POPULATION-LEVEL ANALYSIS AND VALIDATION OF AN INDIVIDUAL-BASED CUTTHROAT TROUT MODEL

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ABSTRACT. An individual-based model of stream trout is analyzed by testing its ability to reproduce patterns of population-level behavior observed in real trout: (1) "self-thinning," a negative power relation between weight and abundance; (2) a "critical period" of density-dependent mortality in young-of-the-year; (3) high and age-specific inter-annual variability in abundance; (4) density dependence in growth; and (5) fewer large trout when pool habitat is eliminated. The trout model successfully reproduced these patterns and was useful for evaluating their theoretical basis. The model analyses produced new explanations for some field observations and indicated that some patterns are less gen-

eral than field studies indicate. The model did not reproduce
field-observed patterns of population variability by age class,
discrepancies potentially explained by site differences, preda-
tion mortality being more stochastic than the model assumes,
or uncertainty in the field study's age estimates.

Introduction.   In a recent review of individual-based models
(IBM's), Grimm [1999] identified reasons why IBM's have contributed
little to ecological research and management. Prominent among these
reasons are that modelers have not (1) explored IBM results to un-
derstand why they occurred, (2) tested and validated the realism of
IBM's, and (3) compared IBM results to conventional ecological the-
ory. Railsback [2001] suggested that evaluating an IBM's ability to
reproduce a wide range of observed patterns is a productive way to
test the model, understand how results emerge from properties of in-
dividuals and evaluate ecological theory using the model. We present
such a pattern-oriented exploration and validation of an IBM of stream
trout. We examine population-level simulation results, comparing the
IBM's predictions to patterns of trout population dynamics observed
in natural systems or predicted by ecological theory.

The model we examine is the cutthroat trout model of Railsback
and Harvey [2001], which was designed as a research and management
tool for understanding how stream flow and habitat alterations affect
trout individuals and population dynamics. In this model, selection
of habitat is the primary means by which individual trout adapt to
changing conditions. A previous analysis showed that this model
can reproduce a wide range of realistic habitat selection behaviors in
response to changes in habitat and competitive conditions that affect
growth and mortality (Railsback and Harvey [in press]). However, the
population dynamics that emerge as individuals respond to habitat
and each other have not previously been examined for this model.
Clark and Rose [1997] conducted an extensive population-level analysis
of a different stream trout model, but did not precede this analysis
by demonstrating that their model could produce realistic individual
behaviors.

This paper addresses three objectives. First is to analyze and un-
derstand the population dynamics produced by the IBM and how
they emerge from processes acting at the individual level. Second is
to test the model's ability to reproduce observed patterns of popula-

tion response, providing evidence of the model's validity for predicting population-level phenomena. Third is to compare model results to population-level patterns that might be expected theoretically. These objectives are addressed by (1) establishing a priori patterns of expected population response that have been observed in natural populations or derived from theory, (2) simulating the conditions under which the expected population response patterns arose, and (3) comparing simulated responses to the expected patterns and examining why the simulated responses did or did not match the expected patterns.

2. Methods.

2.1 Trout IBM. The model we analyze is described in full by Railsback and Harvey [2001]; a description of the model except for the reproductive cycle is provided by Railsback and Harvey [in press]. The model has the following key properties.

(1) A one-day time step is used, but within a day fish are assumed to feed during day and hide at night.

(2) The external driving variables are stream flow, water temperature and food availability. Daily flow and temperature values are input. Drifting food items are assumed to occur at a constant concentration (grams food per cubic m of water), and stationary food items are assumed to be produced at a constant rate per unit of wetted stream area. Food production therefore varies with flow but not with season.

(3) Space is represented as a collection of two-dimensional (vertically averaged) cells that are one to several m on each side. Water depth and velocity in each cell is a function of stream flow, determined using a hydraulic model.

(4) Trout are not assumed to be territorial but instead compete in a size-determined hierarchy for the food available in each cell on each day. Competitive interactions are not simulated, but a fish has access only to the food not consumed by bigger fish in its cell.

(5) Growth is modeled as a function of food intake and metabolic energy costs, using standard bioenergetics methods. Metabolic costs increase with swimming speed. Swimming speed is assumed equal to the water velocity in the fish's cell, except that fish may use velocity

shelters to reduce swimming speed while feeding on drift, and swimming is zero at night.

(6) Mortality risks to trout include poor condition (starvation and disease resulting from low weight), terrestrial predation (which increases with trout size and decreases with water depth and velocity), cannibalism (a risk to small juveniles that is lower in shallow water), exhaustion due to extreme velocities and the stranding and excess predation risk of extremely shallow habitat.

(7) Every day trout move, if there is any better habitat available within an area of "known" habitat. This area increases with trout size. Trout select habitat using the "expected reproductive maturity" measure (Railsback et al. [1999]), an estimate of expected probability of future survival and growth to reproductive size. This approach causes fish to select habitat that provides a good tradeoff between mortality risks and growth. In general, fish seek habitat that provides minimal risks and sufficient growth to avoid starvation and reach reproductive size. These assumptions are simple but produce realistic movement at a daily time scale (Railsback and Harvey [in press]).

(8) Redds (nests of trout eggs in the stream gravel) are modeled explicitly. Redds are vulnerable to scouring at high flows and dewatering at low flows.

(9) There is no emigration or immigration in the model. The effects of this assumption on population dynamics have not been examined.

The model was programmed using the Swarm simulation system (Minar et al. [1996]). The software allows users to observe the individual fish to test and understand simulations, and includes an experiment manager that automates the generation and execution of replicate simulations of multiple scenarios. The software was tested extensively by comparing output of its key components to independent implementations of these components in spreadsheet software, and is fully documented (EPRI [1999]).

The modeled site is on Little Jones Creek, about 1000 m above its confluence with the Smith River, Del Norte County, in northwestern California. Little Jones Creek is a third-order mountain stream of moderate gradient. The climate is moderate year-round due to marine influence, but flows are highly seasonal because rainfall is rare between June and September. Cutthroat trout are the only fish species at the

site, and ocean migrations are precluded by a downstream waterfall.

