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Ecological Modelling 187 (2005) 247–258
ECOLOGICAL MODELLING
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An individual-based simulation model for mottled sculpin (*Cottus bairdi*) in a southern Appalachian stream

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Received 6 January 2003; received in revised form 15 October 2004; accepted 21 January 2005
Available online 23 February 2005

Abstract

We describe and analyze a spatially explicit, individual-based model for the local population dynamics of mottled sculpin (*Cottus bairdi*). The model simulated daily growth, mortality, movement and spawning of individuals within a reach of stream. Juvenile and adult growth was based on consumption bioenergetics of benthic macroinvertebrate prey; benthic macroinvertebrate densities were a function of flow, season, and habitat quality. We based mortality rates of individual sculpin on their condition. Fish movement was determined by a growth maximization rule. We adjusted selected parameters to calibrate the model for a sculpin population in a southern Appalachian stream, in terms of adult and juvenile abundance and mean adult weight and length. Sensitivity and correlation analysis of the calibrated model suggested that this population was regulated by overwinter density-dependence among juveniles and adults.
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Keywords: Density-dependence; Population regulation; Stream fish; Individual-based model; Density-independent

1. Introduction

Unlike standard population models, which assume that most or all individuals are identical and merely track the number of individuals over time, individual-based models track individuals in terms of their unique biological characteristics such as length, weight, and location. Individual-based model enable researchers to incorporate biologically meaningful intra-individual differences (Wootton, 1998) and to evaluate the effects of biotic and abiotic processes on these characteristics. In addition, individual-based models allow greater complexity (i.e., may be more realistic) than standard models, but can be robust because individual-level biology and behavior are better studied than population-level parameters for many species (DeAngelis and Gross, 1992). There have been several previous applications of individual-based models to lotic fishes, including assessments of the effects of varying flow on populations of brown and rainbow trout (Van Winkle et al., 1998), chinook salmon in regulated Western rivers (Jager et al., 1997), rainbow trout and brook char in the southern Appalachians (Clark and Rose,

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doi:10.1016/j.ecolmodel.2005.01.047

1997), and striped bass in the Potomac River (Rose and Cowan, 1993). Nonetheless, most, if not all previous individual-based models for fish have examined game species, despite the fact that non-game fishes typically dominate freshwater fish assemblages in both abundance and biomass (Matthews, 1998; Wootton, 1998; Moyle and Cech, 1999).

This paper considers how individual behaviors and habitat conditions affect population dynamics in *Cottus bairdi*, the mottled sculpin, in southern Appalachian high-gradient streams. *C. bairdi* is a benthic, non-game fish that is widely distributed across temperate North America and commonly dominates cold-water stream fish assemblages (Grossman et al., 2002). Much is known about its biology as a result of 20 years of study in Coweeta Creek of western North Carolina, a drainage that is characteristic of many streams in the southern Appalachian Mountains (Grossman et al., 1998). Sculpin are the most abundant fish in the upper portion of this drainage (Freeman et al., 1988), and previous studies demonstrate that interspecific competition and predation have little effect on diet and habitat selection by sculpin in this system (Stouder, 1990; Grossman et al., 1995, 1998), thus a population-level approach is justified for this species. Sculpin populations display high levels of stability in this system (Freeman et al., 1988; Grossman et al., 1990).

Habitat selection in sculpin is based on macroinvertebrate prey density rather than physical habitat attributes (Petty and Grossman, 1996). Highest quality habitats occur in fast riffles (Wohl et al., 1995), and Petty (1998) demonstrated that survival among juveniles and younger adults is higher in higher quality habitats. Adult sculpins are territorial, and Petty (1998) demonstrated that larger sculpin (i.e., adults) exclude smaller individuals (i.e., juveniles) from high quality patches, and individuals in poor quality habitats displayed lower growth rates and survival. Nonetheless, when juveniles occupy high-quality patches, their survivorship and growth rates do not differ significantly from adults (Petty, 1998). Freeman and Stouder (1989) have also shown that larger sculpin can displace smaller individuals. Our individual-based model for sculpin represents stream habitat as spatially explicit in two dimensions, and uses a size-based dominance structure to control access to habitat. These features are used in other IBMs for stream fish: a two-dimensional spatially explicit approach has been used by Jager et al. (1999), and Van Winkle et al. (1998) use a length driven dominance structure that controls access to feeding stations for trout in the a California river. Our model is unique in combining these features.

