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ANALYSIS OF HABITAT-SELECTION RULES USING AN INDIVIDUAL-BASED MODEL

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Abstract. Despite their promise for simulating natural complexity, individual-based models (IBMs) are rarely used for ecological research or resource management. Few IBMs have been shown to reproduce realistic patterns of behavior by individual organisms. To test our IBM of stream salmonids and draw conclusions about foraging theory, we analyzed the IBM's ability to reproduce six patterns of habitat selection by real trout in simulations contrasting three alternative habitat-selection objectives: maximizing current growth rate, current survival probability, or ''expected maturity'' (EM). EM is the product of (1) predicted survival of starvation and other mortality risks over a future time horizon, and (2) the fraction of reproductive size attained over the time horizon. Minimizing the ratio of mortality risk to growth rate was not tested as a habitat-selection rule because it produces nonsensical results when any habitat yields negative growth rates. The IBM simulates habitat selection in response to spatial and temporal variation in mortality risks and food availability as fish compete for food. The model fish move each daily time step to maximize their habitat-selection objective with no other restrictions (e.g., territoriality) imposed.

Simulations with habitat selected to maximize growth reproduced three of the six habitat-selection patterns; maximizing survival reproduced two patterns; and maximizing EM reproduced all six patterns. Two patterns (shifts in habitat with changes in temperature and food availability) were not reproduced by the objectives that consider only current growth and risk but were explained by the EM objective that considers how future starvation risk depends on current energy reserves and energy intake. In 75-d simulations, population-level survival and biomass accumulation were highest for fish moving to maximize EM. These results support the basic assumptions of state-based dynamic-modeling approaches to habitat selection. Our IBM appears successful because it avoids restrictive assumptions, incorporates competition for food, assumes salmonids make good habitat-selection decisions at a daily time step, and uses a habitat objective (EM) that provides reasonable trade-offs between growth and mortality risks.

Key words: foraging; habitat selection; individual-based model; model testing; modeling, state-based; movement motivation; rules for habitat selection, trout; salmonidae; stream fish.

INTRODUCTION

One of the most promising uses of individual-based models (IBMs) is to test and develop ecological theory (Huston et al. 1988). This promise remains largely unfulfilled, in part because the ability of IBMs to produce realistic behavior has rarely been tested (Grimm 1999). Analyzing the ability of IBMs to produce realistic behavior is not only important for establishing the credibility of the models, but also because it can be a productive way to test and develop theory for complex systems like animal communities (Auyang 1998). We present simulation experiments that test the validity of an IBM and that contrast three theories of habitat selection.

Habitat-selection behavior is of great importance in both ecological theory and individual-based modeling because this behavior is a primary way that mobile organisms adapt to changing conditions. Both net energy intake (growth) and mortality risks can influence habitat selection. For example, habitat use by stream salmonids has been predicted from net energy intake alone (e.g., Fausch 1984, Hughes 1992*a*, 1998, Nislow et al. 1999) but other research indicates that avoiding risk can be an important factor in habitat selection for fish (e.g., Gilliam and Fraser 1987, Lima and Dill 1990, Tabor and Wurtsbaugh 1991, Roussel and Bardonnet 1999). Because energy intake and survival are both critical to fitness, habitat-selection models that consider both are more likely to be generally applicable.

Few approaches have been developed for predicting how animals select habitat among sites varying in energy intake and mortality risk. One such approach is the ''minimize μ/g rule'' where μ is the mortality risk currently being experienced and g the current growth rate (in grams per day). The concept that minimizing μ/g maximizes an animal's fitness has been derived for

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specific conditions (Gilliam and Fraser 1987, Mangel 1994) but used in more general models (e.g., Bennett and Houston 1989, Werner and Anholt 1993, Van Winkle et al. 1998). Leonardsson (1991) proposed the ''maximize *SG*'' habitat-selection objective, where *S* is the survival rate ($1 - \mu$) and *G* equals $(M + g)/M$ and *M* is the fish's mass (''weight'' [*W*] in original). Reviewing movement rules for fish IBMs, Railsback et al. (1999) found that because the μ/g and *SG* approaches are based on assumptions that can rarely be accommodated in IBMs of stream salmonids, these rules can produce unrealistic results. For example, both of these rules depend on the unrealistic assumption that all habitats provide positive growth. Also, maximizing *SG* usually produces choices very similar to maximizing growth rate because *S* (evaluated as a daily rate) typically ranges only between 0.99 and 1.0 for stream salmonids (see Methods: Individual-based model for stream salmonids: Risks, below). Railsback et al. (1999) proposed approaches, adapted from Mangel and Clark (1986), that treat survival over a time horizon as a common ''currency'' for food intake and mortality risks and use an animal's current state and energy intake to predict the risk of future starvation.

Two obstacles have limited attempts to ''validate'' IBMs. One has been the lack of software that allows observation of the model's individuals (Grimm 1999). Such software is crucial because an IBM cannot be considered valid until its ability to reproduce realistic individual behaviors has been demonstrated (Bart 1995). We implemented our model in the Swarm (Swarm Development Group, New Mexico, USA)[4] simulation system (Minar et al. 1996), which provides tools for observing individual fish. The second obstacle is the difficulty of quantifying the major factors driving habitat selection (food availability and mortality risks) in the field at appropriate spatial and temporal scales (Railsback et al. 1999). To avoid this obstacle, we tested our model's ability to reproduce a range of observed *patterns* of habitat selection in response to known stimuli (Grimm et al. 1996, Railsback 2001).

Our objectives in this study were to: (1) test the ability of our IBM of stream salmonids to predict realistic habitat-selection behavior, and (2) contrast alternative rules for habitat selection. We identified six patterns of habitat selection from the literature and used the IBM to simulate the conditions of physical habitat, competition, and food availability under which the patterns have been observed in nature. In otherwise-identical simulations, fish selected habitat to maximize one of three objectives: (1) current daily growth (net energy intake), (2) current daily survival probability, or (3) expected maturity (EM; Railsback et al. 1999), an estimate of the fish's probability of surviving starvation and other risks and attaining reproductive maturity over a future time horizon. We contrasted the three habitat-selection objectives by comparing model results to patterns of habitat selection by real fish.

[4] URL: ⟨www.swarm.org⟩

Methods

Here, we describe the trout IBM (individual-based model) conceptually, then briefly outline how we tested its ability to reproduce observed patterns of behavior using three alternative habitat-selection objectives. Appendix A contains a complete description of modeling methods. To understand our analysis of habitat-selection objectives, readers need not understand the details of how feeding, growth, and survival probabilities are modeled, but they do need to understand how simulated growth and survival probabilities vary with habitat. We therefore provide graphical depictions of how growth and survival vary with key habitat variables.

Individual-based model for stream salmonids

The IBM is a discrete simulator with a daily time step. Stream flow, temperature, and food availability are the external driving variables. We model how trout select habitat for daytime foraging but we ignore habitat use during non-feeding activities. We assume model fish can correctly evaluate food availability and mortality risks at potential destinations.