Habitat input was collected on a 187-m reach of the stream, which includes several sequences of riffles and pools created by bedrock and large wood. The site is described in more detail by Harvey [1998]. To increase the number of fish in our analyses and reduce errors due to the lack of emigration and immigration in our model, we doubled the size of the modeled area by duplicating the entire 187-m habitat sequence.

Simulations were conducted using parts or all of a 12-year period representing October, 1987 through September, 1999. Daily stream flows were estimated from flows measured at a gaging station on the Smith River, using a regression relationship developed from approximately one year of daily flow measurements made at the study site. Water temperature at the study site varies little and is almost always within a range (5-15° C) considered normal for trout; therefore, we used daily temperatures measured at the study site for a one-year period in 1999–2000 to represent all the simulated years.

To avoid bias in our results, we used only a minimal calibration of the full model. Each separate component of the IBM (e.g., feeding methods, growth calculations, etc.) was parameterized and tested using the best information available from the literature and our field site. After assembling the full model, the only calibration we conducted was adjusting two mortality parameters (controlling terrestrial predation and cannibalism) and two food parameters (availability of drifting and stationary food). These parameters were adjusted to approximately match growth and mortality of three age classes (age 0, 1, and 2+) observed at the study site over a single 75-d summer period.

2.2. Analysis patterns. We analyzed the model by examining its ability to reproduce five population-level patterns. These patterns are explained in detail in our presentation of results for each.

(1) A "self-thinning" relation, a negative power relation between mean weight and mean abundance among age classes. Self-thinning with an exponent of $-4/3$ was suggested from theoretical considerations by Begon et al. [1986] and observed in stream trout by Elliott [1993].

(2) The "critical survival time", the duration of intense, density-dependent mortality in newly hatched trout. This pattern is based on the observations of Elliott [1989].

(3) Age-specific patterns in population variation over time observed in a trout stream similar to our study site (House [1995]). While these patterns are based only on field observations and not theoretical considerations, the observations correspond with the "complex ecology" perspective that population equilibrium or stability should not be expected even in relatively simple and undisturbed systems.

(4) Density dependence in growth. Some observations (especially Elliott [1994]) have indicated that abundance has little effect on the size of age 0 trout, whereas the experiments of Jenkins et al. [1999] found strong effects of abundance on size.

(5) Fewer large adult trout when deep pool habitat is eliminated. This pattern is based on the observations of Bisson and Sedell [1984].

3. Results. For each of the patterns used in analyzing the IBM, we describe the pattern and its basis, how we attempted to reproduce it and how simulation results compare to the expected pattern.

3.1 Self-thinning. Begon et al. [1986] suggested that animal populations may exhibit a power relationship among age classes in which mean weight decreases with the $-4/3$ power of mean density. The theoretical self-thinning relationship is:

$$W = a\,N^S$$

where W is the mean weight of individuals in an age class at some time, N is the number of individuals in the age class at the same time (assuming habitat area is constant), a is a constant and S is the exponent determined as the slope of a regression of $\log(W)$ against $\log(N)$.

The theory that $S = -4/3$ results from assuming (a) metabolic rates are proportional to weight^b, where the parameter b is equal to 0.75, and (b) food production rates are constant. Elliott [1993] studied self-thinning in brown trout at his Black Brows Beck study site. Elliott found the expected negative power relation between W and N, with S varying considerably among year classes. When data from all age classes over the 25-yr period were combined (excluding several outliers), Elliott found S to match the theoretical value of $-4/3$. Armstrong [1997] provided several reasons why the $-4/3$ power

self-thinning relation may not occur in freshwater salmonids: the availability of food varies with the trout size and habitat, and metabolic rates and growth vary with temperature (e.g., often there is no growth in winter).

Given that self-thinning with $S = -4/3$ has been observed in stream salmonids while its theoretical basis has been questioned, we combined model validation with examination of the theory. Using a sensitivity analysis approach, we varied the metabolic parameter b in the trout growth component of the IBM to see if S responded as predicted by theory. We simulated seven scenarios in which the value of b was varied from 0.6 to 0.9 in increments of 0.05. Three replicates of each 5-yr simulation were produced. ("Replicates" are repeated simulations in which only the random number sequence is changed.) The sea-going trout studied by Elliott [1993] have only two age classes (they migrate to the sea after their first year), but our modeled cutthroat trout have four age classes. Elliott examined data observed in both early and late summer. We only examine data observed in late summer (October) to avoid (1) the "critical period" of high mortality for age 0 trout, which occurs in summer because the cutthroat trout spawn in spring, and (2) winter, when low temperatures may affect growth. Simulation started on October 1, 1995, and the first observations used in the analysis were from October 1996.

Like the field observations of Elliott [1993], our simulations produced a relationship between the W and N fit fairly well by a power curve; also like Elliott's data, our simulations showed the relationship to vary considerably among age classes. With b equal to 0.75, we found S to be -1.25, with the relationship having an R^2 of 0.85 (Figure 1); Elliott found an exponent of -1.33 and R^2 of 0.87 over all year-classes. (In preliminary experiments using various numbers of replicates, initial fish abundances, and random number sequences, we found S over all age classes to vary; in one case we matched Elliott's value of -1.33 but this appeared to be coincidental.)

