beta = -5.114 \times 10^{-3}$. Velocity at 0.05 fish lengths from the bottom (V_{bott}) has units of m/sec, fish length (L) is in mm, and turbidity (T_b) is in Jackson turbidity units. V_{bott} is calculated from Equation 10.

A large fraction of mortality predicted for larvae and juveniles in the simulations reported here resulted from the combined effects of starvation and size-dependent

mortality. We report these together because they are correlated: when the condition of an individual drops below a threshold, it is lost to the population, whether due to predation, disease, emigration, or other causes. We assume that predation on larvae prior to dispersal depends on the size of the guarding male rather than that of the larva. After dispersal from the nest, juvenile smallmouth bass in the model are exposed to a preda-

tion mortality risk that decreases with juvenile size. Because we consider this a non-mechanistic representation of predation, we refer to it as size-dependent mortality. Individual model fish are exposed to the mechanistic sources of mortality first, and then to an empirically fitted size-dependent mortality risk. Model formulations for both sources of mortality are described in more detail in DeAngelis et al. (1991).

SIMULATIONS OF THE NORTH ANNA RIVER

Site Description and Model Parameters

The model was parameterized for a representative reach of the North Anna River in Virginia, a tailwater stream below a storage dam on Lake Anna (Figure 4). The average gradient is 0.4 m/km (King et al. 1991). We obtained long-term flow and temperature records from the U.S. Geolog-

ic Survey data and the Virginia Power Company. The average width of the stream is 35 m. Each model cell within a transect is defined by aggregating five contiguous measurement stations until the opposite bank is reached. Habitat suitability curves for smallmouth bass, which play a limited role in the model, have been developed in the North Anna River for spawning and for the juvenile and adult life stages (Lukas

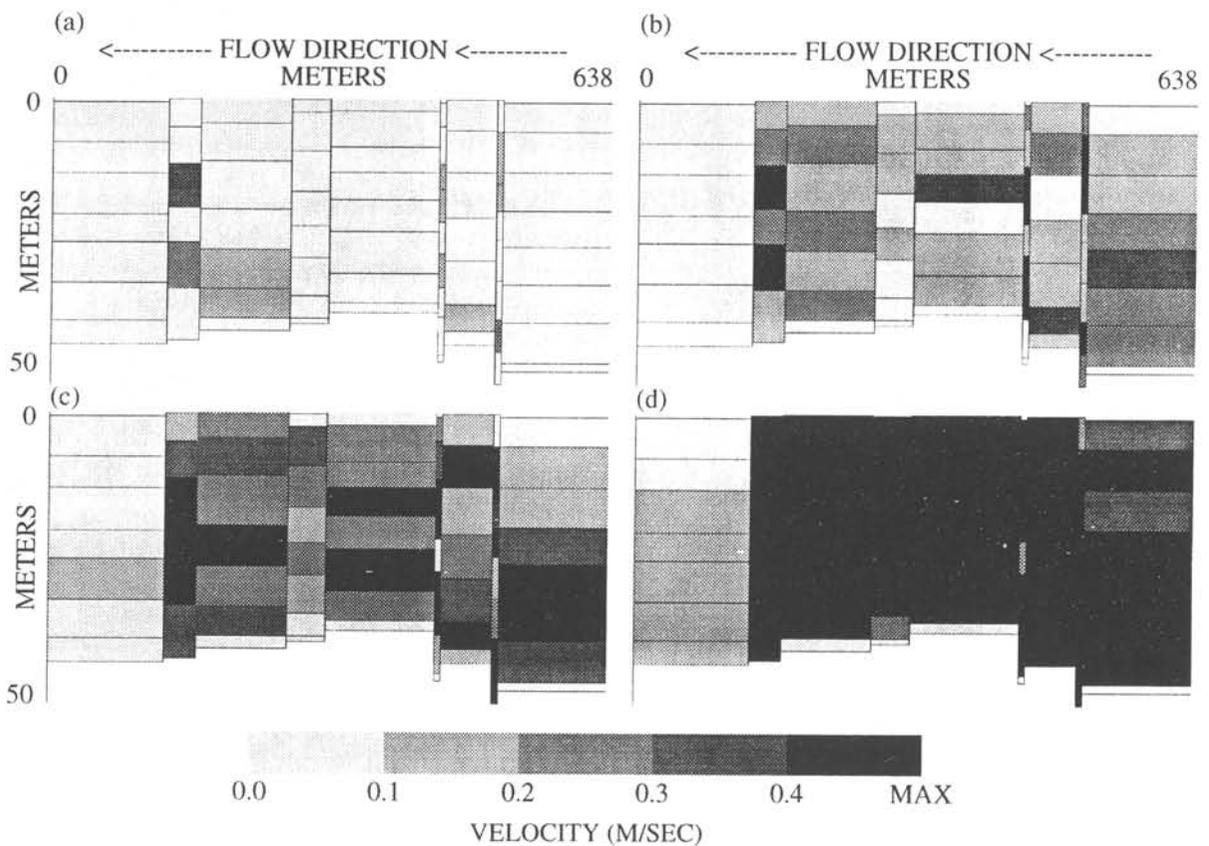


FIGURE 5. A view of the representative reach (looking down at water surface) showing the cell structure used in the model and predicted velocities at four flows: (a) 1 m³/sec, (b) 5 m³/sec, (c) 10 m³/sec, and (d) 50 m³/sec.

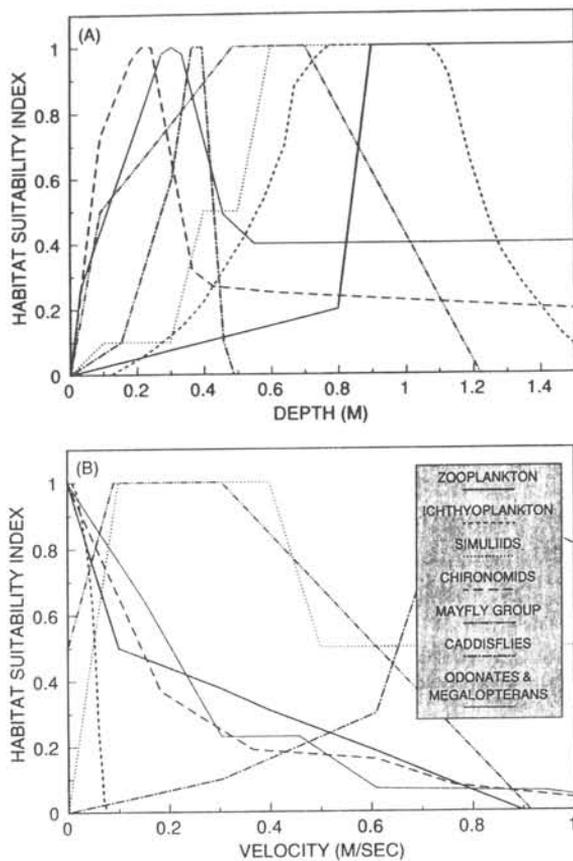


FIGURE 6. Habitat suitability index (HSI) curves for simulated prey taxa with respect to (a) depth and (b) velocity. References are listed in Table 2.