Habitat.—We model stream reaches in two-dimensional space using rectangular cells of varying size. In collecting field data, we place cells so (1) each contains relatively uniform conditions of depth and velocity and (2) the size of each cell is large compared to the amount of space one fish uses for feeding (to reduce boundary errors that result from having an integer number of fish competing for a cell's food). Habitat conditions are assumed uniform within each cell, except that only a specified fraction of each cell provides velocity shelter for drift feeding. The average distance a fish must travel to hiding cover is also input for each cell. A hydraulic model determines the depth and velocity in each cell from the daily flow rate. We do not model locations of fish within cells, but track which cell each fish occupies.

The availabilities of benthic and drift food in each cell are modeled separately. For benthic food we assume a constant production rate (in grams per square centimeter per hour); hourly availability of benthic food in each cell is simply the cell's surface area times the production rate. The availability of drift food in a cell (A_D, in grams per hour) is modeled as:

$$A_D = \frac{C_D \times W \times D \times V \times 3600}{R}$$

where C_D is a constant concentration of drift food (in grams per cubic centimeter); *W* and *D* are the cell width and depth (in centimeters) respectively, and *V* is velocity (in centimeters per second). The factor *R* (in centimeters) simulates how drift food is regenerated from the benthos, and can be considered to represent the distance over which food depletion by fish is re-

placed by new drift. This factor makes the availability of drift food per unit area of stream independent of habitat cell size.

Risks.—Mortality risks are depicted as daily survival probabilities that vary with habitat and fish characteristics. We simulate five sources of mortality:

1) *Starvation.* Survival of starvation is modeled as an increasing logistic function of condition factor (K). Following Van Winkle et al. (1998), K is the fraction (between 0 and 1) of ''healthy'' mass a fish is, considering its length.

2) *Predation by terrestrial animals.* Survival of this risk increases with depth and velocity (which make fish harder to see and catch, and less vulnerable to wading birds), and increases sharply as fish length decreases below 6 cm (small fish are harder to detect and less attractive to larger predators). Survival decreases with increasing distance to hiding cover.

3) *Predation by fish.* Survival of this risk increases with fish size and is higher at depths shallow enough to exclude large fish.

4) *High velocity*, representing fatigue and inability to maintain position in fast water. Survival of this risk decreases as the ratio of cell velocity to the fish's maximum sustainable swimming speed increases.

5) *Stranding* as habitat goes dry when flows decrease. Survival of this risk increases with the ratio of cell depth to fish length.

Habitat-selection decisions in the IBM are based in part on how the probability of surviving all risks varies with habitat. Survival probability (of risks other than starvation) varies more with depth than velocity, except at high velocities (Fig. 1). For small fish (<4 cm length), total daily survival probability is generally highest in shallow cells where risk of predation by bigger fish is reduced. Larger fish have higher daily survival probabilities in deep cells that offer protection from terrestrial predators. The 5-cm juveniles used in some of our analyses are vulnerable to both aquatic and terrestrial predators when in intermediate depths, so survival is greatest in either very shallow or deep habitat. Survival of all fish is low at extreme velocities, and is improved at moderate depths and velocities by proximity to hiding cover (Fig. 1).

Fish.—Fish conduct three actions in each daily time step: movement, growth, and survival. Movement (habitat selection) occurs first but is based on predicted growth and survival. Growth is a function of food intake and metabolic energy costs. Whether a fish survives each day is a stochastic function of the survival probability for each kind of risk.

Food intake is a function of food availability, a fish's size-dependent feeding ability, and competition. Feeding is modeled separately for drift- and benthic-feeding strategies. For drift feeding, the ''capture distance'' over which a fish can detect and capture food decreases with water velocity and increases with fish length (Hill and Grossman 1993). We assume drift-feeding fish capture all the food that passes within a rectangle that is perpendicular to flow with a width of twice the capture distance and a height equal to the minimum of the capture distance and the water depth. Because the rate of drift passing through the rectangle increases with velocity but the rectangle's size decreases with velocity, and because metabolic costs increase with swimming speed, net energy intake from drift feeding peaks and then declines as velocity increases (Fig. 2).

Benthic feeding is a potentially important but less studied alternative available to stream salmonids (Nislow et al. 1998). We assume capture rate of benthic food is proportional to the benthic food production rate times a factor representing the area a fish searches daily. Benthic intake is also reduced linearly as water velocity increases, reaching 0 when velocity equals the fish's maximum sustainable swimming speed—we assume intake declines as fish must dedicate more effort to maintaining position in faster water. Because metabolism increases rapidly with fish size but benthic-feeding rate does not, benthic feeding provides higher growth for smaller fish (Fig. 2).

We treat competition as a component of food intake: the food available to a fish is equal to the cell's total food availability minus the food consumed by all the larger fish in the cell. The competition for benthic and drift food are separate; we assume fish choose the feeding method that offers highest net energy intake, and use that method for a full daily time step. Our modeled salmonids feed only during daylight hours and in this paper we compare model predictions only to daytime observations of fish.

To model growth, we follow the standard bioenergetics approach of assuming net energy intake and growth are proportional to food energy intake minus metabolic energy costs (Hanson et al. 1997). Metabolic costs include a ''standard'' term that increases with temperature and fish size, and an ''activity'' term that increases with swimming speed and the number of hours spent feeding per day. Drift-feeding fish that have access to velocity shelters are assumed to swim at only 30% of their cell's mean water velocity, while other fish are assumed to swim at their cell's mean water velocity during feeding hours. Daily growth rate (in grams per day) is proportional to net energy intake. Especially for trout that are small or not using velocity shelters, there is a wide range of habitat where growth would be negative (Figs. 2 and 3). Predicted growth is highly dependent on velocity, while depth is influential only for larger trout at depths <50 cm.

In simulating movement, we use the departure and destination approaches recommended by Railsback et al. (1999). Each day, fish determine the value of a habitat-selection objective for the cell they occupy and all other potential destination cells. Fish then move to the cell offering the highest value of the objective. Potential destination cells are all those within a distance of 200 times the fish's length, a distance conservatively