Our simulation experiment varying b, partially supported both the theoretical concept of a self-thinning relationship determined by how metabolic rate varies with body weight, and the limitations of this theory suggested by Armstrong [1997]. As predicted by the theory, S from our simulations increased (became less negative) in a nearly linear fashion as the value of b increased (Figure 2). However, the modeled S is
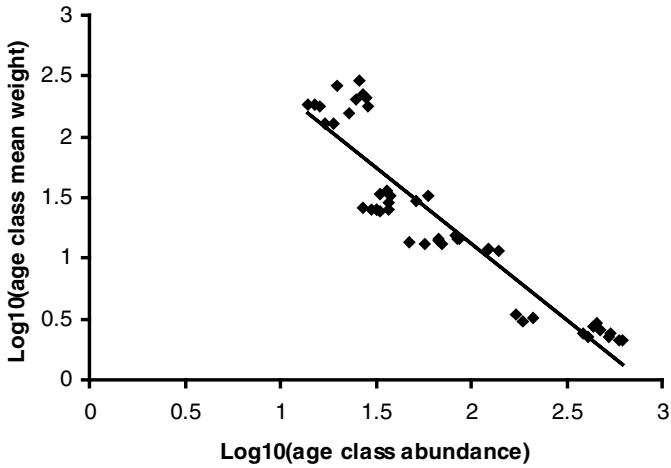
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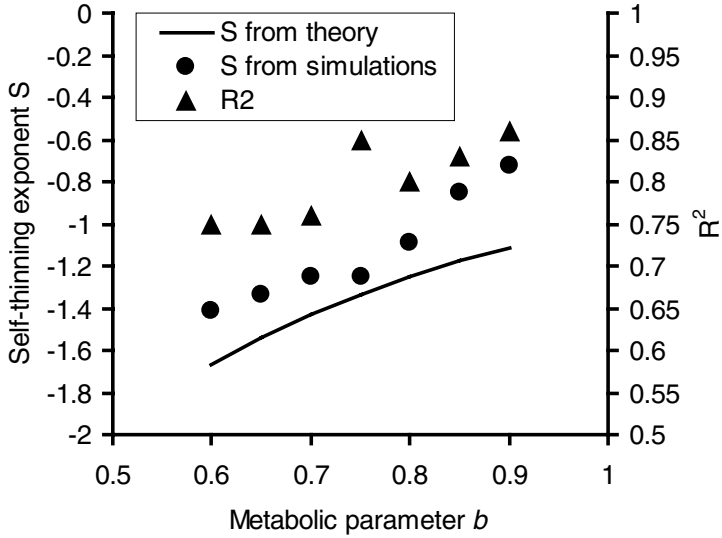FIGURE 1. Self-thinning relationship for metabolic parameter $b = 0.75$.

FIGURE 2.   Relation between theoretical self-thinning exponent S and S observed from IBM simulations.

consistently less negative than the theoretical value. The value of R^2 for the self-thinning relationship also generally increased with b (Figure 2). As proposed by Armstrong [1997], varying importance of food competition (the process assumed by theory to drive self-thinning) may explain these patterns. Our model assumes that predation mortality is always present and density independent, so some apparent "thinning" is unrelated to food competition. Less density-dependent mortality sources like predation may explain why simulated S values were higher than theoretical ones. The increase in the self-thinning R^2 as b increases is expected because food competition should become more intense, and therefore dominate mortality more, as b increases. Higher values of b mean that a fish's metabolic rates are higher, requiring more food intake to obtain growth. The result, in our IBM, is greater competition for habitat that offers higher intake. At lower metabolic rates, fish give greater preference to habitat with low predation risks. Therefore, we expect actual self-thinning to more closely match the theory of Begon et al. [1986] as b increases.

3.2 Critical survival time. This pattern is based on the observations by Elliott [1989] of age 0 brown trout at his Black Brows Beck study site. Critical survival time (CT) is Elliott's term for the duration of a "critical period" of intense density-dependent mortality that commences as soon as trout fry emerge from their natal gravel. The critical period ends when mortality rate decreases and becomes less density-dependent. Elliott [1989] estimated CT by censusing trout fry repeatedly, usually at intervals of 30 d, and plotting the logarithm of the number of fry alive over time. Elliott found that these plots showed a distinct change in slope and defined CT as the number of days between peak abundance of trout fry and the change in slope. For his brown trout fry, Elliott [1989] found CT to fall within the range of 30–70 d.

Our experiment closely reproduced Elliott's methods. We estimated CT for each of the five years in 2 replicates of three scenarios. The scenarios differed in the starting abundance of spawning trout, so they created variation in the number of age 0 trout. Abundance was observed from the model every 30 d. Like Elliott [1989], we defined the start of the critical period as the census date on which age 0 abundance was highest. We used a graphical method similar to that of Elliott to

define the end of the critical period. On a plot of log(abundance) vs. date, we fit a line through the first two–three points to define the mortality rate during the critical period (the third point was included if it fell approximately on the line defined by the first two points). The points representing the last two–three censuses were used to define the mortality rate after the critical period. The intersection of these two lines was assumed to occur at the CT.

During 18 of the 29 years simulated, the IBM results showed a distinct critical period with CT values ranging between 30 and 65 d, except for one CT of 86 d (Figure 3). With this one exception, the CT values fell within the range of 30–70 d observed by Elliott [1984]. However, our simulations also produced a phenomenon not reported by Elliott: the absence of a distinct critical period when age 0 abundance was low. All of our simulations produced age 0 densities well below those reported by Elliott [1984], most likely due to differences in productivity of the two study sites and Elliott's spawners' being large sea-going trout that produce many more eggs than our small cutthroat trout. In 11 simulation years when age 0 trout abundance was low, the mortality rate (slope of the logarithmic graph of number of survivors vs. date) remained approximately constant (shown on Figure 3 as having CT of zero). The absence of a distinct critical period in years of low age 0 abundance makes intuitive sense; density-dependent mortality should be absent or hard to detect when density is low.

Like Elliott [1984], we found a negative relation between initial age 0 abundance and CT. For the 18 cases in which we observed a distinct CT (Figure 3), linear regression of CT vs. initial abundance had a negative slope and R^2 of 0.17.

3.3 Population variation over time. House [1995] examined a wild cutthroat trout population similar in many ways to the one at the Little Jones Creek site of our IBM. Similarities between House's Dead Horse Canyon Creek site in Oregon and our model site include (1) being small watersheds in the Pacific Northwest with similar patterns of flow variation among seasons, (2) resident cutthroat trout as the only fish, (3) low flows in the range of 0.03–0.07 m^3/s and (4) a history of little recent timber harvest, angling, or other human disturbance. However, an important difference is that House's study site had flow variation moderated by spring inflows and winter peak flows in the range of 5 to
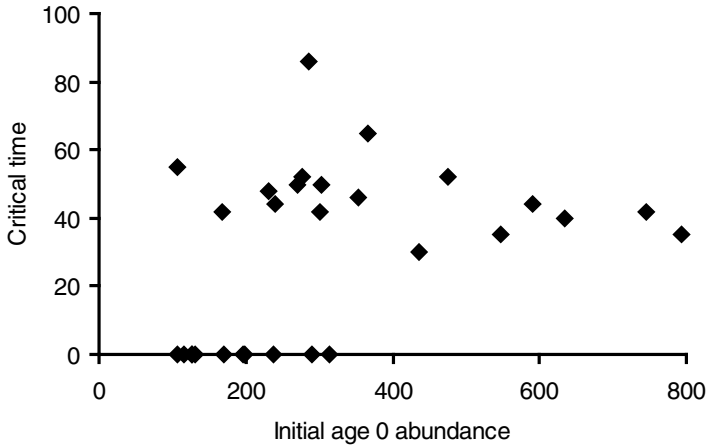
FIGURE 3. Relation between age 0 initial abundance and critical time. For years when no critical period was observed, the value of critical time is shown as zero.