In this paper, we describe the individual-based model for a *Cottus* population, the methods used to calibrate for a specific site in the southern Appalachians, and the results from calibration and sensitivity analysis. Our model simulates daily growth, mortality, movement and spawning of sculpin. Juvenile and adult growth was based on consumption bioenergetics of benthic macroinvertebrate prey; mortality rates of individual sculpin were based on their condition. Fish movement was determined by a growth maximization rule. We calibrated the model to 10 years of data from a stream reach in lower Ball Creek, a tributary to Coweeta Creek. Relationships of population abundance and growth rates to population density and flow variables in the calibrated model were examined using correlation analysis. The calibrated model can be used to provide a better understanding of *Cottus* population dynamics and facilitate prediction of how populations of this abundant and widely distributed species will response to future stressors such as climate change.

2. Model description

2.1. Overview

Our model represents daily dynamics of a mottled sculpin population in a stream channel of fixed length. Daily temporal resolution was used because it is common in other IBMs; shorter time steps require excessive computation and longer time steps increase the likelihood of missing transient dynamics. A spatially explicit approach was used because of the high variability in the stream channel and the significance of this variability to fish biology. The spatial resolution of the model was in two dimensions because sculpin are known to be territorial and occupy discrete habitat patches (Petty and Grossman, 2004). The environment consists of daily water temperature, flow, and depth measures. Temperature was included because it is known to affect fish respiration and consumption (e.g., Hanson et al., 1997). Wetted width, calculated from flow, determines the amount of habitat available for sculpin. Velocity, calculated from flow and depth, af-

fects benthic macroinvertebrate growth rates (Resh and Rosenberg, 1984). Other factors such as water quality were not considered here. Macroinvertebrate density is modeled explicitly because habitat selection is based on macroinvertebrate prey density rather than physical habitat attributes (Petty and Grossman, 1996, 2004).

The biological processes represented in the model for fish are growth, survival, movement and spawning. Juveniles and adults are tracked as individuals by the model, in terms of weight, length, age, sex, and spatial position, using a daily timestep. The individual-based approach is used in order to relate the consequences of intra-individual biological differences to population regulation (Wootton, 1998). The model simulates the sculpin life stages of egg, larvae, and young-of-year (YOY) indirectly as cohorts, because there is insufficient biological information about these life stages to characterize individual differences. Because this species maintains a stable population (Freeman et al., 1988), we assumed that immigration and emigration are negligible.

The model description is organized as follows: physical habitat, benthic invertebrate biomass dynamics, fish growth, fish survival, fish movement, and fish spawning and early life stages. The submodels were implemented in Matlab in this order. In general, the model structure and equations were designed to be similar to published IBMs for fish. Parameter values and definitions are listed in Table 1. We verified all software components to ensure that results were mathematically stable and yielded biologically realistic values.

2.2. Physical habitat

Our model represents daily dynamics of a mottled sculpin population in a stream channel of fixed length λ (m). We gridded the stream system into square patches of area A (m^2), based on a maximum stream width ω_{max} (m). The area of habitat patches (A) was set to 1 m^2, which is consistent with measured values for this species at this site (Freeman and Stouder, 1989; Petty, 1998). Patches are indexed with the coordinate system of i (across the stream) and j (downstream direction).

The model uses an input time series of mean daily flow (Q, $m^3\,s^{-1}$) obtained from Forest Service Weir 9, just above the sample site on Ball Creek. Flow is used in a regression to calculate wetted area, which is divided by the length of the stream segment to give wetted width (ω, m):

$$\omega = \frac{\omega_a Q + \omega_b}{\lambda}. \tag{1}$$

Regression parameters for Eq. (1) (Table 1) were derived by Grossman et al. (unpublished data). If $\omega > \omega_{max}$, $\omega = \omega_{max}$. Average velocity ($\bar{v}$, $m\,s^{-1}$) is calculated as

$$\bar{v} = \frac{Q}{d\omega}, \tag{2}$$

where d (m) is the average depth, defined as

$$d = (D_a \omega)^{D_b}; \tag{3}$$

D_a and D_b are parameters. This formulation for d was taken from Richards (1976) and was successfully used in the individual-based trout model of Clark and Rose (1997). The parameters D_a and D_b (Eq. (3)) were taken from individual-based model of Clark and Rose (1997) for streams in a nearby geographic location. Using Eqs. (1) and (3), the average flow in Ball Creek (0.28 $m\,s^{-1}$) corresponds to an average depth of 0.21 m, which is similar to that measured in Ball Creek by Houston (1994).