1993; Groshens, Virginia Polytechnic Institute and State University, unpublished data).

A PHABSIM survey of nine transects spanning 0.639 km of stream was conducted for this reach during low (1.38 m³/sec), medium (2.27 m³/sec), and high (8.78 m³/sec) flow conditions. Predictions of average model cell velocity are shown for four levels of flow in the North Anna River (Figure 5). We specified bankful flow for this system as 14.16 m³/sec.

We used benthic invertebrate and prey-fish densities collected by the Virginia Power Company to define initial prey densities. Prey taxa used to simulate YOY smallmouth bass foraging are listed in Table 2. We used the following prey size classes: 0–2 mm, 2–5 mm, 5–10 mm, 10–15 mm, 15–20 mm, 20–50 mm, and 50–75 mm. Terrestrial sources of prey are not currently simulated because stomach analyses of YOY smallmouth bass in the North Anna River suggest that they constitute less than 10% of intake by weight (Easton 1992).

TABLE 3

Initial size and age distribution of adult smallmouth bass used in simulations of the North Anna River.

Age class (yr)	Total fish length (mm)		Proportion of population
	Mean	Minimum Maximum	
1	112	66 184	0.48
2	206	152 271	0.26
3	274	217 362	0.13
4	318	297 389	0.08
5	352	321 407	0.05

Variables for each prey taxa were obtained from the North Anna River, where possible, and from the literature otherwise (Table 2). Habitat suitability information for prey taxa was obtained from the Instream Curves Library maintained by the Habitat Evaluation Procedures Group of the U.S. Fish and Wildlife Service in Fort Collins, Colorado (Figure 6).

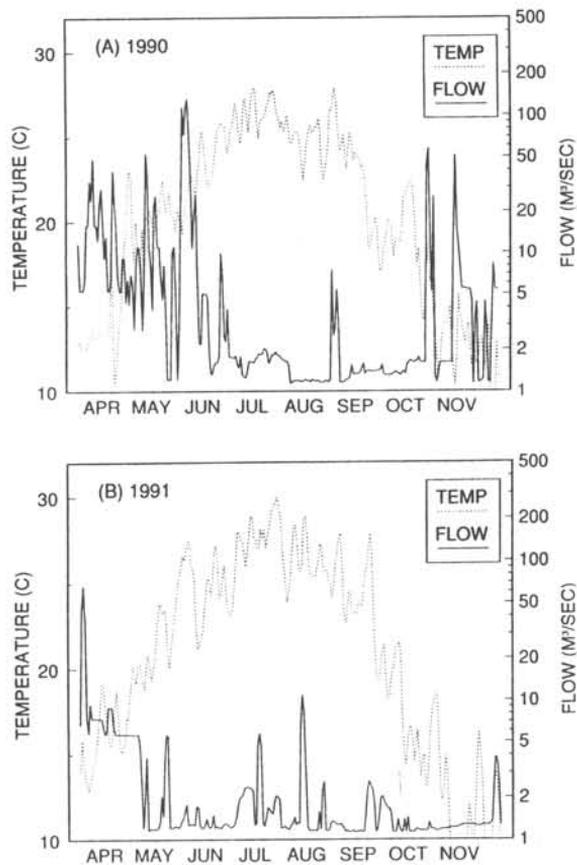


FIGURE 7. Water temperature and streamflow near the representative reach of the North Anna River during the (a) 1990 and (b) 1991 growing seasons for smallmouth bass.



Life stage	1990		1991	
	Average number	Standard deviation	Average number	Standard deviation
Nests ^a	12	2	14	2
Eggs	29,838	3,783	29,330	3,551
Larvae	19,847	3,162	24,224	2,756
Juveniles	9,816	1,267	11,161	1,115
Yearlings	17	7	131	7

^a Model nests with smallmouth bass that survive to swim-up.

The smallmouth bass population was initialized in the model with 47 yearling and older fish based on fish counts in 1991. The size distribution used for this initial population is shown in Table 3; size and age statistics were collected by Virginia Power Company from 1989 through 1991 (Graham 1991; King et al. 1991). A 50:50 sex ratio is assumed for the adults, and the sizes of individual adults are generated from a normal distribution with the specified mean and a standard deviation equal to one-fourth of the range. The temporal order of use (ranking) and the locations of potential nests are specified from observations at this site from 1990 through 1992. The historical 1990 and 1991 daily average flow and temperature records are shown in Figure 7.

We selected 1990 and 1991 for these baseline simulations because field data are available that describe YOY growth. The purpose of these baseline simulations is two-fold. First, they demonstrate the capabilities of the model. Second, they highlight areas in which further study is needed.

Results

The averages and standard deviations reported in Table 4 include five replicate simulations for each year. Variability among these replicates has many potential sources because of the stochastic nature of the model. For example, random differences in the initial sizes of adult males and

the rate that they reach spawning condition can lead to differences in the order that they nest, in the selection of a female and the number of eggs provided, and in the risk of nest destruction associated with the cell selected for nesting. Within a replicate simulation, variability among YOY fish results from differences in the habitats encountered, foraging success, and metabolic costs.

Reproduction. Our comparison of model reproduction with field data relies on back-calculated swim-up dates estimated from the otoliths of juveniles sampled in August of 1990 and 1991 in the North Anna River. The following description of model events demonstrates the types of predictions made by the model and, where possible, compares those predictions with field information about spawning during these two years.

The simulated spawning season of 1991 began earlier and ended later than that of 1990 (Figure 8). Juvenile otoliths suggest that spawning in the North Anna River started and ended earlier in 1991 than the onset of spawning in 1990. It is possible that spawning occurred at times other than those represented by juveniles that survived to August.

In 1990 simulations, the few early spawners that initiated nesting in the model in mid-April lost their nests when temperatures dropped a few days later. Conditions between 15 and 22 April 1990 were so poor that no spawning activity was attempted. A pulse of spawning activity on 22 April 1990 involved most of the reproductive males in the model, including spawners that lost earlier nests.