13 m^3/s, whereas our site has unusually rapid and strong variation in flow, with annual peak flows typically in the range of 30–50 m^3/s. Over an 11-year period, House censused trout in late summer, sampling an area approximately half the length of the reach we model. Data were reported for three age classes: age 0, 1, and 2 and older (designated as "age 2+").

House [1995] observed the following patterns (omitting those affected by House's admitted inability to census age 0 trout accurately). (1) Fourfold interannual variation in abundance of age 0 trout (the highest abundance was four times the lowest abundance). (2) Age 1 had the most stable abundance, with the highest abundance only twice the lowest. (3) Age 2+ was the most variable age class, with sixfold interannual variation. (4) No correlation between the number of age 1 fish one year and the number of age 2+ fish the following year. (5) A weak correlation between peak flow in winter and abundance of age 1 trout the following summer. (6) No correlation between summer low flow and trout abundance.

We compared our trout IBM to the observations of House [1995] by conducting one 11-year simulation (1989–99), observing abundance from the IBM once per year in September. (We actually simulated

12 years and discarded results from the first year to reduce effects of the initial population.) Our model with input from Little Jones Creek produced much higher interannual variation than observed by House [1995] (Table 1). The range of variation (highest annual abundance divided by the lowest) was more than an order of magnitude greater than the values of 4 and 2 reported by House for ages 0 and 1. The high interannual variation in abundance observed in our simulations was caused by the frequent peak flow events, which scoured out redds (eliminating almost all redds in 1996) and caused high mortality in age 0 trout (especially in 1998). Our observations at Little Jones Creek indicate that high flow impact on age 0 abundance predicted by the model is not unrealistic. Other studies have found strong effects of flood flows on age 0 salmonids (e.g., Thorne and Ames [1987]).

TABLE 1. Variation in abundance over an 11-yr. simulation,
with actual flows for Little Jones Creek.

Age	0	1	2+
Maximum abundance	1144	202	96
Minimum abundance	17	4	19
Range of variation	67	51	5

To make our simulations more comparable to House's study site with its relatively stable flows, we repeated the simulations using flow input smoothed by replacing each day's flow with a 10-day running average of the measured flows (Figure 4). In this smoothed flow input, peak flows ranged between 10 and 25 m^3/s. With the smoothed flow input, our IBM simulations produced ranges of variation similar in magnitude to those observed by House [1995] (Table 2). The simulations with smoothed flows were used for all the following comparisons to House's observations.

Our simulations did not match House's observed pattern of variation among age classes. Whereas House found age 1 to have the least interannual variation and age 2+ the highest, we found the opposite (Table 2). There are several potential explanations for these differing patterns. The first is habitat differences between the two sites; our
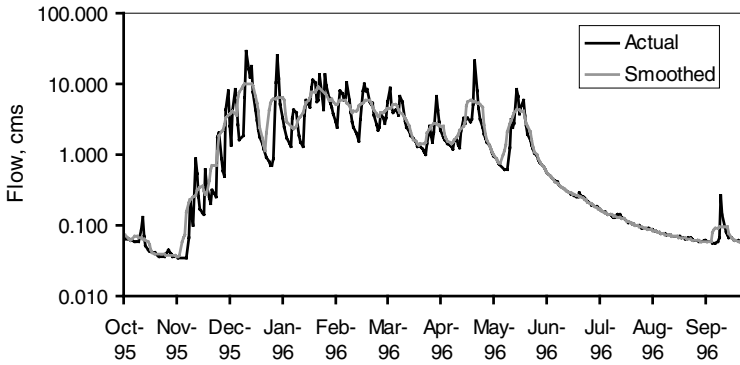
FIGURE 4. Natural and smoothed flows for water year 1996.

Little Jones Creek site appears to have a higher fraction of deep pool habitat that offers high survival to adult trout. As discussed below (Section 3.5), the availability of such pools affect population dynamics. A second potential explanation is that our model lacks some process, making mortality of age 2+ trout more stochastic. Our simulations predict that terrestrial predators account for most mortality of adult trout, with this mortality being a stochastic function of habitat (depth, velocity and hiding cover all reducing the risk). Terrestrial predation may be stochastic at longer time scales than we assume; for example, otters may thoroughly search a stream reach for trout prey only at rare intervals. Mortality due to spawning stress may be a more common and variable source of mortality than we assume. A third explanation is the uncertain method used by House [1995] to estimate fish ages. House used a length-frequency relation to estimate age from length,

TABLE 2. Variation in abundance over an 11-yr. simulation, with smoothed flows for Little Jones Creek.

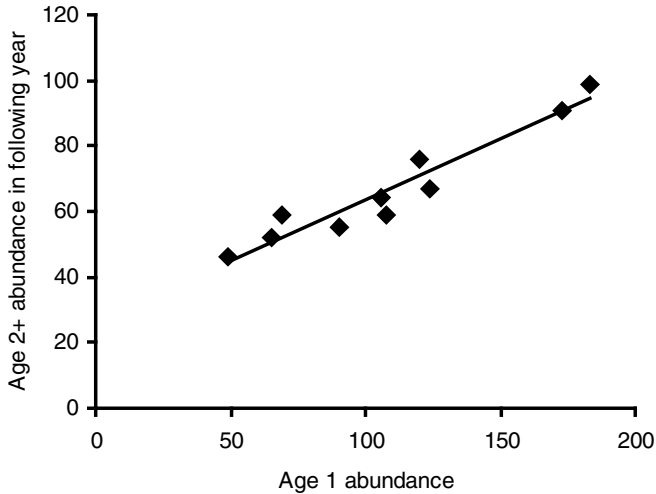| Age	0	1	2+
Maximum abundance	961	183	99
Minimum abundance	338	49	46
Range of variation	3	4	2

FIGURE 5. Relation between abundance of age 1 trout and age 2+ trout the following year in an 11-year IBM simulation.

a method that is inherently uncertain and the fraction of age 1 fish misidentified as age 2 is higher in years of high growth. As a result, variation in growth among years likely induced errors in determining age that explain some of House's observed variation in age 2+ abundance.