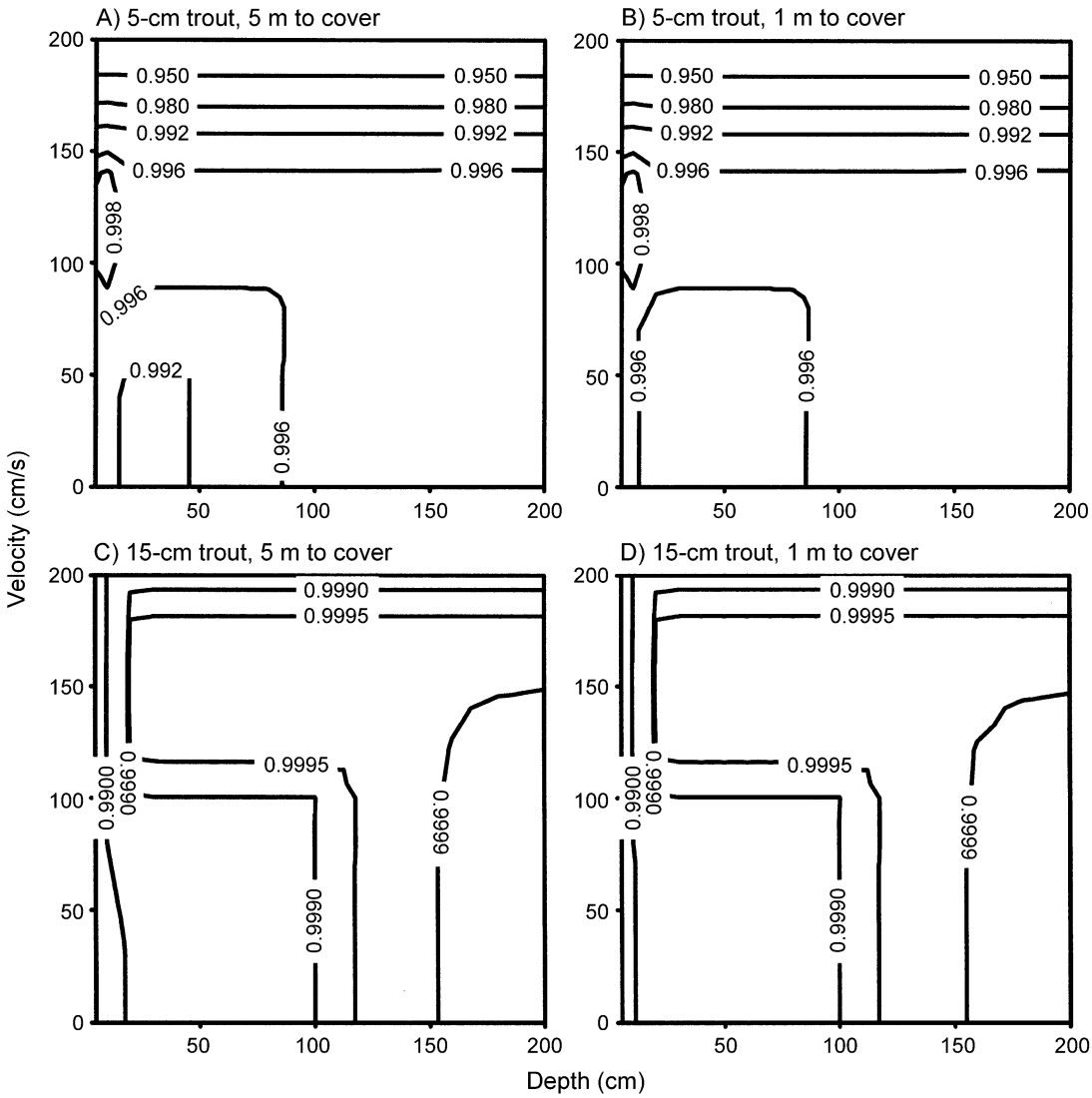

FIG. 1. Simulated daily probability of surviving risks other than starvation, as a function of depth and velocity. Plots are for age-0 trout (5-cm length) with distance to hiding cover of (A) 5 m and (B) 1 m, and for adults (15-cm length) with distance to cover of (C) 5 m and (D) 1 m. All plots are for fish using velocity shelters to reduce swimming speed and risk of exhaustion.

based on literature (Appendix A) showing that trout select habitat over 10s to 100s of meters within a day. Other than this distance limit and a prohibition against moving to cells with zero depth, the habitat-selection objective is the only factor affecting movement—there are no such limitations as a maximum fish density or minimum food intake.

We compared movement rules that maximize three different objectives: (1) daily growth rate provided under current conditions (MG); (2) current survival probability (MS), including survival of all risks except starvation (at a daily time step, the probability of starvation is nearly independent of location because one day's food intake has little effect on starvation probability); and (3) EM (expected maturity), as defined by Railsback et al. (1999). EM is the product of (1) the probability of surviving risks other than starvation over a specified fitness time horizon; (2) the probability of surviving starvation over the time horizon, based on projected net energy intake and change in K (a condition factor: the fraction [between 0 and 1] of ''healthy'' mass a fish is, considering its length); and (3) the fraction of reproductive size the fish will be at the end of the time horizon, also projected from energy intake. Reproductive size is 15 cm in these simulations, so for fish >15 cm, the reproductive size term no longer affects the movement decision. Determining EM for a potential destination requires predicting the net energy intake and survival probabilities in that cell over the time horizon; in this model the fish simply predict that

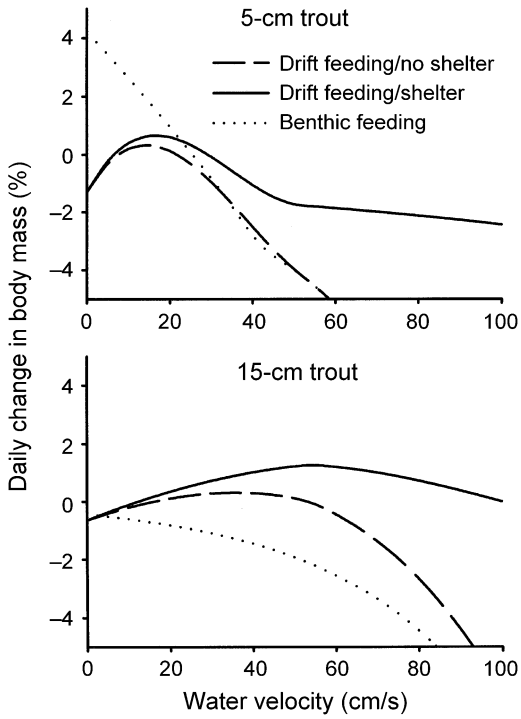

FIG. 2. Growth (daily percentage change in body mass) as a function of water velocity for two sizes of trout using the drift- and benthic-feeding strategies. Separate functions are shown for drift-feeding fish with and without velocity shelter that reduces swimming metabolic costs by 70%.

the current day's conditions will persist over the time horizon. For example, if the current daily net energy intake for a cell produces growth of 0.1 g/d, the fish predicts growth of 9.0 g over a 90-d horizon. Using this approach, the fish's expected probability of surviving starvation over a 90-d horizon varies sharply with predicted growth (Fig. 4).

Several considerations influenced our decision to use a 90-d horizon for calculation of EM. Fitness ideally should be evaluated over an animal's lifetime, but the need to predict habitat conditions over the fitness time horizon limits its length. Bull et al. (1996) used a model conceptually similar to ours and assumed overwintering juvenile salmon use the remaining winter period as a time horizon. Thorpe et al. (1998) proposed using the duration of various salmonid life stages as time horizons. The habitat that maximizes EM varies with the length of the time horizon. At short time horizons (e.g., 10 d) starvation over the time horizon is unlikely even if growth is strongly negative. Consequently, with a short time horizon EM depends mainly on non-starvation survival and the variation in EM with depth and velocity is similar in pattern to that of daily survival probability. Starvation over the time horizon becomes more likely as the horizon increases. A time horizon of 90 d restricts high levels of EM to regions with both high daily survival probabilities and growth rates near or above 0; even longer time horizons result in little additional change in the variation of EM with habitat. Considering how EM varies with the time horizon and our assumption that trout make decisions by predicting that habitat conditions remain constant over the time horizon, we chose a time horizon of 90 d.