We assume that the stream channel is symmetric and that the cross-sectional velocity profile can be represented as parabolic. For each patch i across the stream, we assign a current velocity v_i based on the mean velocity and the distance between the midpoint of the patch and the center of the stream:

$$v_i = \frac{6\bar{v}}{\omega^2}\left(i - \frac{\sqrt{A}}{2}\right)\left(\omega - \left(i - \frac{\sqrt{A}}{2}\right)\right). \tag{4}$$

We assigned each habitat patch a habitat quality value, $q_{i,j}$ that represents generalized habitat features. These values were assigned randomly but sorted across each row so that the largest values occurred in the stream center. We used this constraint because high quality erosional habitats for sculpin generally do not occur in shallow stream margins (Grossman and Ratajczak, 1998; Petty, 1998). Petty (1998) found that a critical velocity (v_c) of 0.20 $m\,s^{-1}$ determined whether a patch was erosional or depositional and described the differential effects on sculpin fitness of occupying either type of patch. In brief, the higher prey abundance

Table 1
Parameters used in the model

Parameter	Definition (units)	Value
A	Patch area (m^2)	1
α	Overlap among juveniles	0.15
B	Benthic macroinvertebrates maximum production ($g\,m^{-2}$)	$B^* = 6$
C_a, C_b, C_c	Parameters in the C_{max} calculation	0.08, 0.69, 0.0693
c_r, c_t	Costs for reproduction (r) and travel (t)	0.75, 0.55
D_a, D_b	Parameters for calculating depth	0.075, 1.57
d	Mean depth (m)	
E	Fish assimilation efficiency	0.5
F_a, F_b	Parameters for determining sculpin fecundity	0.00597, 2.295
h	Half-saturation constant ($g\,m^{-2}$)	6
K	Fish condition	$K_c = 0.75$
L	Standard length of individual fish (mm)	$L_{min} = 43.6$
L_a, L_b	Parameters in the sculpin length–weight regression	32.02, 0.364
λ	Stream length (m)	30
m	Movement parameter for benthic macroinvertebrates (d^{-1})	0.003
P	Coefficient for benthic macroinvertebrate growth rate	0.25
Q	Stream flow ($m^3\,s^{-1}$)	From Weir 9
q	Habitat quality (randomly assigned to patches)	0.1–1
R_a, R_b, R_c	Coefficients for fish respiration equation	0.008, 0.69, 0.0693
r_d, r_e	Growth rate for benthic macroinvertebrates (d^{-1})	0.0175, 0.035
S	Age of sculpin senescence (years)	6
s_y, s_j, s_a	Survival probabilities for different fish life stages (d^{-1})	0.9975, 0.9978, 0.9983
T	Stream temperature (°C)	$T_0 = 10$
T_a, T_b, T_c, T_d	Parameters used in stream temperature equation	10.9, 5.7, 365.6, 4.3
t_{spawn}	Julian day of spawning in the model	90
t_{spring}, t_{fall}	Julian day of "sampling" in the model	135, 260
v	Velocity ($m\,s^{-1}$)	$v_c = 0.2$
W	Weight of individual (g)	
ω_a, ω_b	Parameters for wetted width regression	74.42, 128.67
ω	Wetted width (m)	$\omega_{max} = 6.0$

and prey replenishment rates of erosional patches probably produce the higher growth and survivorship rates of sculpin occupying these patches (Petty, 1998; Petty and Grossman, 2004).

Daily water temperature data (T, °C) was obtained from a submerged thermograph located in a shaded section of Coweeta Creek, approximately 400 m downstream from the Ball Creek study site. Because the temperature data set was incomplete, we fit a sine curve to the daily means of available data ($r^2 = 0.97$):

$$T = T_a + T_b \sin\left(\frac{2\pi t}{T_c} + T_d\right), \tag{5}$$

where t is the julian day of the year (1–366). Sine functions have also been used in other IBMs to represent water temperature (e.g., Rose and Cowan, 1993; Jager et al., 1997). We used parameters from this curve in the model (Table 1). Because the stream is well mixed (G. Grossman, personal observation), we assume that temperature variation is minimal throughout the reach.

2.3. Benthic macroinvertebrate biomass

We calculate benthic macroinvertebrate biomass at a particular patch ($B_{i,j}$, $g\,m^{-2}$) as:

$$\frac{dB_{i,j}}{dt} = P_{i,j} - C_{i,j} + M_{i,j}, \tag{6}$$

where P is production ($g\,d^{-1}$), C is consumption of benthic macroinvertebrates by fish predators ($g\,d^{-1}$, see Section 2.4), and M is the net immigration from other patches ($g\,d^{-1}$). This equation is analogous to the formulation of by McDermot and Rose (2000). We

represent production (P) with a logistic function,

$$P_{i,j} = r_i \left(1 + p \sin\frac{2\pi t}{365}\right)\left(1 - \frac{B_{i,j}}{q_{i,j}B^*}\right) B_{i,j} \quad (7)$$

where r_i (d^{-1}) is the growth rate for benthic macroinvertebrates, p is a term to account for the variation that occurs in benthic macroinvertebrate growth rate due to temperature (Petty and Grossman, 1996), $q_{i,j}$ is a habitat quality value for each patch (see Section 2.2), and B^* ($g\,m^{-2}$) is maximum production. Growth rate depends on velocity in the patch: $r_i = r_e$, $v_i < v_c$ and $r_i = r_d$, $v_i \geq v_c$, where v_c ($m\,s^{-1}$) is the critical velocity determining whether a patch is erosional or depositional. Net immigration from other patches (M) is represented as a first-order process with a constant value m (d^{-1}). Net immigration from patch (i, j) to patch $(i, j-1)$, is:

$$M_{i,j} = m(B_{i,j} - B_{i,j-1}). \quad (8)$$

Net immigration to patch (i, j), is the sum of diffusion of biomass from all neighboring patches. If a patch is dewatered, its benthic macroinvertebrate density is set to zero.