These potential explanations for differences in abundance variability among age classes may also explain why our simulations did not match the observation of House [1995]—that abundance of age 2+ trout in one year was not correlated with the abundance of age 1 trout the previous year. We found a high correlation between these variables (Figure 5) with $R^2 = 0.92$. While we did not thoroughly investigate this discrepancy, the IBM could be a useful tool for doing so. For example, the IBM-simulated length of each fish could be used to estimate fish age using House's method, to determine how the method's uncertainty affects results.

Like House [1995], the IBM produced a weak correlation between peak winter flow and age 1 abundance the following summer (Figure 6), although the correlation in our simulations was stronger ($R^2 = .29$) than that observed by House ($R^2 = .05$). The stronger correlation
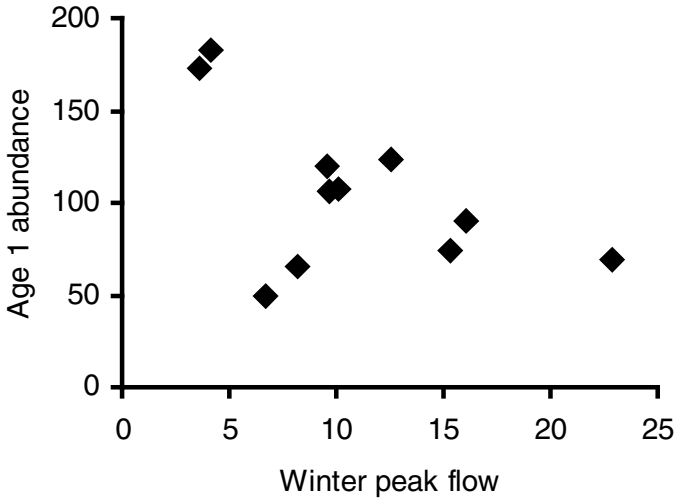
FIGURE 6. Relation between peak flow in a winter and age 1 abundance the following summer, from an 11-year IBM simulation.

likely resulted from peak flows' in the model simulation being higher and varying over a wider range than at House's site.

Also like House [1995] we found no correlation between low flow and abundance. We examined the relation between the lowest flow in a year (typically occurring in September or October) and the abundance of age 1 and 2+ trout the following summer, and found no relation (Figure 7). The lack of correlation observed by House and in our simulations is likely to result in part from the low interannual variation in low flows.

Although our IBM simulations did not reproduce all the abundance patterns observed by House [1995], this analysis did show our IBM capable of reproducing several important relationships. First, our simulations reproduced the most basic conclusion of House's study, that interannual variation in trout abundance can be high even in relatively simple and undisturbed systems. Second, we found the interannual variation in abundance (and how it differs among age classes) to be highly dependent on flow variability. Especially, winter peak flows have strong effects on recruitment and abundance in succeeding years, in both our model and in nature (e.g., Strange et al. [1992]). Finally, our simulations reproduced the observations of House that abundance in
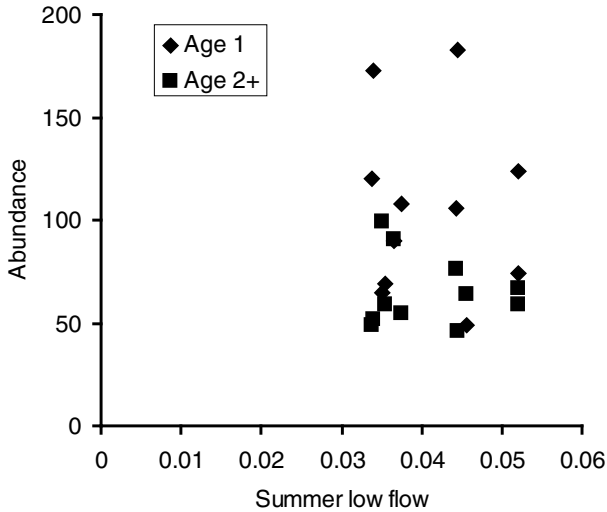
FIGURE 7. Summer low flow vs. abundance the following summer.

summer is affected by peak flow in the previous winter but not related to minimum flow in the previous summer-fall low-flow season.

3.4 Density dependence in growth. Field observations and experiments have produced conflicting answers to the question of whether trout density affects growth of age 0 trout. Elliott [1994] examined abundance and size of age 0 trout observed once in each of 17 years at his Black Brows Beck study site and concluded that abundance had little effect on growth. Jenkins et al. [1999] observed abundance and size of age 0 trout in natural and controlled stream channels, in some cases manipulating trout density. Jenkins et al. observed that abundance had a strong negative effect on age 0 size and concluded that growth was density-dependent. Major differences between the studies of Elliott [1994] and Jenkins et al. [1999] include that Jenkins et al. made observations over relatively long stream reaches (> 90 m), used multiple treatments with varying density in the same year, and in some cases blocked immigration and emigration.

We conducted experiments resembling those of both Elliott [1994] and Jenkins et al. [1999]. Output of one 11-year simulation (the same used to examine population variation over time, above) was examined for

density-related variation in age 0 size and growth among years, similar to Elliott's observations. We also conducted an experiment in which trout abundance was manipulated in otherwise identical simulations over a one-year period, conceptually similar to the design of Jenkins et al. In this experiment, we ran the model over calendar year 1994. In five scenarios of increasing initial abundance, the total initial abundance of age 1, 2, and 3 trout was varied from 17 to 240. This variation in initial abundance affected the number of age 0 trout produced via spawning in spring. Five replicates were conducted for each of these scenarios. These simulations used smoothed flow input to eliminate the redd scouring that otherwise reduced spawning success. Like Jenkins et al. [1999] we observed age 0 abundance and size in late November or early December.