Two key differences between EM and the MG and MS habitat-selection objectives are that EM (1) considers both energy intake and mortality risks, and (2) causes the choice of habitat to vary with a fish's physiological state. Under non-starvation conditions, a fish maximizing EM prefers habitat that provides 0 to positive net energy intake while otherwise minimizing risks. When a fish's energy reserves are low, starvation is more likely and the fish gives more preference to higher energy intake. To reach maturity, smaller fish put greater emphasis on growth than do mature fish.

Parameterization and calibration.—We conducted our simulations using input data and parameters representing a resident cutthroat trout (*Oncorhynchus clarki clarki*) population at a study site on Little Jones Creek, Del Norte County, California USA. The modeled habitat is a 184-m reach of riffles and pools containing the diversity of habitat typically encountered in mountain streams with moderate gradients.

For each model component, we estimated parameter values from the literature or via calibration. We calibrated the full model only to ensure that survival and growth rates were reasonable, because these rates directly affect habitat selection. Full-model calibration used observed survival and growth from a 75-d period from mid-July to early October. We calibrated mortality of young-of-the-year (age-0) fish using the aquatic predation-risk parameter and mortality of older fish using terrestrial predation risk. Growth rates of yearling (age 1) and older trout were calibrated with the drift-food-availability parameter, after which growth of age-0 trout was calibrated with the benthic food-availability parameter.

The standard scenario used for most simulations was a 10-d period in mid-July with a typical population age and size structure (Table 1). The initial length of each fish was randomly drawn from a normal distribution with mean and standard deviation equal to those observed at the study site for each age class. Initial masses were characteristic of healthy fish. We modeled three age classes: age 0, age 1, and all post-age-1 fish combined (age 2 and older). In July at our site the stream flow rates are typically low and gradually declining and temperatures are near their annual peak of 14–16°C. We used a steady flow rate of 0.4 m^3/s and temperature of 15°C. Under this standard scenario the model has 91 habitat cells with non-zero depth, with a total area of 1370 m^2. Depth and velocity are not correlated in these cells ($r = 0.014$).

Analyzing habitat-selection rules

The habitat-selection rules were analyzed by determining whether, when used in the IBM, the rules re-

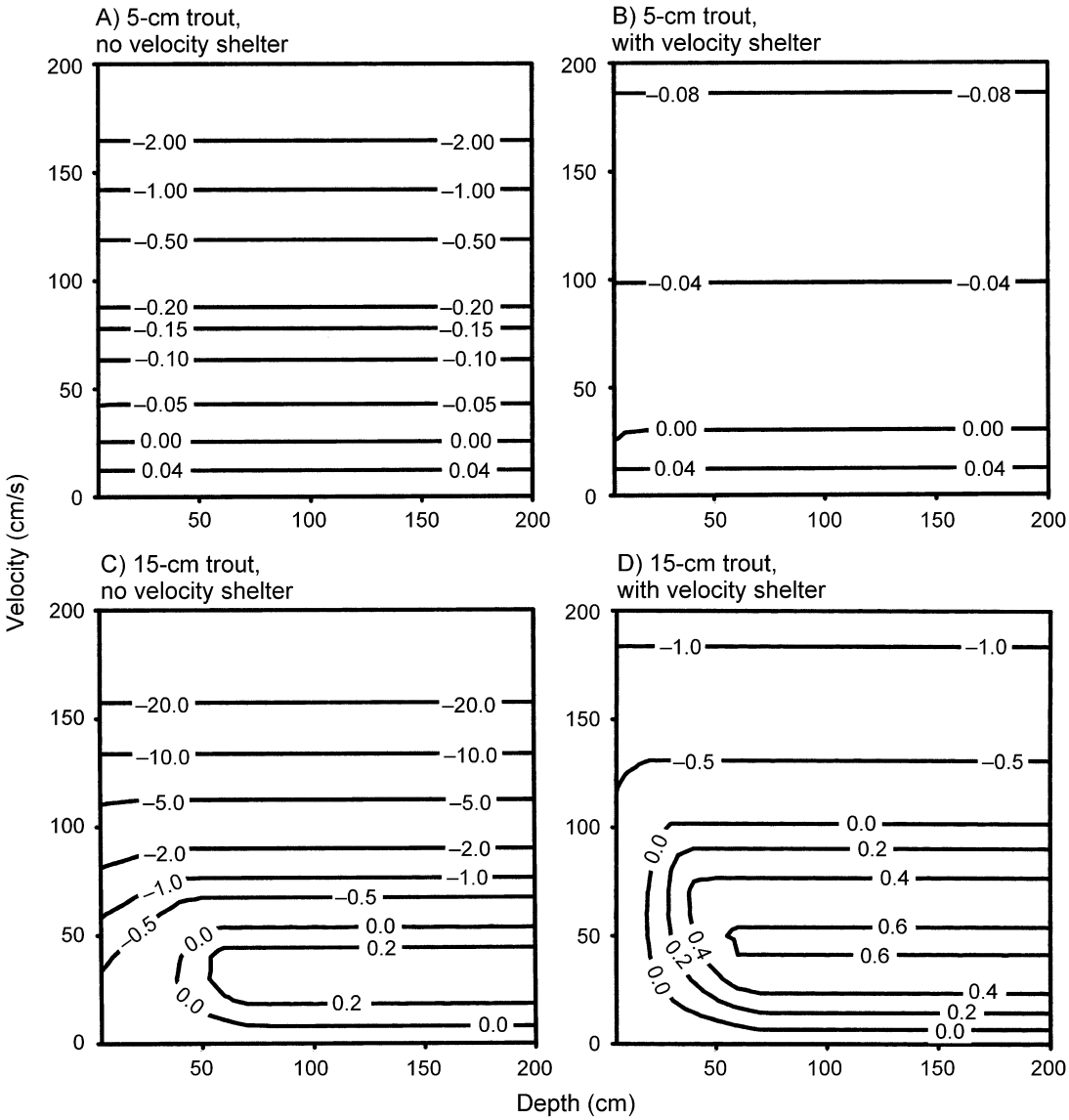

FIG. 3. Simulated daily growth rate (in grams per day) as a function of depth and velocity. Plots are for age-0 trout (5-cm length) (A) without and (B) with velocity shelter, and for 15-cm adults (C) without and (D) with velocity shelter.

produced patterns of habitat selection observed in real trout. We identified six patterns that: (1) are general responses to relatively well-understood changes in growth and risk conditions, (2) are documented in the literature, and (3) occur over spatial and temporal scales compatible with the model. These tests were made without simulating mortality–mortality risks were modeled, but fish did not actually ''die'' so the number of fish remained constant during each simulation. We also used the three habitat-selection objectives in longer-term simulations to compare their population-level consequences. These simulations used the same 75-d period and input used for model calibration. Mortality in these simulations is a stochastic function of survival probabilities, so we arbitrarily ran 10 simulations for each objective. Survival, mean growth, and production of each age class were compared among habitat-selection objectives using one-way ANOVAs followed by pairwise comparisons using Bonferroni *t* tests with $\alpha = 0.05$.

RESULTS

We used six patterns of habitat selection to analyze the three habitat-selection objectives with the individual-based model (IBM). We describe the characteristics of each pattern identified a priori as criteria for model ''success,'' how we simulated the conditions under which the pattern is expected, and the results of the simulations. (Appendix B contains animations of simulations for three of these patterns.)