Field observations in 1990 suggest that there was no successful spawning until June, much later than predicted by the model. Larval fish that were observed in late May appeared diseased and disappeared soon afterward. The fate of May broods is unclear. They may have been destroyed (by flooding, disease, or other factors), they may have left the reach, or they may not have been sampled. Surviving juveniles collected in August 1990 have estimated swim-up dates in mid-June.

In 1991 simulations, a pulse of spawning activity involving six to seven nests occurred on 5 April. Most of these nests were successful and produced swim-ups on 18

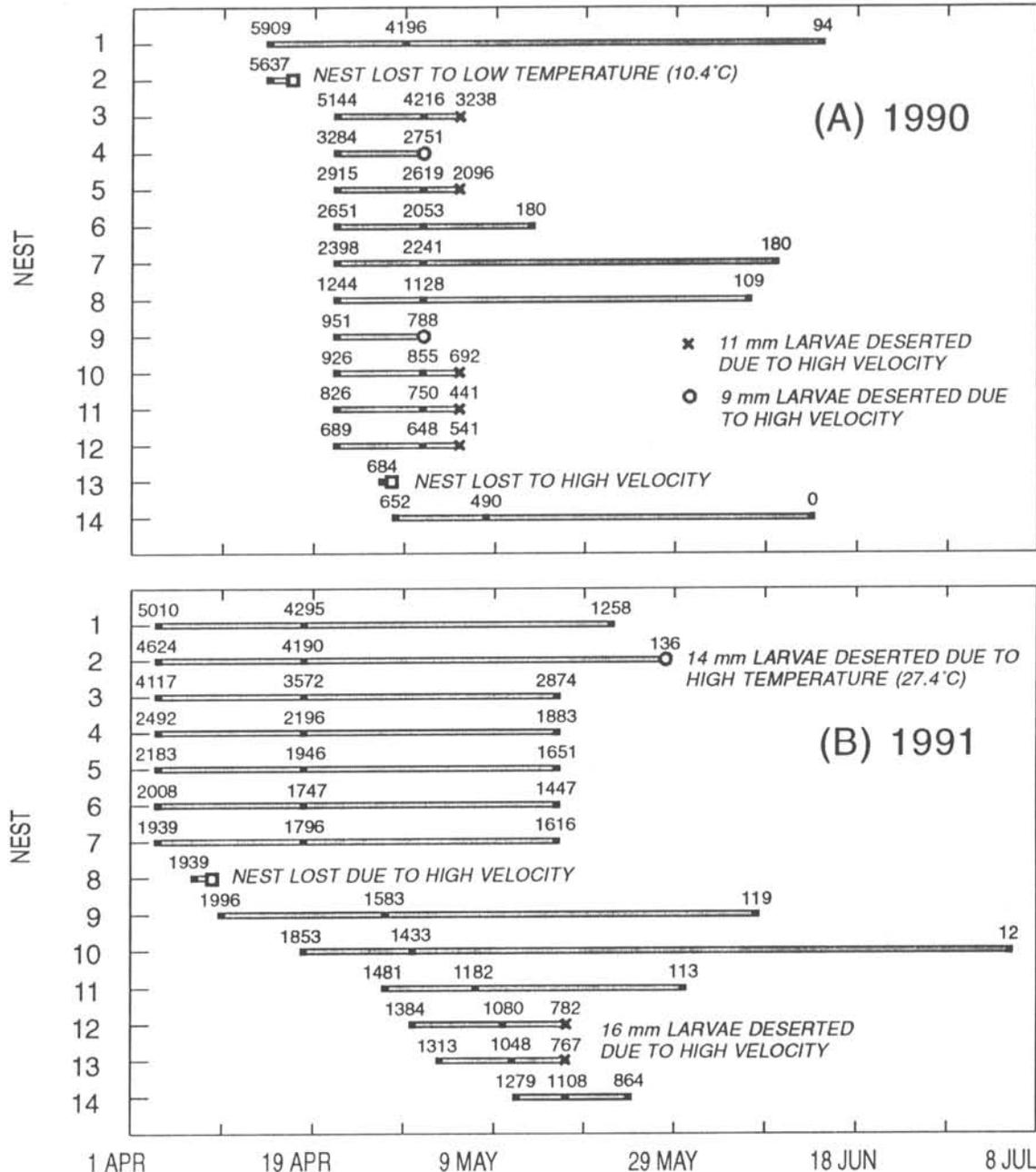


FIGURE 8. A typical sequence of spawning events during a simulation of (a) 1990 and (b) 1991. For each of 14 model nests, we indicate the number of eggs on the date at which spawning occurs, the number of larvae on the date of swim-up, and the number of juveniles on the date of dispersal from the nest. Causes of nest mortality or premature abandonment are indicated on the dates that they occur.

April. Later nests were built between early April and mid-May of 1991.

Field observations in 1991 were made of larvae from three nests on 15 April, all of which disappeared by the following week. Surviving larvae that were observed later have estimated swim-up dates in the first week of May.

The simulated duration of the larval stage in some cases exceeds the maximum durations reported (ca. 30 days). In the North

Anna River, the guarding male generally left between 4 and 21 days after swim-up.

The map of our representative reach in Figure 9 shows the locations of nests and the fate of the brood until dispersal from the nest. The velocities of cells where high velocities led to nest destruction or premature nest abandonment by the guarding male can be compared at different flows in Figure 5.