We used information from multiple studies on Ball Creek to estimate r, the growth rate parameter for benthic macroinvertebrates (Huryn and Wallace, 1987; Houston, 1994) and B^*, benthic macroinvertebrate maximum production (Wohl et al., 1995; Gibson et al., 2004).

2.4. Individual growth

We represent daily growth in mass for juveniles and adults using the bioenergetic equation

$$\frac{dW}{dt} = EC - R, \quad (9)$$

where W is wet weight (g), C is consumption ($g\,d^{-1}$), R is respiration ($g\,d^{-1}$), and E is assimilation efficiency, which account for losses due to egestion, excretion, and specific dynamic action. The factors incorporated into assimilation efficiency are sometimes calculated separately in individual-based models, but can be combined if the assumption is made that they are all fractions of consumption (Hanson et al., 1997). We assumed an assimilation efficiency (E) of 0.5, which is in the range of parameter values used in similar individual-based models (e.g., Clark and Rose, 1997; McDermot and Rose, 2000).

Consumption is represented by a Holling Type II equation with interference (Holling, 1959)

$$C = \frac{C_{max} B_{i,j}}{h + B_{i,j} + \alpha(N_{i,j} - 1)}, \quad (10)$$

where C_{max} is maximum consumption rate ($g\,d^{-1}$), h represents the half-saturation constant, $B_{i,j}$ represents the biomass density of benthic macroinvertebrates in the patch, α is a coefficient of interference, and N is number of individuals in the patch. Juveniles may overlap within patches, and hence, experience competition, however, adults have exclusive territories so the $(N_{i,j} - 1)$ term is zero for adults in territories (Petty, 1998). Half-saturation was adjusted in calibration. The interference coefficient (α) was estimated at 0.15, based on field observations of juvenile overlap by Petty (1998).

Maximum consumption is calculated as

$$C_{max} = C_a W^{C_b} e^{C_c(T - T_0)} \quad (11)$$

where T is temperature and C_a, C_b, and C_c are parameters. We derived the C_a parameter by doubling the half-saturation estimate from Davis and Warren (1965). A reference temperature (T_0) of 10 °C was used. The parameter C_b was set based on common values for other bioenergetic equations (Hanson et al., 1997). The parameter C_c was set to 0.0693, assuming that a twofold change in a physiological process occurs in response to a 10 °C change in temperature (i.e., $Q_{10} = 2$).

We represent respiration with a temperature-dependent power function:

$$R = R_a W^{R_b} e^{R_c(T - T_0)}, \quad (12)$$

where T is temperature and R_a, R_b, and R_c are parameters (Hanson et al., 1997). The parameter R_a, respiration at the reference temperature T_0 (a reference temperature of 10 °C was used) was obtained from Facey and Grossman (1990). The oxygen-based measure from Facey and Grossman (1990) was converted to a carbon-based measure assuming that Respiratory Quotient (RQ) was equal to 1. We have not corrected respiration for activity, which is used in some fish models but is less significant for a sedentary, benthic fish such as *Cottus* (Facey and Grossman, 1990). The parameter R_b was set based on common values for other bioenergetic equations (Hanson et al., 1997). The parameter R_c was set to 0.0693, assuming that a twofold

change in a physiological process occurs in response to a 10 °C change in temperature (i.e., $Q_{10} = 2$).

If the change in weight (Eq. (9)) is positive, standard length (L, mm) is updated by a length-weight regression,

$$L = L_a W^{L_b}, \tag{13}$$

where L_a and L_b are constants derived from a linear regression of log-transformed data on fishes collected at the Coweeta laboratory ($r^2 = 0.93$, $N = 175$). If the individual loses weight, its length does not change. We solved the differential Eqs. (6) and (9) using a Runge–Kutta approach.

2.5. Individual survival

Individual survival is determined by the survival probability of juveniles (s_j, d^{-1}) and adults (s_a, d^{-1}) multiplied by K, a measure of condition, which is calculated as the ratio of actual weight to expected weight calculated from current length (Van Winkle et al., 1998):

$$K = \frac{W}{(L/L_a)^{1/L_b}}. \tag{14}$$

We assume that an individual juvenile or adult dies if a randomly generated number that is uniform on (0, 1) is less than $1 - s_j K$ or $1 - s_a K$, respectively. This approach is used in order to stochastically simulate the mortality for an individual. Survival probabilities for juveniles and adults were estimated from Petty (1998) (Table 1). All individuals die once they reach the age of S years; parameter values for age of senescence (S) were taken from Grossman et al. (2002) (Table 1).