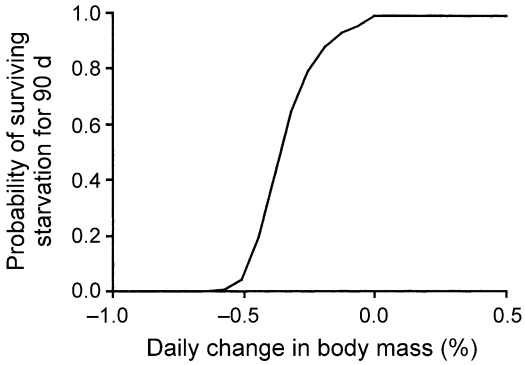

FIG. 4. Expected probability of surviving starvation over a 90-d time horizon as a function of daily growth (as percentage of body mass per day) over the time horizon. This relation applies to all sizes of trout and assumes a starting condition factor K of 1.0.

Hierarchical feeding in heterogeneous habitat

Hierarchical feeding was described by Hughes (1992*a, b*) for arctic grayling (*Thymallus arcticus*) and is commonly observed in other stream salmonids where food availability varies sharply over space (e.g., Nielsen 1992). This pattern is defined by: (1) a consistent preference for specific feeding sites, (2) dominant fish displacing others from the most preferred sites, and (3) subdominant fish occupying the most preferred sites when the dominant fish are removed. Our model's spatial resolution is lower than the field observations and model of Hughes (1992*a*), but we expected the key features of the pattern to be reproduced at a slightly greater spatial scale. Following Hughes' (1992*b*) field observations, the model assumes dominance is determined by fish length.

We modeled a part of the Little Jones Creek (California, USA) study reach that resembles the habitat studied by Hughes (1992*a*). The model included 31 habitat cells representing the downstream end of a riffle and a single deep pool. Like Hughes' site and model, our cells have varying amounts of cover that provide velocity shelter for feeding and possible protection from predators. For this test we initialized a population of 10 age-2 trout with lengths drawn from a normal distribution with a mean of 15 cm and standard deviation of 2.2. We allowed five initial time steps and then, on every other time step, removed the largest remaining fish from the model. Patterns of habitat selection were observed using the software's animation window.

The model reproduced the hierarchical feeding pattern using both the maximize-growth (MG) and expected-maturity (EM) objectives. The largest fish always occupied the same specific habitat cell, with the remaining fish distributed among nearby cells (Fig. 5). As the largest remaining fish were successively removed, their position was immediately occupied by the next largest fish. The maximize-survival (MS) objective did not produce hierarchical behavior: all fish remained in the single cell offering the highest survival probability for risks other than starvation. Hierarchical behavior is caused by competition among members of the hierarchy and our model includes no competition for resources that influence mortality risks other than starvation.

The most preferred cell differed between the MG and EM simulations (Fig. 5). The EM objective resulted in fish preferring a deep cell with moderate velocity. This cell offered the lowest mortality risks of all the cells in the model (daily survival probability of 0.9999) and enough intake for fish to maintain their energy reserves and completely avoid starvation risk. The MG objective caused fish to prefer a shallower cell with higher velocity (closer to the optimal velocity for growth; Fig. 5) and lower survival probability (0.9962). These probabilities translate to mean survival times of 180 d for fish using the MG objective vs. 6900 d for EM fish.

Response to high flows

Movement in response to events that cause major changes in habitat quality can be critical for avoiding mortality or low food intake. Floods are such events for stream salmonids. Radio-tagged adult trout in Little Jones Creek respond to high flows by simply moving to stream margins until flows subside (Harvey et al. 1999); other stream fishes respond similarly (Ross and Baker 1983, Jowett and Richardson 1994, Matheney and Rabeni 1995). We tested whether model trout move to stream margins during flood flows and return to previous locations as flows recede.

We modeled our standard population of trout in the 184-m study reach at Little Jones Creek during a characteristic brief flood. Modeled discharge increased from a base level of 0.6 m^3/s to 5 m^3/s on day 2, to 17 m^3/s on day 3, then gradually receded over the next 15 d.

The MG, MS, and EM habitat-selection objectives all reproduced the pattern of fish moving to stream margins as flow increased and returning to mid-stream as flow receded. (Age 0 fish generally selected margin habitat even at base flows.) This result occurred because high mid-channel velocities (>200 cm/s) produced both negative growth and low survival (Figs. 1 and 3). During the flood, locations that were preferred at base flows imposed: (1) velocities exceeding the maximum sustainable swimming speed, (2) little or no

TABLE 1. Population characteristics of trout used to initialize model runs.

Age (yr)	No. of fish	Length (cm)	
		Mean	1 SD
0	800	5.0	0.82
1	50	11.4	1.3
≥2	20	16.9	2.8

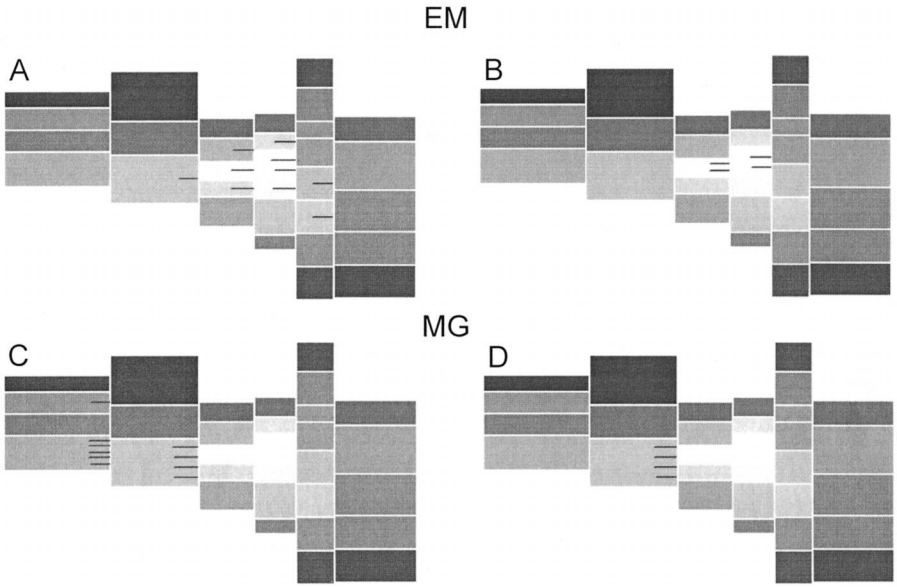

FIG. 5. Hierarchical feeding in the expected-maturity (EM) and maximize-growth (MG) simulations, in plan view with flow from right to left. Habitat cells are shaded by depth; lighter cells are deeper. Trout are represented by dark lines aligned with the right edge of the cells; the lengths of these lines are proportional to trout length. With 10 trout, competition for food required smaller fish to use suboptimal cells (A, C). After the six largest trout were removed, remaining trout occupied cells with highest expected maturity (B) or growth (D). The optimal cell for EM is the right-most cell with two trout in (B); the optimal MG cell is the one with four trout in (D).

food intake because fish were unable to capture drift or benthic food, and (3) high metabolic costs. For this scenario, the same response maximized both food intake and survival.