Renesting occurred in three instances in

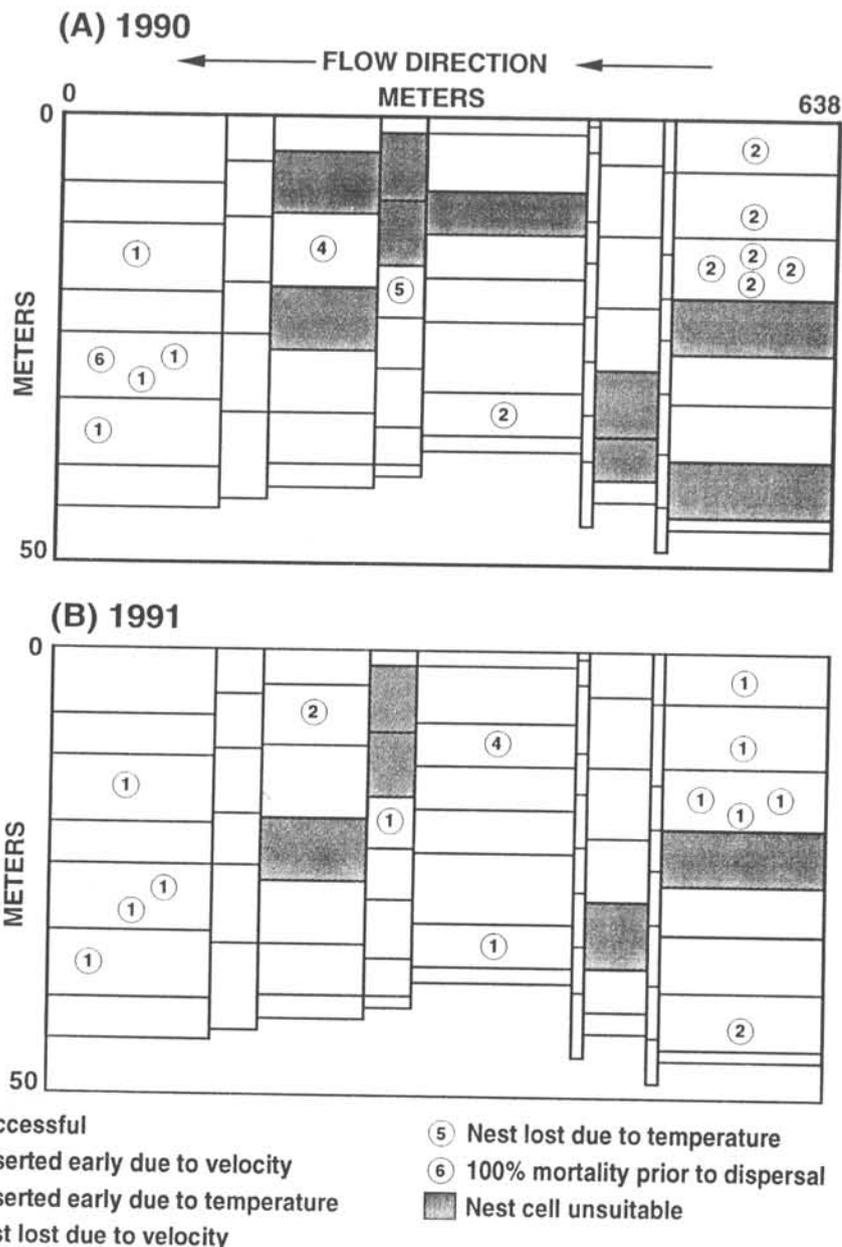


FIGURE 9. The locations of those nests observed between 1990 and 1992 and used in simulations and predicted outcomes for (A) 1990 and (B) 1991 are shown looking down at the representative reach.

simulations for the two years. Nest #3 was built by the model male that abandoned nest #2 due to low temperature on 16 April 1990. Nest #14 was built by the male that lost nest #13 due to high velocity at a flow of $6.9 \text{ m}^3/\text{sec}$ on 27 April 1990 (Figure 8a). In simulations for 1991, nest #9 was built by the male that lost nest #8 due to high velocity (Figure 8b).

More model broods survived to swim-up in 1990 than in 1991 (Table 4). The number of model eggs deposited by females in the representative reach in the two years was similar: 29,838 in 1990 and 29,330 in 1991.

Foraging. Table 5 summarizes our baseline simulation results for YOY foraging in 1990 and 1991. The average amount of time spent foraging by model fish is initially about 1 hr, during which time the larvae receive a full daily ration (100% of C_{max}). Later, during the transition period when larvae in some nests have reached 16 mm and are dispersed from the nest, foraging intake drops to an average of 30% of C_{max} and the fish spend 9 hr foraging. This suggests that depletion of prey is occurring in the nest cells, and that dispersal occurs at an opportune time. From 16 to 70 mm, model fish are receiving nearly a full

TABLE 5
Foraging characteristics of simulated YOY smallmouth bass^a.

Average fish length (mm)	Average foraging time (hr)	Average percent of C_{max}	Average prey size (mm)		Average diet breadth ^b
			Mini-mum	Maxi-mum	
9.4	1.1	100	1.3	2.5	4.5
10.5	1.0	100	1.3	3.8	6.0
16.0	9.4	30	1.3	5.0	6.2
17.5	4.6	92	1.3	4.1	5.0
19.4	5.0	90	1.3	6.8	8.2
24.2	1.5	100	1.3	7.5	7.1
31.2	4.4	100	3.8	10.5	7.1
43.8	6.4	99	3.8	16.0	10.3
50.8	5.1	100	3.8	17.5	9.7
55.6	7.3	100	3.8	17.5	10.0
60.6	6.5	100	3.8	17.5	9.5
69.9	7.3	99	3.8	17.5	9.2
76.2	8.1	56	7.1	18.3	8.1
86.0	7.3	65	7.5	24.5	8.3
88.7	6.3	68	7.5	27.0	8.2
101.7	5.3	92	7.5	35.0	9.0
104.9	7.5	66	7.5	34.8	9.5
117.2	7.5	88	7.5	36.3	9.7

^a Statistics based on a subsample of 10 simulated fish from each year.

^b Average number of taxon-size classes of prey in the optimal diet.

ration and they tend to spend more time foraging as the summer progresses. In the fall, the expected percentage of C_{max} for these model fish decreases (56–92%) whereas the expected time spent foraging remains the same (5–8 hr).

The smallest prey initially used by first-feeding larvae of 8.0–8.8 mm in the model are simuliids, small chironomids, small caddisflies, and small benthic insects in the mayfly-stonefly-hemipteran category. At 10 mm in length, larvae feed on chironomids, simuliids, microcrustaceans, mayflies, and trichopterans. As the larvae continue to grow, ichthyoplankton and larger classes of benthic insects such as caddisflies and odonates are used. Smaller prey such as microcrustaceans do not disappear completely from the diet until the model fish reach 75 mm.

Growth. The growth of YOY bass in the model is shown over the first growing season for a typical simulation (Figure 10). We show observed values for three dates during the summers of 1990 and 1991. At the

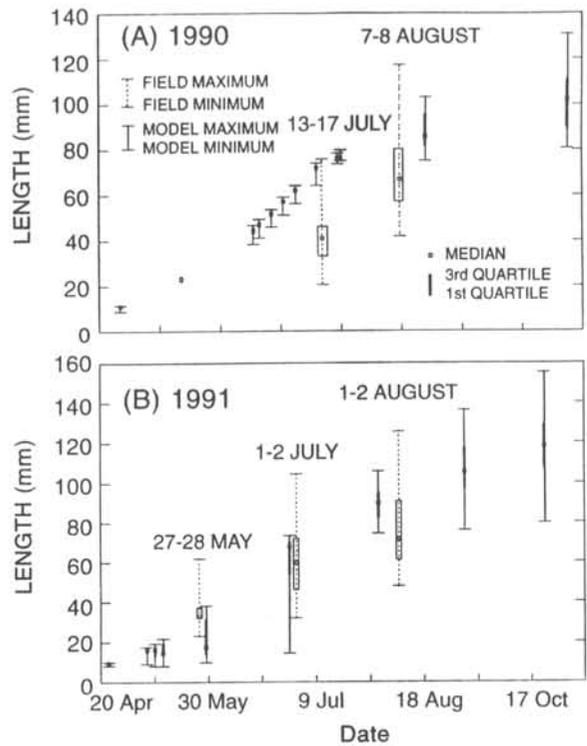


FIGURE 10. A comparison of young-of-year growth with field observations in (a) 1990 and (b) 1991. Fish length distributions are plotted over the first growing season. Dates below the field distributions indicate the range of sample dates included.