2.6. Individual movement

On each day, all fish examine adjacent patches and move if their foraging rate is higher in an adjacent patch (Clark and Rose, 1997). This is a growth maximization rule, which is appropriate when mortality risks and metabolic costs are not spatially variable (Railsback et al., 1999). We assumed that if a target patch is occupied by a larger individual, a move to that patch is not possible (Petty, 1998). The potential benefit of occupying a target patch $(i+1, j)$ is calculated as

$$G_{i+1,j} = \max\left(\frac{B_{i+1,j} - B_{i,j} - c_t}{B_{i,j}}, 0\right) \times \max\left(\frac{L_{i+1,j} - L_{i,j}}{L_{i,j}}, 0\right). \tag{15}$$

where $B_{i,j}$ and $L_{i,j}$ are the benthic macroinvertebrate biomass and the standard length of the individual fish in patch (i, j), respectively. Petty (1998) found that adults abandon a patch when prey density falls below a threshold level that is lower than the mean prey density of randomly selected patches. This suggests that there is a cost to movement, which is represented here as a travel cost c_t. Hence, our movement rule for the model is as follows: if a move is advantageous, the fish moves to the patch with the greatest gain, and if a smaller fish is present, it is switched with the larger fish.

At each time step, each juvenile also evaluates the habitat quality in all adjacent patches. We assumed that patches outside the study area, patches with no velocity, and those that are inhabited by adults are unavailable to juveniles. The potential benefit of a neighboring patch is calculated as

$$G_{i+1,j} = \max\left(\frac{B_{i+1,j}}{N_{i+1,j} + 1} - \frac{B_{i,j}}{N_{i,j}}, 0\right), \tag{16}$$

where the measure of destination is the amount of food available divided by the number of competitors in the patch. Movement cost is not included for juveniles, since field studies do not show evidence of this (Petty, 1998). If movement is not possible and an individual's current patch is dewatered, the individual dies. Once juveniles reach the minimum length for adult size (L_{min}), they are able to defend a patch and inhabit it exclusively (Petty and Grossman, 2004).

Previous work on movement by sculpin in this system indicates that the model's movement constraints (i.e., short movements, growth maximization, lack of predation effect) are consistent with what occurs in the natural system (Grossman et al., 1995; Petty, 1998; Petty and Grossman, 2004). Nonetheless, we recognize that in other systems predation risk may constrain movement, and other movement rules may be more appropriate (White and Harvey, 2001). Similarly, temperature has been shown to constrain fish movement (Wildhaber and Lamberson, 2004), however, our system is well mixed and shallow so it is unlikely that significant temperature differences exist among patches.

2.7. Spawning and early life stages

We assumed that females spawn one time per season on the day t_{spawn} (April 1, DeHaven et al., 1992). Females spawn only if they are above the minimum length for adult size (L_{min}) and only if their condition factor is above a critical value, $K > K_c$. The critical condition value for a female to spawn (K_c) was set at 0.75, a value used in other individual-based fish models (Van Winkle et al., 1998). Initial clutch size for each female was determined by fecundity, which is a function of female length,

$$F = F_a L^{F_b}, \tag{17}$$

where F_a and F_b are constants taken from Grossman et al. (2002). The weights of reproductive females and males are multiplied by a parameter c_r to reproductive cost; the value for this parameter is based on measurements of *C. bairdi* in this system made by DeHaven et al. (1992) (Table 1). Males are included because they expend energy guarding nests (Fiumera et al., 2002).

We assumed that the development from eggs to young-of-year to juveniles takes a year. For each clutch, at their spawn day in the next year, the number of juveniles from the clutch is determined by

$$N = s_y F \tag{18}$$

where s_y, the survival of YOY, is a constant (Table 1). Each clutch of juveniles is randomly assigned a location in the set of wetted patches that do not contain adults. We assigned each of the N juveniles a weight calculated from the minimum length for juveniles (25 mm, Petty, 1998) using Eq. (13), assigned gender by drawing from a binomial random variable with mean value 0.5 (McDaniel, 1999), and tracked each individually.

3. Model calibration

3.1. Site description

We calibrated the model for a sculpin population inhabiting Ball Creek in the USDA Forest Service Coweeta Hydrological Laboratory in Otto, North Carolina. This laboratory is situated in the Blue Ridge province of the southeastern Appalachian mountains. A thorough description of the study drainage can be found in Freeman et al. (1988), Grossman et al. (1998), and Thompson et al. (2001). The site is located at an elevation of 690 m, has an average gradient of 7%, a drainage area of 689.6 ha, and a mean depth of 0.14 m (Houston, 1994). Maximum wetted width (ω_{max}) is approximately 6 m, and the site is dominated by high velocity riffles and shallow pools with bedrock, cobble, gravel, and sand substrata.