Response to interspecific competition

The effects of interspecific competition on habitat selection have been examined by comparing habitat preferences of one species at sites with and without a competing species (e.g., Everest and Chapman 1972, Gatz et al. 1987) and in controlled experiments (e.g., Fausch and White 1986, Bugert and Bjornn 1991). Interspecific competition among juvenile salmonids is often influenced by body size (e.g., Everest and Chapman 1972, Fausch and White 1986, Strange et al. 1992). Salmonids may respond to larger competitors by using higher velocities, but shifts in velocity selection can be subtle (Gatz et al. 1987, Bugert and Bjornn 1991). Competition-driven changes in depth preference have been less consistent among studies. We tested whether competition with a larger species produces a shift in habitat selection by age-0 trout, with the most likely shift being toward higher velocities.

We simulated habitat selection by age-0 trout of one species with and without a second, larger species. This scenario typifies competition between spring-spawning rainbow trout (*Oncorhynchus mykiss*) and fall-spawning brown trout (*Salmo trutta*). We thus refer to the observed species as rainbow trout and the competing species as brown trout. As a baseline scenario, the model was initialized for a standard population (Table 1) of rainbow trout. To simulate interspecific competition, a brown trout population was also initialized; each species had half the number of fish as in our standard scenario so total trout abundance was constant between scenarios. The only difference between species was a typical brown trout size advantage of 2 cm (e.g., Moyle and Vondracek 1985).

Results varied substantially for the three habitat-selection objectives. The MS objective did not result in a habitat shift in the presence of competitors, an expected result because our model does not simulate any effect of competitors on daily survival probability (unless the competitors are large enough to be predators). The MG objective produced the expected shift toward higher velocities in the presence of competitors (an increase in mean velocity from 21 to 23 cm/s), but very little change in depth selection (Fig. 6). This shift appears to result from competition for the low-velocity habitat that provides highest growth for age-0 trout (Fig. 3). The EM objective produced both the expected shift toward higher velocity (increase in mean from 21 to 23 cm/s) and a shift to shallower habitat (mean depth shifted from 31 to 27 cm/s; Fig. 6). The habitat shift toward higher velocity was very similar to that with the MG objective, indicating that velocity selection is driven mainly by food intake. The shift in depth usage (complete avoidance of depths >60 cm) that occurred in EM but not MG simulations was a result of competition for habitat 70–80 cm deep (Fig. 6). Model brown trout had a stronger preference than the smaller rainbow trout for this deeper habitat because the gra-

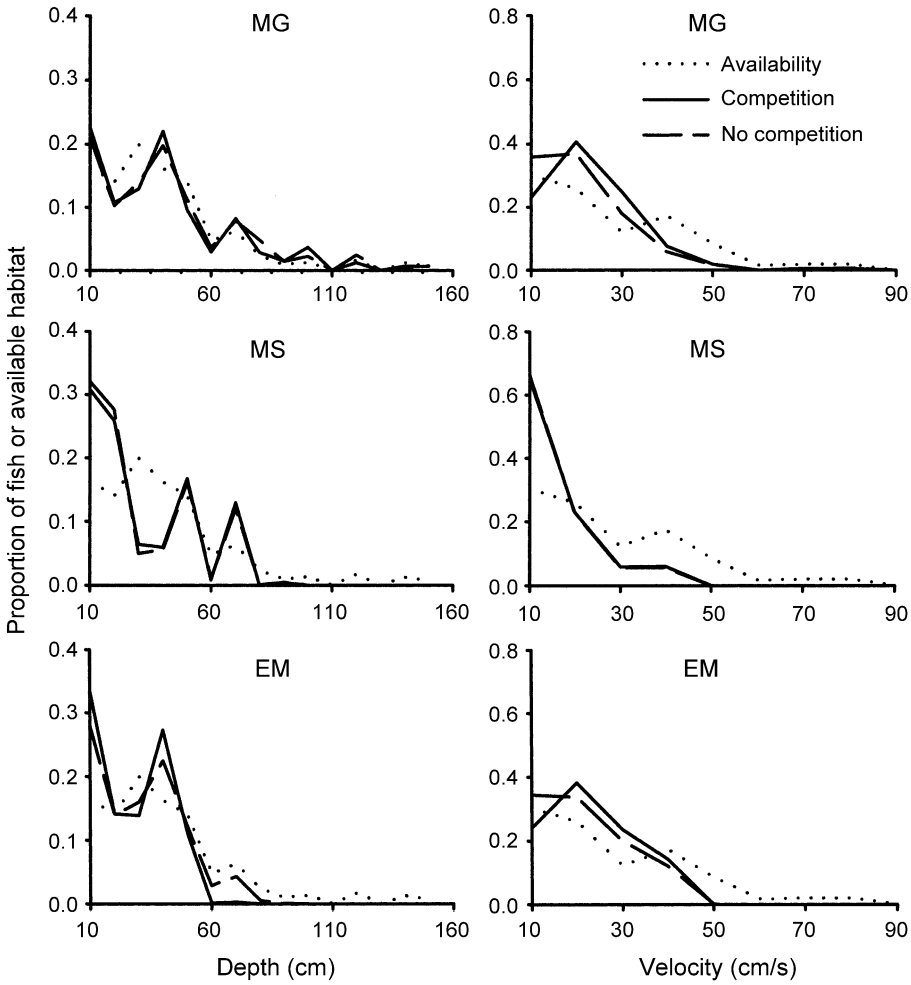

FIG. 6. Frequency of depth and velocity use by age-0 rainbow trout with and without sympatric brown trout, comparing simulations using maximize-growth (MG), maximize-survival (MS), and expected-maturity (EM) habitat-selection objectives. At each 10-cm increment along the *x*-axis, the lines represent the fraction of total age-0 trout using depth or velocity within the preceding 10-cm category. The dotted lines show habitat availability, the proportion of stream area within the depth or velocity category.

dient in survival with depth was stronger for larger trout (Fig. 1). Competition for deep habitat occurred because fish maximizing EM evaluated both growth (a function of food competition) and survival (a strong function of depth).

Response to predatory fish

A number of studies have indicated that piscivorous fish affect daytime habitat selection by small trout. For example, Brown and Moyle (1991) observed rainbow trout selecting faster and shallower habitat in the presence of piscivorous Sacramento pikeminnow (*Ptychocheilus grandis*). Campbell (1998) showed age-0 rainbow trout spent less time in a deep pool after introduction of a large brown trout. The key habitat-selection pattern observed in these studies is a shift by juvenile trout to faster and shallower habitat in the presence of predators.