end of the growing season, we compared the distribution of individual YOY lengths predicted by the model with the distribution of back-calculated YOY lengths obtained from scales of 3-yr-old and younger fish collected in the North Anna River (Figure 11). The average length of fish surviving to the end of the model growing season was 106.4 ± 5.1 mm in 1990. The average fish size at the time of annulus formation reported for YOY fish in the North Anna River in 1990 was 114.0 ± 27.8 mm (King et al. 1991). We do not have field data for comparison with 1991 simulations yet, but the lengths of model fish in 1991 simulations averaged 122.1 ± 1.6 mm—an average of 18 mm longer than 1990 model yearlings.

Movement. The rate of movement is presented as the percentage of opportunities to move that were taken by model YOY fish. In 1990 simulations, only 9.3% of opportunities to move were taken. Thirty percent of these movements were instigated by changes in habitat suitability and 70% were instigated by our growth-based departure rule. In 1991 simulations, YOY fish moved more frequently than in 1990

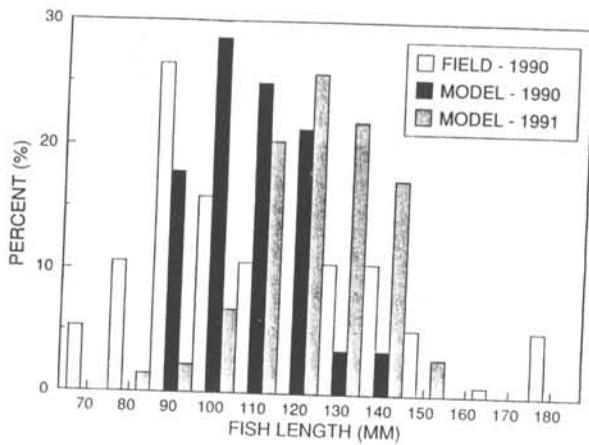


FIGURE 11. Simulated length distribution of young-of-year at the end of the growing season are shown for years 1990 and 1991 and compared with lengths for the 1990 year class back-calculated from scale measurements of smallmouth bass collected in the North Anna River by Robert Graham of Virginia Power Company.

(19.2% of opportunities). Most of the between-day movements were initiated in response to inadequate growth relative to the fish's past experience (97%), whereas a small percentage of moves were made because of habitat degradation (3%).

Mortality. Field estimates for YOY numbers were estimated from snorkel counts

during the summers of 1990 and 1991. During the period from 13 July to 8 August 1990, we estimated that 80–84 juveniles were present in the representative reach. We estimated that 49–63 juveniles were present in the representative reach from three successive counts conducted between 27 May and 4 August 1991. Model predictions for the average number of juveniles in early spring (131 ± 7) are higher than the average of the three field estimates (56 ± 7) (Table 4).

Figure 12 shows the sequence of mortality events for the first replicate for both years. Starvation and size-dependent mortality are responsible for most of the fish deaths in these baseline simulations. There is a distinct peak in starvation and size-dependent mortality near 10 May for the 1991 simulations, whereas predicted starvation and size-dependent mortality in 1990 occurs throughout May. The second leading cause of mortality in simulations of 1990 is the sweeping away of larvae by high currents. This factor was responsible for 6,038 larval deaths, peaking during a 6 May high-flow event in 1990. A modest 226 larvae are swept away around 17 May in the 1991 simulation.

DISCUSSION

Comparison of Observed and Predicted Results

The individual-based approach is well suited to an iterative process of model validation and improvement. In this paper we have compared observed and predicted results for smallmouth bass reproduction and the dynamics of YOY smallmouth bass in a representative reach of the North Anna River. When discrepancies appeared, we were able to identify likely mechanisms causing the problem by comparing intermediate variables. These discrepancies obligate us to ask more questions about the field data and the model, and then to design appropriate follow-up studies. Ultimately this process focuses attention on important processes that require more attention and targets the remaining processes for removal or simplification (Murdoch et al. 1992). With this strategy in mind, we discuss our results for reproduction, foraging, and growth.

Reproduction. The spawning process simulated here is characterized by a high degree of variability that is influenced by its event-driven nature and the small number of nests simulated. Changes in flow and temperature from the conditions at the time nests are built can greatly decrease reproductive success in the model. Renesting by males and multiple-clutch spawning by females can, however, mitigate these effects, which were important in the 1990 and 1991 simulations and would be even more so in years of higher and more variable flows.

The predicted timing of events in 1991 agrees reasonably well with field observations. In contrast, the predicted timing of events in 1990 deviates from field observations. Our prediction that a large pulse of swim-ups from successful nests in late April was not observed in the field and, consequently, there were no model spawn-

ers nesting later as suggested by field data. We have three hypotheses to explain this discrepancy. First, many of these early model nests were abandoned prematurely because of high flows just after swim-up, and, if broods had been at this stage in the field during these flows, it is quite possible that the males would have attempted to renest. This is not currently allowed in the model once the brood reaches swim-up. Second, the diseased appearance of early larvae in the field suggests that a factor not predictable from the model, disease, was the cause of early nest failure. Our third hypothesis is that the period of several days between nest construction and spawning, which is not currently simulated, delayed some of the early spawners in the field.

This validation process has suggested several mechanisms that deserve further examination. Our 1990 results suggest that the ability of males to renest when nests are lost after swim-up should be examined. The importance of the waiting period between nest building and spawning will also be evaluated with the help of the model. A thorough validation of the reproduction module will soon be possible based on a detailed study of spawning conducted in the North Anna River during 1992.

Foraging. The predicted diet of YOY smallmouth bass shows general agreement with reported diets and with casual observations of YOY foraging in the North Anna River. In our model results, microcrustaceans are important early on and larval fish appear only in the diets of YOY with lengths ≥ 40 mm. Microcrustaceans and chironomids dominate in the stomachs of YOY < 15 mm in length in the New River, West Virginia (Easton 1992). Easton observed that mayflies and caddisflies increased in importance for 20–85-mm juveniles. This is in contrast to observations of Livingstone and Rabeni (1991) in the Jacks Fork River, Missouri, where fish ≤ 15 mm were important for small (10–35-mm) YOY fish. Livingstone and Rabeni (1991) showed chironomids and mayflies, but not microcrustaceans, to be important. Both field studies noted an increase in the importance of mayflies as the YOY fish grew larger.