3.2. Calibration procedure

We quantified sculpin abundance in a 30 m section of stream in Ball Creek twice a year for 10 years (1984–1993) and these data form the basis of our model calibration. A basic description of the sampling methodology can be found in Freeman et al. (1988). In short, during spring and fall of each year we block-netted the upstream and downstream boundaries of the site, and then used a backpack electrofisher to collect fish within the site. We made a minimum of three passes through the site and used the depletion estimator of the CAPTURE program (White et al., 1982) to estimate abundances of juvenile and adult sculpin within the site. For some of the estimates, adult abundance data exceeded the number of adults plus juveniles at the previous time step. These discrepancies were due both to immigration and sample error, which were not included in the model. For comparison to model output, adult abundance data was constrained such that it could not exceed the number of adults plus the number of juveniles at the previous sampling time.

We obtained data from the model on specific dates t_{spring} and t_{fall} that fell within the ranges of actual spring and fall sample dates. Because actual sample dates varied from year to year, the length cut-off used to distinguish small adults from juveniles also varied; our model, however, used a single sampling day, so we calculated a mean cut-off value from the actual cut-off data (spring: $\bar{x} = 40.2$ mm, S.D. = 1.7; fall: $\bar{x} = 47.0$ mm, S.D. = 0.9) to use in the model.

We initialized the model with the number of fish adults present in the first spring sample ($N = 41$, Spring 1984), and used their actual lengths and weights. The length of one individual was adjusted from 39 to 40.2 to agree with the spring length cut-off used in the model. In 1984, the estimated numbers of juveniles from the

spring and fall samples were 3 and 22, respectively; and given that it is biologically impossible for YOY to grow to juvenile size in this time interval, we increased the spring estimate by 19 juveniles of length 25 mm and weight determined by Eq. (13). No YOY were observed in the spring 1984 sample, so five YOY cohorts, each containing 71 individuals (corresponding to the mean fecundity of age-3 fish, Grossman et al., 2002), were generated in order to produce the juveniles measured in the spring 1985 sample. We initialized benthic macroinvertebrate densities at half of their maximum production.

Our calibration criteria were as follows: (1) the population persisted through the simulation, (2) the model produced a realistic length-age relationship, and (3) the observed and predicted values for abundance, mean number of juveniles, and mean adult length and weight had to be in reasonable agreement (Bart, 1995). Because an individual-based model is stochastic by nature, multiple runs were necessary to be able to compare output values with field data. First, we ran the model with 100 different random seeds to determine expected values for adult abundance, and we then sequentially reduced the number of runs and recalculated the expected values for each data point. Using this method, we determined that 25 runs were needed to approximate the expected model values within ±0.001. To calibrate the model, we adjusted selected parameter values (Table 1) until good agreement was obtained.

3.3. Calibration results

The calibrated model provided a reasonable fit to the observed abundance of adult sculpin in Ball Creek (Fig. 1). The average absolute difference between observed and predicted adult abundance values over the 10-year period was 20.8%, which was moderate. For example, Van Winkle et al. (1998) reported average absolute differences of 23–60% between the observed abundances for two species of trout and abundances predicted by an individual based model. The largest differences between observed and predicted sculpin abundance occurred in 1989, 1990, and 1992, and coincided with the highest flows recorded during the study (Fig. 1). The discrepancies between observed and predicted abundance data could be due to uncertainties in the observed data, for example the variability in sampling days as opposed to the constant sampling day

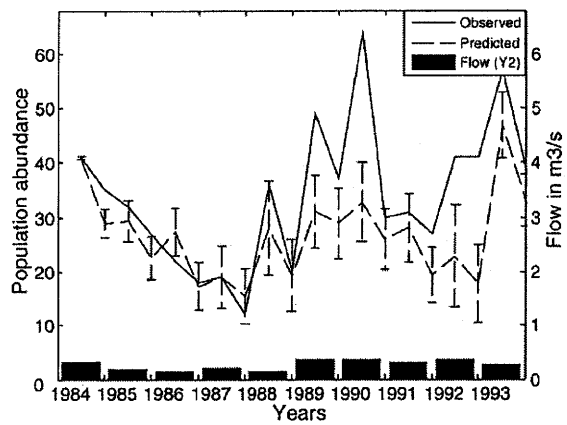

Fig. 1. Observed vs. model predicted abundance (±1S.D.) of adult sculpin in Ball Creek. Inset gives flow for the same time period.

imposed in the model. Also, it is possible that the sampling efficiency varied. At higher water levels, depletion with the 3-pass method tends to be lower, which leads to larger predicted abundance ranges and may overestimate abundance (G. Grossman, personal observation).