We tested the model's ability to reproduce these responses to predators by measuring habitat selection by age-0 trout with and without the presence of large piscivorous trout. Simulations were based on our standard scenario. Like Campbell (1998), we examined the response of age-0 trout averaging 5 cm in length. The absence of predators was modeled by: (1) initializing the model with no age-1 or older trout, and (2) removing predation by fish (cannibalism) from the risks considered by age-0 trout. Predator presence was modeled by including all ages of trout and including the risk of cannibalism among those considered by age-0 trout. To simulate predation risks similar to those in Campbell's experiment (in which proximity of predator and prey was artificially maintained), we used a risk of predation by fish 10 times higher than that calibrated for our study site, where large trout and cannibalism are rare. Like many studies of real fish, this modeling

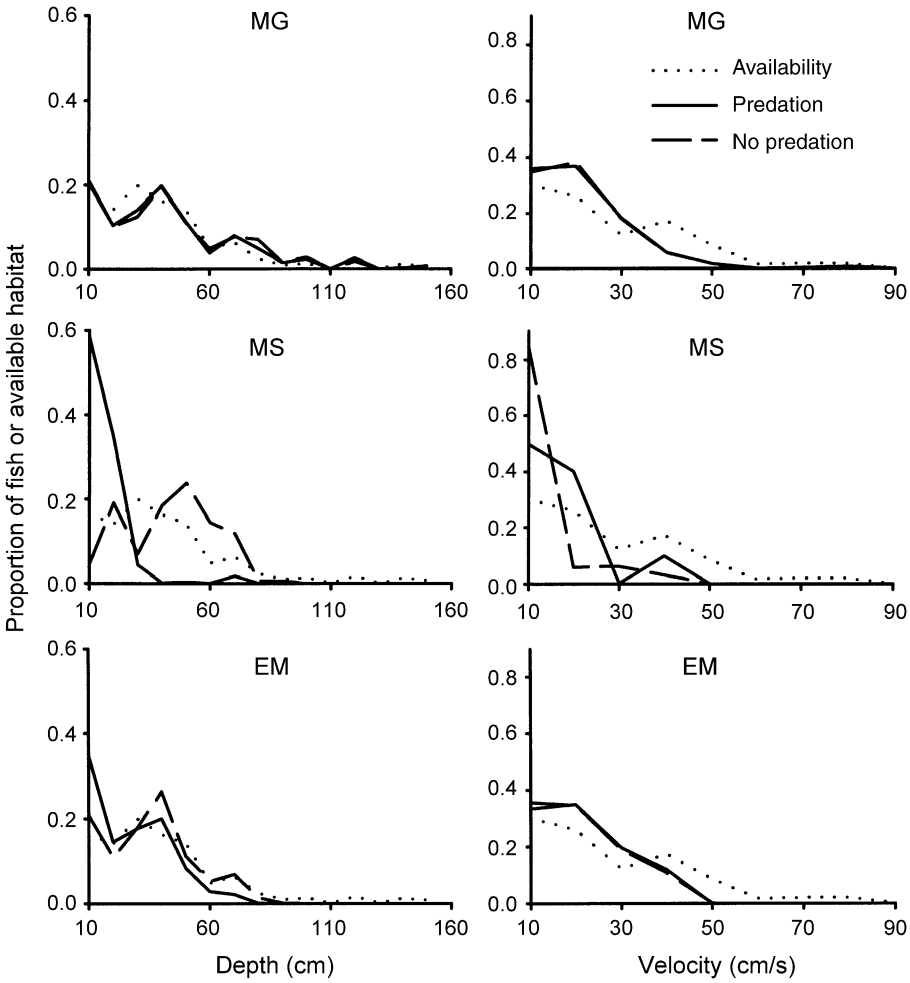

FIG. 7. Frequency of depth and velocity use by age-0 trout with and without risk of predation by larger fish, comparing MG (maximize-growth), MS (maximize-survival), and EM (expected-maturity) objectives.

exercise potentially confounds the effects of predation and competition, because of overlap in the diets of age-0 and older trout.

Depth and velocity selection were little affected by predator presence in the MG simulations (Fig. 7). With MG habitat selection driven only by energy intake, this result indicates negligible food competition between age-0 and older trout. (There is little overlap in high-growth habitat for 5- vs. 15-cm trout; Fig. 3.) The MS simulations produced the expected shift to shallower depths with predators present: mean depth used by age-0 trout decreased from 43 to 16 cm and depths >40 cm were strongly avoided. Mean velocity use increased from 13 to 17 cm/s, mainly due to a shift out of habitats with velocities <20 cm/s. The large change in depth in the MS simulation indicates that using shallower water was the primary way juvenile trout avoided piscine predators. This result was expected because our model formulation reduces risk from fish predators as depth decreases.

The EM habitat objective yielded a weaker shift to shallower water when predators were present (mean depth changed from 35 to 27 cm), but little change in velocity selection (Fig. 7; mean velocity increased only from 20.5 to 21 cm/s). For the 5-cm trout using moderate depths and velocities in this simulation, growth varies mainly with velocity (Fig. 3) and survival probability varies mainly with depth (Fig. 1). The predation risk we simulated caused age-0 trout maximizing EM to shift to shallower and less risky habitat while still using velocities that provide positive net energy intake. Most shallow habitat in the experimental channel used by Campbell (1998) was in its riffle section where velocities were higher. In contrast, our modeled habitat included shallow water with a wide range of velocities, so fish could shift to shallower habitat without being forced to use higher velocities.

Variation in velocity preference with season

Stream salmonids commonly exhibit seasonal changes in habitat preference. For example, Vondracek and Longanecker (1993) found a positive relation between

the velocities preferred by feeding adult trout and water temperature, over temperatures ranging seasonally 5°–22°C at a site where flow (controlled by a dam) remained stable. In another study where flows were stabilized by a dam, feeding cutthroat trout preferred higher velocities in summer compared to winter (Bowen 1996).

We simulated temperatures and day lengths representing four seasonal conditions: winter (1–10 January) with a water temperature of 5°C, fall (1–10 October) at 10°C, early summer (19–28 July) at 15°C, and late summer (15–24 August) at 20°C. Flow was 0.4 m^3/s for all simulations but the number of daylight hours was adjusted by date. Our model assumes fish feed during all daylight hours, so day length affects food intake and differences among these scenarios can result from day length as well as temperature. For comparison to the studies of Vondracek and Longanecker (1993) and Bowen (1996), we examined habitat selection by age-2 and older trout.

In our model, spatial variation in both net energy intake and survival probability are negligibly affected by temperature and day length: temperature and day length affect the magnitude of energy intake and survival but the effects are uniform among habitat cells. Consequently, the MG and MS objectives produced negligible change in water-velocity selection with season. Over the four seasonal conditions the mean velocity occupied by fish with the MG objective was 45–46 cm/s and the mean velocity occupied by MS fish was 25 cm/s.

Trout using the EM objective used mean velocities of 25, 29, 29, and 31 cm/s, respectively under the four seasonal conditions with temperatures from 5° to 20°C. This trend resulted from metabolic demands that increase with temperature, requiring higher food intake (provided at higher velocities) to avoid starvation over the time horizon. The effect of temperature on starvation risk over the time horizon caused a shift in the trade-off between food intake and mortality risks that maximizes EM. The model predicted no change in velocity selection between 10° and 15°C. Comparing these conditions, metabolic rates are slightly higher and day length 2.7 h longer for the 15°C scenario; the longer feeding time allows fish to meet their food requirements without using faster, riskier habitat. At 5°C, metabolic rates are low so trout need little food to avoid starvation. The EM objective consequently predicted velocity use that was almost identical to that under the MS objective, apparently to avoid nonstarvation risks.