Other aspects of foraging predictions did not match our expectations based on field

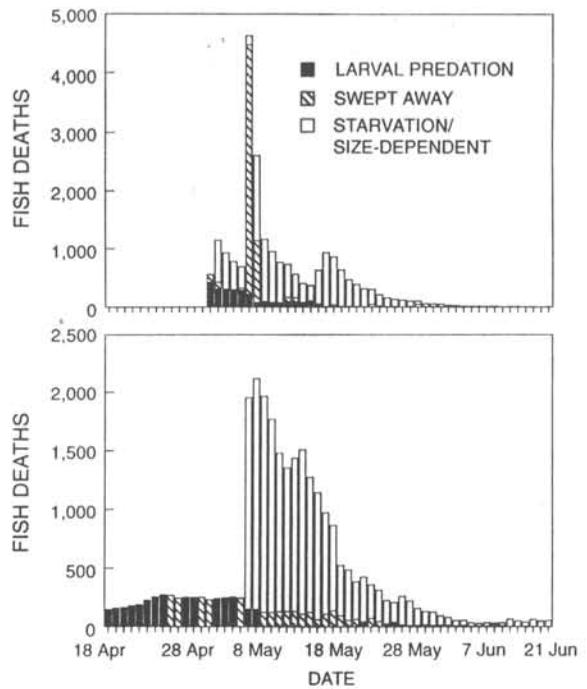


FIGURE 12. A typical sequence of mortality events during a simulation of (a) 1990 and (b) 1991. The number of deaths associated with each source of mortality is stacked to show the total mortality on each date.

observation. The model predicts that nearly all larvae receive the maximum daily ration for lengths up to 70 mm. This contradicts field observations of larvae foraging more or less continuously during daylight hours. Later in the season, during August 1991, the proportion of maximum intake observed through video observation of foraging (40–50%) was lower than that predicted by the model (56–68%).

Growth. The duration of the larval stage, bounded by two events, swim-up and dispersal, is variable among nests and it is too long for some nests (Figure 8). Some model broods take much longer to reach the threshold length of 16 mm than others. We suspect that the model underestimates the maximum ration consumed by larval smallmouth bass, leading to early growth that is too slow (see Post 1990). Simulations in which we allowed larval fish to consume up to three times their body weight daily brought model predictions of the larval period closer to those observed in the field for all nests.

Field measurements in 1990 show that the YOY fish are smaller than predicted by the model (Figure 10a). This difference is consistent with the later spawning dates

inferred from field data. Predicted sizes in 1991 are much closer to field observations. The model, because it is individual-based, predicted the full distribution of fish lengths as well as the average. The variability in size among individuals was underpredicted by the model. The maximum back-calculated length at the time of first annulus formation was greater among sample North Anna River smallmouth bass than among individuals in our simulations at the end of the growing season (Figure 11). We suspect that the low variability was caused, in part, because all larvae received the same, maximum daily ration early on. If larval fish are allowed a larger maximum daily ration in the model, variability would increase because they would receive smaller (and different) proportions of the maximum ration.

Bottlenecks: Limiting Resources

A model designed to simulate the dynamics of a population must incorporate the restrictions imposed by windows of resource limitation that occur in time and space. In this model we explicitly simulate the resource limitations imposed by inadequate levels of prey and by poor habitat conditions. These features of the model allow us to investigate both the individual-level impacts of resource limitation and the potential for compensation at the population level.

Model recruitment was limited in 1990 simulations by the egg and larval mortality that resulted from high flows during the spawning season. High flows later in the season were mitigated by movement of model fish. Thus, habitat degradation during the immobile life stages did, apparently, act as a bottleneck on the simulated year class, whereas flow events during the juvenile life stage did not. Windows during which prey resources limited fish growth seemed to occur just before dispersal and in late fall (Table 5), but not necessarily due to depletion effects.

Future Research

An important goal for this model is to investigate the effects of flow on smallmouth bass. Further model validation is needed to give credence to model results.

In the next round of model validation we intend to concentrate on one model process at a time. To validate reproduction, we will conduct a comparison of model predictions with comprehensive field observations of spawning in 1992. To validate movement and energetics of juveniles, predicted and observed patterns of habitat use in 1990 and 1991 will be compared.

There are many areas for improvement, some of which were identified by this validation process. First, our results pointed to a need for research in the area of larval metabolism for smallmouth bass, similar to that conducted by Post (1990) for yellow perch. Second, expanding the spatial context of the model away from the "representative reach" on which PHABSIM analysis is based would make the spatial scale of the model appropriate for the simulation of the adult lifestage. Third, expansion of hydraulic simulation to predict the range of available velocities within cells would allow more realistic linkage between microhabitat and fish activity. Finally, sensitivity analysis is needed to determine the most critical elements in population response to altered flow regimes.

All models are wrong—they represent an idealistic simplification of a real system. This model is no exception, but the ability to subject this mechanistic model to a process of iterative refinement brings the goal of addressing instream flow issues within our grasp.

Acknowledgments

This model application benefited greatly from the cooperation of Virginia Power Company, especially Robert Graham and Judson White. They provided time, equipment, and input data in the form of long-term records of water temperature and flow, seasonal densities of benthic invertebrate and fish prey, and data on individual sizes of smallmouth bass in the North Anna River. Research projects conducted by graduate students at Virginia Polytechnic Institute and State University in Blacksburg provided useful information: Tom Grohens provided us with the age distribution and density of adults and Ed Pert shared insights into young-of-year foraging. Alan Moos served as our hydraulic simulation expert and modified an IFG4 code to provide us with hydraulic parameter estimates for each cell.

We thank John Smith and John Wojtowicz of the Environmental Sciences Division at Oak Ridge



National Laboratory, whose classification of a long list of benthic invertebrate taxa into size and habitat groups was used to determine prey categories and avoidances. Jeff Tyler of Oak Ridge National Laboratory contributed the learning aspects of our departure rule for fish and provided a thoughtful review. Ray Newman (University of Minnesota) provided valuable input to the modeling process. R. G. Otto (Otto Associates), M. S. Ridgway, and B. J. Shuter (Ontario Ministry of Natural Re-

sources) provided helpful reviews of this manuscript.