Both our 11-year simulation and the one-year scenarios produced fall age 0 mean weights that varied with the density of age 0 trout, following a power curve as did the observations of Jenkins et al. (Figures 8 and 9). This result appears to conflict with Elliott's observation that age 0 size was not related to density, but the relation between size and abundance we observed from the IBM is noisy, and if confined to high densities (as Elliott's data were), could lead to the conclusion that size is not related to density.

However, examination of our IBM results indicates that the observed negative relation between size and density is not necessarily an indication that growth was density-dependent. The fall mean weight of age 0 trout is a function not just of growth rate, but also of when trout emerged from their eggs and of size-dependent mortality. When we examined growth rate (change in mean weight of age 0 trout over a 30-d period, expressed as g/d), we found no relation between density and growth in the 11-year simulation (Figure 10). We actually found a weak positive relation between density and growth rate in the multiple one-year simulations (Figure 11). The negative relation between size and age 0 trout density produced by our simulations matches the observations of Jenkins et al. [1999], but appears not to be caused by density-dependent growth. Instead, at least three other processes potentially could explain this relation. One is variation in timing of spawning: in years when more spawning occurred later in the summer, more age 0 trout are likely to still be alive at the time of the fall census (making density higher) but these trout will be younger and therefore
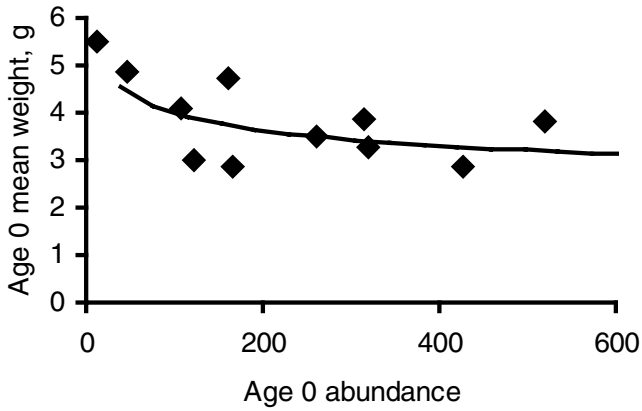
FIGURE 8. Abundance of age 0 trout vs. mean weight (g), observed in late November or early December from a single 11-year simulation. The regression power curve has R^2 of 0.46.
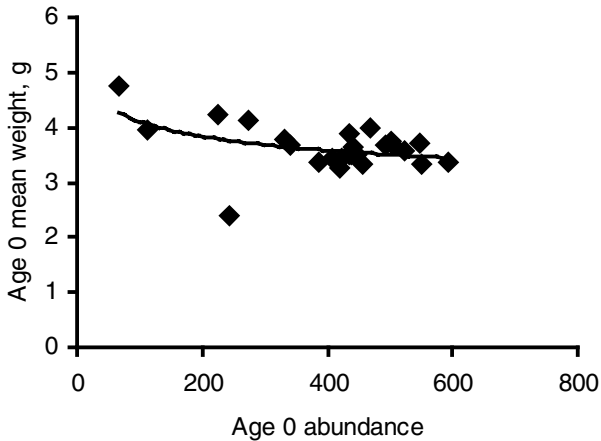

FIGURE 9. Abundance of age 0 trout vs. mean weight (g), observed in late November from multiple one-year simulations. The regression power curve has R^2 of 0.16.
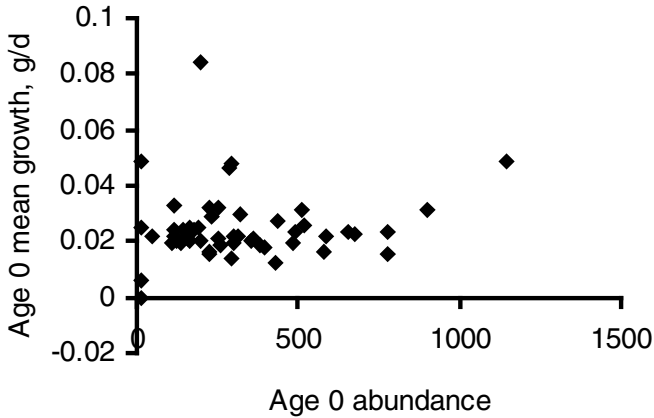
FIGURE 10. Abundance for age 0 trout vs. mean growth rate (g/d; evaluated from the change in mean weight over a 30-d period). Results are from a single 11-year simulation, for all months between fry emergence and late fall. Linear regression R^2 is 0.01 with a slightly positive slope.

smaller. (Spawn timing did not vary much in our simulations, making this explanation unlikely.) A second explanation possibly important in multi-year or multi-site experiments is that both density and mortality are affected by variation in availability of habitat and food (e.g., due to interannual flow variability). When resources are scarcer, mortality of age 0 trout is expected to be higher and smaller trout more likely to die; consequently, abundance is expected to be lower and mean size higher. Third, in our multiple one-year simulations we found late summer and fall mortality of age 0 trout (number dying per day) to be nearly independent of density but apparently greater for smaller fish. (The most prevalent form of mortality, starvation and disease due to poor condition, was positively related to density; however, per-fish predation mortality was negatively related to density. At low densities, predation mortality is roughly as important as poor condition, Figure 12.) We observed a positive relation between mortality and growth rate $(R^2 = 0.10)$, likely a result of size-dependent mortality. Such a size-dependent, but density-independent, mortality rate (deaths per day) would have strongest, positive effects on the apparent growth rate when abundance is small.