There were no significant differences (Wilcoxon rank-sum test, $P < 0.05$) between medians of observed and predicted adult lengths and weights (Fig. 2). However, the number of juveniles predicted by the calibrated model was significantly greater than the ob-

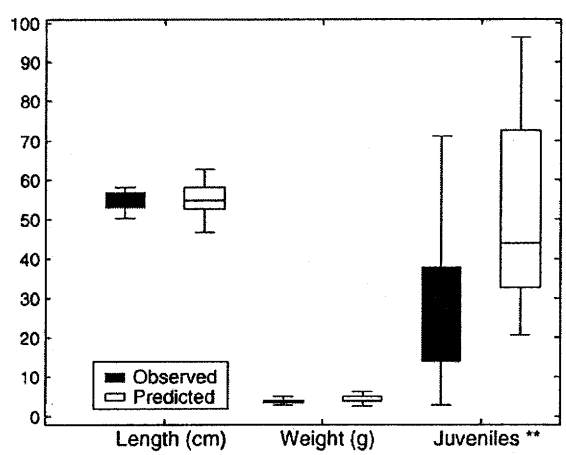

Fig. 2. Observed versus model predicted mean adult length (cm), adult weight (g), and number of juveniles of sculpin in Ball Creek (**, significantly different at the 0.05 level) calculated over the entire study period.

served number (Fig. 2). We attribute this to the fact that the model includes complete capture of juveniles, but the field method may not.

4. Sensitivity analysis

Sensitivity analyses are conducted with individual-based models to assess the effect of selected parameters on model outputs (Bart, 1995). We analyzed model sensitivity by sequentially introducing small changes in the selected parameters and measuring the change in the mean values of abundance, length, and weight. Following Clark and Rose (1997) and McDermot and Rose (2000), we used Pearson correlations to examine the relations of juvenile and adult survival to specific environmental and life history variables.

Our analysis indicated that length was less sensitive to parameter changes than either weight or mean abundance (Table 2). Parameters related to consumption appeared to have the greatest impact on response variables, a result that is consistent with other individual-based fish models (e.g., Van Winkle et al., 1998). As expected, parameters that increased consumption (assimilation, benthic invertebrate production and maximum production, c_1) generally produced positive changes in response variables, whereas parameters that decreased consumption (half-saturation, r_1) yielded opposing results. Increases in parameters related to younger life stages (fecundity, YOY survival) elicited negative responses in mean abundance, length and weight. We might expect that increases in younger life stages would increase population abundance, except in settings where resource competition among juveniles occurs.

Table 2
Percent change in response to 10% increase in selected parameters

Parameter	Adult population		
	Mean abundance	Mean length	Mean weight
C_a	−1.3	1.1	2.7
E	5.8	2.7	8.0
F_a	−1.0	−1.1	−3.2
h	−4.4	−0.5	−1.6
K	4.2	2.7	9.4
r_d, r_e	4.8	0.7	2.2
R_a	−11.4	−1.2	−4.3
s_y	−1.0	−1.1	−3.2
T_a	−0.4	−0.3	−1.1

Response variables are averaged over $N=20$ sample points. See Table 1 for parameter definitions.

Adult and population survival showed moderate positive and negative correlations, respectively, with flow amount and variation; this indicates that stable, high-flow conditions are most conducive to survival (Table 3). Surprisingly, juvenile survival from spring to fall showed a negative correlation with flow amount, however, the most significant response for juvenile survival from spring to fall was a negative correlation with adult survival during the same time period. This could indicate a negative influence of adults on juveniles. The most significant finding among the life history variables was a negative correlation between fall population size (adults plus juveniles) and over-winter population survival. This result is consistent with density-dependent population regulation.

Table 3
Correlations among selected life history and environmental variables

Variable	Juvenile survival (spring–fall, $N=10$)	Adult survival (spring–fall, $N=10$)	Adult and juvenile survival (fall–spring, $N=9$)
Flow amount (spring–fall)	−0.6076	0.2328	–
Flow variation (spring–fall)	−0.2091	−0.3994	–
Number of juveniles (spring)	0.5094	–	–
Number of adults (spring)	−0.1174	−0.0690	–
Adult survival (spring–fall)	−0.7528[a]	–	–
Number of adults (fall)	–	–	0.6424
Number of adults and juveniles (fall)	–	–	−0.8797*
Flow amount (fall–spring)	–	–	0.1874
Flow variation (fall–spring)	–	–	−0.4658

* Significant at the 0.05 level.