This research was sponsored by the Electric Power Research Institute under Contract No. RP2932-2 (DOE No. ERD-87-672) with the U.S. Department of Energy, under Contract No. DE-AC05-84OR21400 with Martin Marietta Energy Systems, Inc. This is Publication Number 4079 of the Environmental Sciences Division, Oak Ridge National Laboratory.

REFERENCES

- Bain, M. B., and J. M. Boltz. 1989. *Regulated Streamflow and Warmwater Stream Fish: A General Hypothesis and Research Agenda*. Washington, DC: U.S. Fish and Wildlife Service (Biological Report 89 [18]).
- Bernstein, C., A. Kacelnik, and J. R. Krebs. 1988. Individual decisions and the distribution of predators in a patch environment. *Journal of Animal Ecology* 57(3):1007-1026.
- , ———, and ———. 1991. Individual decisions and the distribution of predators in a patch environment. II. The influence of travel costs and structure of the environment. *Journal of Animal Ecology* 60(1):205-225.
- Breck, J. E., and M. J. Gitter. 1983. Effect of fish size on the reactive distance of bluegill (*Lepomis macrochirus*) sunfish. *Canadian Journal of Fisheries and Aquatic Sciences* 40(2):162-167.
- Carlander, K. D. 1985. *Handbook of Freshwater Fishery Biology*, Volume 2. Ames: Iowa State University Press.
- Charnov, E. L. 1976. Optimal foraging, the marginal value theorem. *Theoretical Population Biology* 9(1):129-136.
- Cheslak, E. F., and A. S. Jacobson. 1990. Integrating the instream flow incremental methodology with a population response model. *Rivers* 1(4):264-288.
- DeAngelis, D. L., L. Godbout, and B. J. Shuter. 1991. An individual-based approach to predicting density-dependent dynamics in smallmouth bass populations. *Ecological Modelling* 57(1):91-115.
- , and L. J. Gross, editors. 1992. *Individual-Based Models and Approaches in Ecology: Populations, Communities and Ecosystems*. New York: Chapman and Hall.
- Dunbrack, R. L., and L. M. Dill. 1983. A model of size dependent surface feeding in a stream dwelling salmonid. *Environmental Biology of Fishes* 8(3/4):203-216.
- Dunsmoor, L. K., D. H. Bennett, and J. A. Chandler. 1991. Prey selectivity and growth of a planktivorous population of smallmouth bass in an Idaho Reservoir. Pages 14-23 in D. C. Jackson, editor. *Proceedings of the First International Smallmouth Bass Symposium*. Mississippi Agricultural and Forestry Experiment Station, Mississippi State University.
- Easton, R. S. 1992. *Feeding Ecology of Age-0 Smallmouth Bass in the New River, West Virginia*. Master's thesis. Blacksburg: Virginia Polytechnic Institute, Fisheries and Wildlife Sciences.
- Gore, J. A., and R. D. Judy, Jr. 1981. Predictive models of benthic macroinvertebrate density for use in instream flow studies and regulated flow management. *Canadian Journal of Fisheries and Aquatic Sciences* 38(11):1363-1370.
- , and J. M. Nestler. 1988. Instream flow studies in perspective. *Regulated Rivers: Research and Management* 2(2):93-101.
- Graham, R. J. 1991. Annual Report for 1991 including summary of 1989-1991 Lake Anna and the Lower North Anna River. Glenn Allen, Virginia: Prepared by Water Quality Department Corporate Services for Virginia Electric and Power Company.
- , and D. J. Orth. 1986. Effects of temperature and streamflow on time and duration of spawning by smallmouth bass. *Transactions of the American Fisheries Society* 115(5):693-702.
- Gray, D. M., and J. M. Wigham. 1973. Peak flow—Rainfall event. Section VIII in D. M. Gray, editor. *Handbook on the Principles of Hydrology*. Syosset, NY: Water Information Center, Inc.
- Harvey, B. C. 1987. Susceptibility of young-of-the-year fishes to downstream displacement by flooding. *Transactions of the American Fisheries Society* 116(6):851-855.
- Herricks, E. E., J. B. Stall, J. W. Eheart, A. B. Libby, S. F. Railsback, and M. J. Sale. 1980. Instream flow needs analysis of the Little Wabash River Basin. Urbana, IL: University of Illinois, *Environmental Engineering Series No. 61* (UILU-ENG-80-2026).
- Hubert, W. A. 1976. Estimation of the fecundity of smallmouth bass, *Micropterus dolomieu*