The trout IBM reproduced the observations of Jenkins et al. [1999] that the fall mean size of age 0 trout has a negative power relation with trout density. However, our simulations do not support the implicit
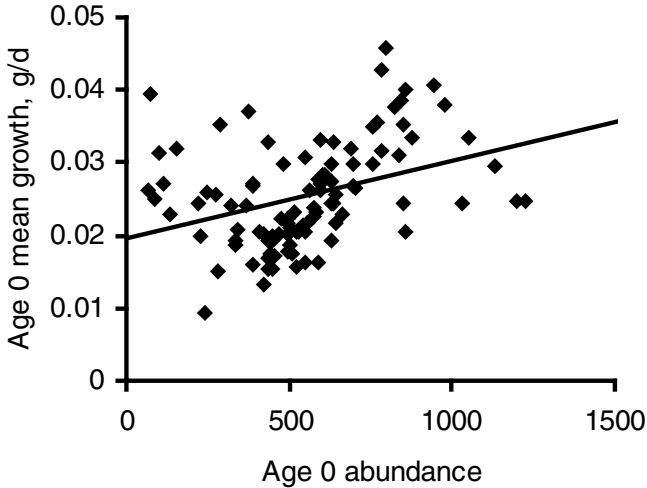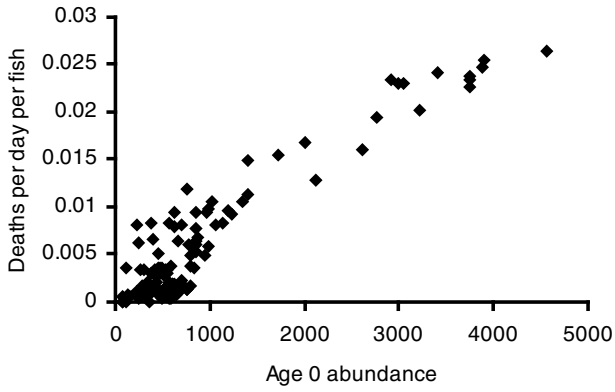
FIGURE 11. Abundance of age 0 trout vs. mean growth rate (g/d; evaluated from the change in mean weight over a 30-d period), between when all trout have emerged and the end of December. Results are from multiple one-year simulations. Linear regression has R^2 of 0.13.

assumption of both Elliott [1994] and Jenkins et al. that fall mean size of age 0 trout is a good indicator of growth rate, or the conclusion of Jenkins et al. that growth rate is negatively density-dependent. In fact the IBM simulations show that growth rate can increase with density while fall size decreases with density. Our experiment indicates that, especially when mortality is as high as it is in the first year of life for trout, relations between size, growth, abundance, and mortality are unlikely to be simple.

3.5 Fewer large trout in the absence of pools. Under this pattern we expect streams lacking deep pool habitat to produce fewer large adult trout, and to have lower relative abundance of older trout. Bisson and Sedell [1984] provide example observations supporting this pattern: they observed that in watersheds with clearcut timber harvest both the pool volume and the relative abundance of older trout were lower, in comparison to control watersheds.

The Little Jones Creek habitat input for our IBM simulations includes six pools with depth of approximately 1 m at summer flow. We compared results from this "with pools" scenario to results obtained

A.
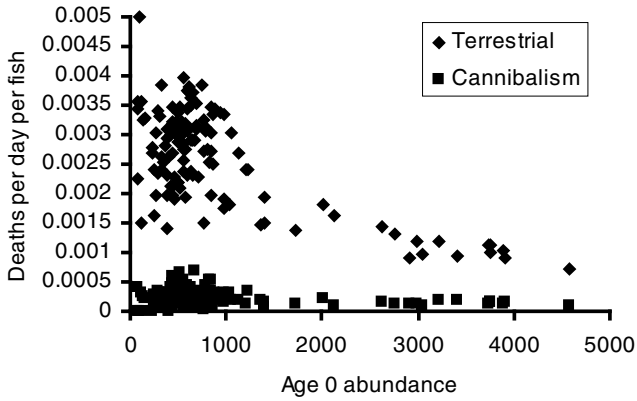
B.

FIGURE 12. Abundance of age 0 trout vs. per-fish mortality due to (A) poor condition and (B) predation. Predation due to terrestrial animals and cannibalism are shown separately. Note the difference in scale between A and B.

when each of the simulated pools was removed from the model and replaced by adjacent habitat that is shallower and faster. The stream length and surface area was similar for both scenarios. The "without pools" scenario approximates filling in the deepest part of all the pools, affecting the overall distributions of both depth and velocity (Figure 13).

The effects of removing pools was examined using five-year simulations, with 10 replicates of the with and without pools scenarios. Abundance and mean weight of each age class were observed from the IBM once per simulated year, in late August.

Removing the pools resulted in lower abundance of all age classes, with the decrease being greater for higher age classes (Table 3). An observed increase in the frequency of mortality by terrestrial predation in the absence of pools appears to be the ultimate cause of lower abundance. This result was expected because our IBM assumes depth provides protection from terrestrial predation (making fish harder to see from the surface). Increased predation on adult trout reduced the number of spawners, and lower growth of adult trout, (discussed below) reduced the number of eggs per spawner. We observed a much lower number of eggs laid in the without-pools scenario, the likely cause of reduced abundance of juvenile trout.

TABLE 3. Differences in abundance and mean weight between scenarios with and without pool habitat. "Change" is the percent change in value from the "the pools" to "without pools" scenario.

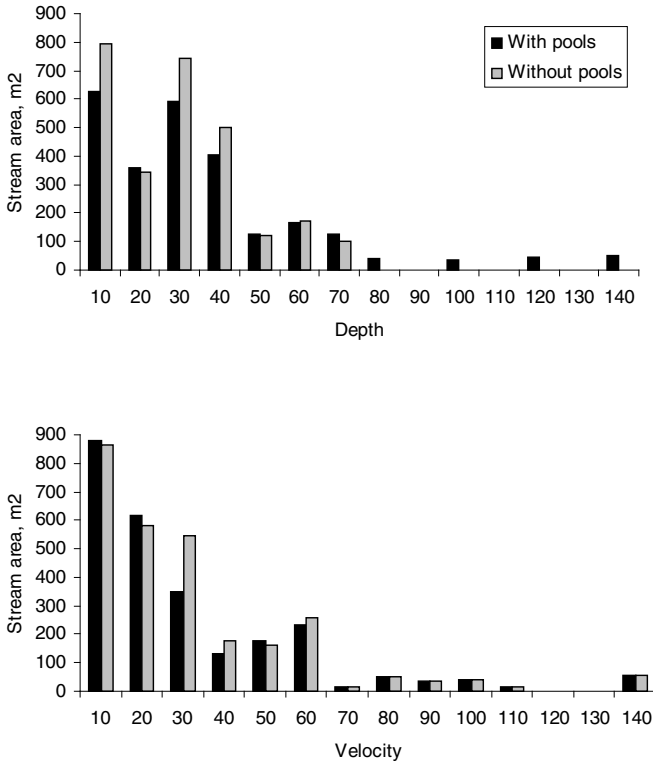| Age class		0	1	2	3+
Mean August abundance	With pools	597	93	36	25
	Without pools	487	65	24	14
	Change	-19%	-29%	-33%	-46%
Mean August weight, g	With pools	1.2	17	76	494
	Without pools	1.4	20	76	32
	Change	+14%	+18%	0%	-35%

FIGURE 13. Depth and velocity distributions for simulations with and without pools, at a typical flow of 0.3 m^3/s.