5. Discussion

We used a spatially explicit, individual based model to simulate the local dynamics of a sculpin population in response to hydrologic variation. Using this modeling approach, we were able to represent spatial variability in habitat quality and ecologically significant differences among individuals, factors that are difficult to incorporate in aggregated models. Our model provided a reasonable fit to data for the Ball Creek sculpin population in terms of adult abundance, length, and weight data. These results suggest that our model was constructed using biologically realistic assumptions and that it should yield insights into the dynamical behavior of sculpin populations in southern Appalachian and other streams. The strongest density-dependent effects in the model occurred in the winter, when food density decreased at the same time that juveniles had grown in size and required more food. Because the model is individual-based, density-dependence occurred through competition between individuals for habitat that provided food resources. Larger individuals excluded smaller individuals from high quality patches, and individuals in poor quality habitats experience lower growth rates and survival. These findings support the mechanism of population regulation postulated by Petty (1998), and are consistent with the Rodenhouse et al. (1997) theory of site-dependent population regulation.

Development of our model was greatly facilitated by the existence of long-term biological data sets for this population. Consequently, we were able to calibrate several aspects of the model from real data, including fecundity, survival, length–weight relationship, and benthic macroinvertebrate dynamics. This approach also has allowed us to identify gaps in our knowledge about this population.

Perhaps the greatest uncertainty in the model is related to survival of young from the egg to juvenile stage. In this model, we assumed a constant survival rate, but in actuality, survivorship may be affected by several factors. Cowan et al. (1993) attributed recruitment variability to a combination of factors, including adult female size distributions, density of prey and competitors, and temperature that could generate variability in an individual-based model. Schlosser (1999) demonstrated that overwinter mortality between ages 0 and 1 for creek chubs in a lotic system was density-dependent, and suggested that the primary mechanism was limitation of growth by a reduction in macroinvertebrate drift resources, and a subsequent increase in mortality due to small size. Johnston et al. (1995) found that larval abundance of white sucker and walleye in the Valley River, Manitoba, was positively correlated to river discharge in the 35 d proceeding the median date of larval drift. Because of our model's sensitivity to parameters for the younger life stages, it will be important to better characterize these rates through additional study.

The fit of our model may have been affected by simplifying assumptions related to multiple factors: macroinvertebrate drift, fish activity, floods, and immigration and emigration. In general, a lack of data prevented the inclusion of these factors in the model. For example, we did not include drift in the model, although it is known to affect benthic macroinvertebrate biomass (e.g., Hynes, 1970). To be represented correctly, drift should be dependent on flow and the presence or absence of a predator (Dunbrack and Dill, 1983). Also, we did not make fish respiration a function of consumption rates or activity, as is done in some individual-based fish models (e.g., Van Nes et al., 2002). As such, our model formulation could produce overestimates of respiration at low feeding rates and underestimates at high feeding rates. Brocksen et al. (1968) observed an increase in respiration with consumption in reticulate sculpin (*Cottus perplexus*), so this factor may be significant, but because sculpin are sit-and-wait predators that do not display extensive movements over seasons or years (Hill and Grossman, 1987; Petty and Grossman, 2004), we did not include the added complexity of activity.

Our model also did not include direct effects of extreme environmental events such as floods. Floods can wash macroinvertebrates out of the system, destroy fish nests and eggs, and wash out or kill free-swimming larval fish (Harvey, 1987; Matthews, 1998). Erman et al. (1988) reported that mortality of Paiute sculpin adults occurred in response to some high-flow events in Sagehen Creek, California, but they attributed this to exceptional shear forces that develop when the stream discharge is confined by deep snowbanks. Movements of individuals in and out of the study area were not included in the model. It is possible that such movements could have occurred as a result of the fluctuations in flow; however, Albanese et al. (2004) found that sculpin movement in a Virginia stream network was not

related to flooding, temperature, or day length. Despite the potential shortcomings of our model, it still yielded reasonable predictions of population abundance, and adult mean length and weight.

In conclusion, our model should yield a better understanding of the dynamics of sculpin populations in the south Appalachian region. Such information will enhance our ability to manage and conserve these populations as well as simulate the potential impacts of anthropogenic disturbances such as global warming. An additional advantage of our model is that it is one of the first attempts to describe population regulation in a benthic non-game fish. Non-game fishes dominate the world's fish fauna (Matthews, 1998; Wootton, 1998; Moyle and Cech, 1999) yet little is known about their population processes or responses to environmental variation. Finally, an individual-based modeling approach allowed us to incorporate individual variation in important biological characteristics such as territoriality, patch quality, growth rate, and fecundity, which allow for greater precision in determining the effects of biological and physical stressors on this population.

Acknowledgments

We would like to acknowledge and thank Todd Petty and Robert Ratajczak for assistance with data, and Craig Barber and Mark Bakker for helpful discussions. We thank all of the reviewers who commented on this manuscript to improve its quality. This paper has been reviewed in accordance with the U.S. Environmental Protection Agency's peer and administrative review policies and approved for publication.

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