- Lacepede, found in the Wilson Dam tailwaters, Alabama. *Journal of the Tennessee Academy of Science* 51(4):142-144.
- , and V. P. Mitchell, Jr. 1979. Ovarian development of smallmouth bass in Pickwick Reservoir. *Journal of the Alabama Academy of Science* 50(2):87-95.
- Huston, M. A., D. L. DeAngelis, and W. M. Post III. 1988. New computer models unify ecological theory. *BioScience* 38(10):682-691.
- Inslie, T. D. 1975. Increased production of smallmouth bass fry. Pages 357-361 in R. H. Stroud and H. Clepper, editors. *Black Bass Biology and Management*. Washington, DC: Sports Fishing Institute.
- King, M. A., R. J. Graham, and W. S. Woolcott. 1991. Comparison of growth of smallmouth bass from two tributaries of the York River, Virginia. Pages 6-13 in D. C. Jackson, editor. *Proceedings of the First International Smallmouth Bass Symposium*. Mississippi Agricultural and Forestry Experiment Station, Mississippi State University.
- Larimore, R. W. 1975. Visual and tactile orientation of smallmouth bass fry under floodwater conditions. Pages 323-332 in R. H. Stroud and H. Clepper, editors. *Black Bass Biology and Management*. Washington, DC: Sports Fishing Institute.
- Latta, W. C. 1963. The life history of the smallmouth bass, *Micropterus dolomieu*, at Wau-goshance Point, Lake Michigan. *Bulletin of the Institute for Fisheries Research* 5(X):5-56.
- Livingstone, A. C., and C. F. Rabeni. 1991. Food-habitat relations of underyearling small-mouth bass in an Ozark stream. Pages 76-83 in D. C. Jackson, editor. *First International Smallmouth Bass Symposium*. Mississippi Agricultural and Forestry Experiment Station, Mississippi State University.
- Lukas, J. A. 1993. *Factors Affecting Reproductive Success of Smallmouth Bass and Redbreast Sunfish in the North Anna River, Virginia*. Master's thesis. Blacksburg: Virginia Polytechnic Institute, Fisheries and Wildlife Sciences.
- Mathur, D., W. H. Bason, E. J. Purdy, Jr., and C. A. Silver. 1985. A critique of the instream flow incremental methodology. *Canadian Journal of Fisheries and Aquatic Sciences* 42(4):825-831.
- Milhous, R. T., M. A. Updike, and D. M. Schneider. 1989. *Physical Habitat Simulation System Reference Manual—Version II. Instream Flow Information Paper No. 26*. Washington, DC: U.S. Fish and Wildlife Service (Biological Report 89 [16]).
- Morhardt, J. M., D. F. Hanson, and P. J. Coulston. 1983. Instream flow: Increased accuracy using habitat mapping. Pages 1294-1304 in *Waterpower 83*, Volume 3. *Environmental Impacts: An International Conference on Hydropower*. Knoxville, TN: Tennessee Valley Authority.
- Morin, A., and N. Bourassa. 1992. Modeles empiriques de la production annuelle et du rapport P/B d'invertebres benthiques d'eau courante. *Canadian Journal of Fisheries and Aquatic Sciences* 49(3):532-539.
- Murdoch, W. W., E. McCauley, R. M. Nisbet, W. S. C. Gurney, and A. M. de Roos. 1992. Individual-based models: Combining testability and generality. Pages 18-35 in D. L. DeAngelis and L. J. Gross, editors. *Individual-Based Models and Approaches in Ecology: Populations, Communities and Ecosystems*. New York: Chapman and Hall.
- Orth, D. J., and O. E. Maughan. 1982. Evaluation of the incremental methodology for recommending instream flows for fishes. *Transactions of the American Fisheries Society* 111(4): 413-445.
- Osborne, L. L., M. J. Wiley, and R. W. Larimore. 1988. Assessment of the water surface profile model: Accuracy of predicted instream fish habitat conditions in low-gradient warmwater streams. *Regulated Rivers: Research and Management* 2(5):619-631.
- Peters, E. J., R. S. Holland, M. A. Callam, and D. L. Brunnell. 1988. *Habitat Utilization, Preference and Suitability Criteria for Fish and Aquatic Invertebrates in the Lower Platte River*. Lincoln, NE: Department of Forestry, Fisheries, and Wildlife, Institute of Agriculture and Natural Resources, University of Nebraska.
- Peters, R. H. 1991. *Critique for Ecology*. New York: Cambridge University Press.
- Pflieger, W. L. 1966. Reproduction of the smallmouth bass (*Micropterus dolomieu*) in a small Ozark stream. *American Midland Naturalist* 76(2):410-419.
- . 1975. Reproduction and survival of the smallmouth bass in Courtois Creek. Pages 231-239 in R. H. Stroud and H. Clepper, editors. *Black Bass Biology and Management*. Washington, DC: Sports Fishing Institute.
- Post, J. R. 1990. Metabolic allometry of larval and juvenile yellow perch (*Perca flavescens*): In situ estimates and bioenergetic models. *Canadian Journal of Fisheries and Aquatic Sciences* 47(3):554-560.

- Reiser, D. W., T. A. Wesche, and C. Estes. 1989. In defense of the instream flow incremental methodology. *Canadian Journal of Fisheries and Aquatic Sciences* 14(2):22-29.
- Reynolds, C. R., and C. J. O'Bara. 1991. Reproductive ecology and spawning habitat of smallmouth bass in two small streams of the Tennessee River system. Pages 61-65 in D. C. Jackson, editor. *Proceedings of the First International Smallmouth Bass Symposium*. Mississippi Agricultural and Forestry Experiment Station, Mississippi State University.
- Rice, J. A., J. E. Breck, S. M. Bartell, and J. F. Kitchell. 1983. Evaluating the constraints of temperature, activity and consumption on growth of largemouth bass. *Environmental Biology of Fishes* 9(3/4):263-275.
- Ridgway, M. S., B. J. Shuter, and E. E. Post. 1991. The relative influence of body size and territorial behaviour on nesting asynchrony in male smallmouth bass, *Micropterus dolomieu* Lacepede, (Pisces: Centrarchidae). *Journal of Animal Ecology* 60(2):665-691.
- Robbins, W. H., and H. R. MacCrimmon. 1977. Vital statistics and migratory patterns of a potamodromous stock of smallmouth bass, *Micropterus dolomieu*. *Journal of the Fisheries Research Board of Canada* 34(1):142-146.
- Sale, M. J., G. F. Cada, L. H. Chang, S. W. Christensen, S. F. Railsback, J. E. Francfort, B. N. Rinehart, and G. L. Sommers. 1991. *Environmental Mitigation at Hydroelectric Projects*, Volume 1. *Current Practices for Instream Flow Needs, Dissolved Oxygen, and Fish Passage*. Idaho Falls, ID: U.S. Department of Energy Field Office (DOE/ID-10360).
- Shuter, B. J., D. L. DeAngelis, M. S. Ridgway, P. Blanchfield, and G. E. Morgan. 1993. Modeling early life history stages of smallmouth bass in Ontario lakes. *Transactions of the American Fisheries Society*. In press.
- , J. A. MacLean, F. E. J. Fry, and H. A. Regier. 1980. Stochastic simulation of temperature effects on first-year survival of smallmouth bass. *Transactions of the American Fisheries Society* 109(1):1-34.
- Smock, L. A. 1980. Relationships between body size and biomass of aquatic insects. *Freshwater Biology* 10(4):375-383.
- Spitze, K. 1985. Functional responses of an ambush predator: *Chaoborus americanus* predation on *Daphnia pulex*. *Ecology* 66(3):938-949.
- Van Winkle, W., K. A. Rose, and R. C. Chambers. 1993. Individual-based approach to fish population dynamics. *Transactions of the American Fisheries Society*. 122(3):397-403.
- Wiegmann, D. D. 1990. On assessing the potential for evolutionary change due to male-male competition and female choice in territorial species. *Journal of Theoretical Biology* 144(2):203-208.
- Williams, F. M. 1984. A fish population model for instream flow assessment. University Park, PA: Prepared for the U.S. Department of the Interior by the Institute for Research on Land and Water Resources, Pennsylvania State University (*Research Project Technical Completion Report A-059-PA*).
- Williamson, S. C., J. M. Bartholow, and C. B. Stalnaker. 1993. Conceptual model for quantifying pre-smolt production from flow-dependent physical habitat and water temperature. *Regulated Rivers: Research and Management*. In press.
- Winemiller, K. O., and D. H. Taylor. 1982. Smallmouth bass nesting behavior and nest site selection in a small Ohio stream. *Ohio Academy of Science* 82(5):266-273.
- Wrenn, W. B. 1984. Smallmouth bass reproduction in elevated temperature regimes at the species' native southern limit. *Transactions of the American Fisheries Society* 113(3):295-303.

Received: 13 December 1992

Accepted: 23 March 1993

Discussion open until: 31 March 1994