Removing pools also resulted in higher mean weight for age 0 and 1 trout, but lower weight of older trout (Table 3). The higher weight of age 0 and 1 trout is explained by two processes. First, the lower abundance occurring in the without-pool scenario results in increased size of age 0 trout (as discussed above in Section 3.4). This process appears to explain the size response of age 0 trout, since these fish prefer shallow habitat and exhibited little change in habitat use when pools were removed. Second, removing pools forces age 1 trout to use shallower, faster habitat where both growth and predation risk are generally higher. Our IBM assumes that as fish approach reproductive size they give greater preference to reducing predation risk vs. maximizing growth. When pools are present, this change in preference results in

increased use of deep habitat and decreased growth as reproductive size is approached; the absence of pools prevents this transition. The much greater mean weight of age 3+ trout with pools appears to result from two processes. First is the higher survival rate with pools—trout on average live longer and attain greater size with the predation protection provided by deep water. Second is that large trout may respond to pool removal by using high velocities instead of depth to reduce risk of terrestrial predation; the IBM assumes that high velocity as well as depth makes trout more difficult for terrestrial predators to see and catch. In the absence of pools, simulated age 3+ trout often used velocities of 100–140 cm/s, which are above optimal for growth.

4. Conclusions. The first objective of this study was to understand how population dynamics in the trout IBM emerge from processes acting at the individual level. A primary conclusion is that relatively simple-appearing responses at the population level may result from complex interactions at the individual level. Our observation that trout size decreased with density while the growth rate was unaffected or increased with density illustrates this conclusion; at least in our simulations, density effects on size are not explained simply by food competition but instead appear to be a complex effect of multiple mortality sources that vary in size- and density-dependence. A second example is the observation that reducing the availability of pool habitat resulted in smaller size of large trout; the size effect appeared to result in part from predation risk causing the trout to use habitat where growth is low.

The following are other ways in which we found individual-level processes to affect population dynamics. (1) The weight coefficient b used to simulate metabolic rates was found to affect the population self-thinning relation, apparently by affecting the strength of food competition. (2) The "critical period" of high density-dependent mortality has strong effects on recruitment of juvenile trout. Our model could explain this mortality as a result of the limited dispersal ability of trout fry and strong food competition. However, simulated recruitment appeared to be limited by spawning success often; when the simulated initial abundance of age 0 trout was low, no critical period was observed. (3) Scouring of redds was found to have strong effects on population variability in situations where flow spates are frequent.

Our second objective was to evaluate the IBM's ability to reproduce observed population-level patterns. Overall, the IBM was highly successful in reproducing the following patterns.

Self-thinning. The IBM produced self-thinning relations qualitatively and quantitatively similar to those observed by Elliott [1993].

Critical survival time. Simulated duration of the critical period closely matched the observations of Elliott [1989]. Unlike Elliott's observations, our simulations included some years when initial abundance of age 0 trout was so low that no critical period was distinguishable.

Population variation over time. Our simulations matched the overall conclusion of House [1995] that natural population variation can be high. We did not reproduce the pattern among age classes in variation observed by House; potential explanations include differences in habitat between our site and House's, error by House in determining fish age, and poor representation by our IBM of the stochasticity of terrestrial predation mortality. The IBM did reproduce the observed effects of peak and low flows on trout abundance.

Density dependence in growth. The IBM reproduced the negative power relation between abundance and size in fall age 0 trout observed by Jenkins et al. [1999].

Fewer large trout in the absence of pools. This pattern was reproduced, with both relative abundance and size of older trout being reduced when pools were eliminated.

The third objective of our study was to evaluate the theoretical basis for some patterns. We evaluated the basis for population self-thinning proposed by Begon et al. [1986] by varying the metabolic parameter b that theoretically determines the exponent of the relation between abundance and mean weight of age classes. Our experiment confirmed the self-thinning theory to the extent that it produced a consistent relation between metabolic rate and self-thinning exponent, but it also indicated that the theory is not completely correct because the observed exponents were consistently different than the theoretically predicted ones. The population variability observations of House [1995] were not related to a specific ecological theory, but House did conclude that his observations contradict the common perspective that undisturbed natural systems tend toward stability or equilibrium. Our simulations support House's conclusion, showing that natural events like spates

and the natural complexities of trout populations can produce highly unstable population dynamics.

This study illustrates several important benefits of using IBM's to study ecological systems. First, we can evaluate ecological theory using simulation experiments that would be impossible in the field or laboratory. Our investigation of how population self-thinning is related to metabolic rates is an example; we cannot manipulate the metabolic rates of real animals. Second, IBM's can provide alternative explanations for observed phenomena. Jenkins et al. [1999] attributed density-dependence in trout size to competition for food or habitat, envisioning that higher densities produced smaller feeding territories for all fish. Our IBM does not include such a process, instead assuming a rigid size-based feeding hierarchy. However, our IBM still reproduced the observed relation between density and size, indicating that other processes (that are in our IBM) can also explain the relation. Third, IBM simulations can investigate a wider range of conditions than are often observed in the field, helping us determine whether observed relationships are situation-specific or truly general. For example, Elliott [1989] concluded that the "critical period" of density-dependent mortality regulates trout abundance, but we found simulated conditions where the critical period was nonexistent. Finally, our experiments showed that even simple-appearing population-level relations are often the complex outcomes of multiple factors like habitat availability, various kinds of mortality, food competition, and initial conditions; and habitat selection to make tradeoffs among these factors further complicates their effects. Attempting to decipher how such relations emerged in the IBM reminds us that asking simplistic questions (e.g., "is growth density-dependent?") or expecting simple cause-effect relationships is unlikely to be productive.

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