Changes in habitat use with food availability and energy reserves

Food availability and the physiological condition of salmonids can affect their trade-offs between net energy intake and mortality risk. Metcalfe and Thorpe (1992) observed an increase in the willingness of overwintering juvenile Atlantic salmon (*Salmo salar*) to take food as food deprivation caused energy reserves (measured as body fat levels) to decline. Wilzbach (1985) observed that when food availability was high, adult cutthroat trout remained in artificial channels with cover that presumably reduced both mortality risk and feeding ability. When food availability was reduced the trout left the channels well before starvation was imminent. We based our test on Wilzbach's (1985) results, by determining if model trout change location when food availability is decreased. Our criterion for model success was a shift to habitat that provides higher food intake, at the cost of lower survival probability, when food availability is reduced.

Our simulation for this pattern used the same 31-cell habitat model used for the hierarchical feeding analysis. We placed five adult trout in the model and provided only drift food. The fish were initialized in healthy condition so starvation risk was initially minimal. The normal concentration of drift food was provided for the first 5 d, then we reduced food by 2/3 and continued the simulation for 15 more days.

Only the EM habitat-selection objective produced the expected habitat shift. Fish maximizing the MG and MS objectives did not move during this scenario because the relative rank of cells by food intake or survival probability did not change: the same cell provided highest growth before and after the change in food concentration even though the magnitude of growth decreased. At the start of the simulation using the EM objective, all trout occupied deep cells with daily survival probabilities >0.998 and food intake adequate to maintain energy reserves. After food was reduced, the four largest trout immediately moved into a cell with twice the daily mortality risk as the previous cell (survival probability = 0.996) but energy intake was the highest available (Fig. 8). These four trout consumed all the food in this cell, so the smallest trout was forced to use another cell where energy intake was lower. Late in the simulation, as its energy reserves declined, the smallest trout moved to a cell where its intake was higher but non-starvation survival was lower (0.994). Under the EM objective, the decrease in food availability makes the possibility of starvation over the 90-d time horizon an important factor in habitat selection. Continued movement as energy reserves declined, parallel to Wilzbach's (1985) laboratory observations, occurred because EM-based decisions are also state based: the trade-off between energy intake and mortality risks varies with the fish's current energy reserves.

Survival and growth over a 75-d period

The three habitat-selection objectives produced different survival and growth rates over a 75-d summer period, for all age classes (Table 2). The EM simulations produced highest survival for all three age classes. The MS simulations produced the lowest survival because many fish starved to death as a consequence of

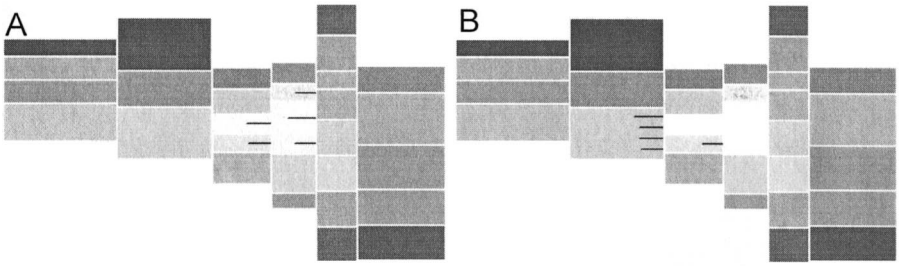

FIG. 8. Habitat selection by adult trout using the EM (expected-maturity) objective, (A) before and (B) after food availability was decreased by two-thirds. Cells are shaded by depth; lighter cells are deeper.

avoiding other risks. Growth is reported as the increase in mean mass of fish alive at the beginning vs. end of the simulation, a measure comparable to growth estimates from field censuses and similarly subject to bias from size-selective mortality. As expected, the increase in mean mass was highest for the MG objective and lowest for the MS simulation. For age-2 and older fish, growth for EM was less than half that of MG because under the EM objective the potential for further growth does not affect habitat selection after reproductive size has been attained. When survival and growth were combined to evaluate the increase in biomass of each age class, EM produced significantly higher values for age-0 trout. MG and EM results were not significantly different for age-1 trout, and for age-2 and older trout MG produced significantly higher values than did EM. For production in age classes near and above reproductive size, the higher survival by fish maximizing EM was offset by higher growth of fish maximizing MG.

DISCUSSION

This analysis of alternative habitat-selection rules provides an example of how individual-based models (IBMs) can be used to draw conclusions about theoretical issues in ecology, using methods similar to those applied to other complex natural and human systems (Auyang 1998). Evaluating an IBM's ability to reproduce a range of observed patterns, while varying the assumptions made in the IBM, appears to be a productive way to conduct such analyses.

Our simulation experiments reinforce the importance of both energy intake (growth) and risk in explaining habitat selection by stream salmonids. Maximizing growth (MG) could explain the hierarchical-feeding, high-flow, and interspecific-competition patterns of habitat selection. Maximizing survival (MS) probability could explain the responses to high flow and predators. Clearly, both growth and mortality risk affect habitat selection by stream salmonids and only the expected-maturity (EM) objective that considers both reproduced all six patterns.

Our experiments also suggest that successful habitat-selection rules must consider future changes in state, not just current growth and survival rates. Only the EM objective could explain the patterns of habitat shift with changing season and food availability. Selecting habitat to minimize the ratio of mortality risk to growth rate, μ/g (see Introduction, above), would not explain these two patterns even if growth rates were all positive; the cell offering minimal μ/g does not change when growth potential is uniformly altered throughout the habitat. Shifting habitat to increase food intake when metabolism increases, food availability decreases, or energy reserves decline is simple, intuitive behavior that we could reproduce only by assuming animals base decisions on an expectation of how future state varies with current state and habitat choices. The 75-d simulations show that giving trout this ability, via the EM objective, also increases their aggregate survival (and accumulation of biomass, among juveniles) compared to maximizing current growth or survival. Our results support the assertion of the ''Unified Foraging Theory'' (Man-

TABLE 2. Results of 75-d simulations with three alternative habitat-selection objectives. The data are means (with 1 SD standard deviation in parentheses) of 10 simulations.

Age class	Survival over 75 d (%)			Increase in mean mass over 75 d (%)			Increase in age class biomass over 75 d (%)		
	MG	MS	EM	MG	MS	EM	MG	MS	EM
0	38 (2)	17 (1)	55 (2)	163 (6)	88 (5)	117 (4)	0 (5)	−67 (1)	18 (4)
1	66 (6)	34 (8)	75 (5)	64 (8)	−21 (6)	50 (9)	8 (13)†	−73 (6)	12 (9)†
≥2	72 (9)	50 (8)	85 (7)	75 (8)	21 (14)	34 (8)	25 (12)	−41 (5)	14 (8)

Notes: Habitat-selection objectives: MG = maximize growth, MS = maximize survival, EM = expected maturity.

† MG and EM results are not significantly different at $\alpha = 0.05$.

gel and Clark 1986) that animals make such state-based, predictive decisions.

Comparison of habitat selection predicted by the three objectives illustrates why investigators using the MG approach have had success predicting habitat selection by stream salmonids (e.g., Fausch 1984, Hughes 1992*a*). The literature we used to formulate our IBM indicates that both growth and survival are improved by shifting to deeper, faster water as trout grow larger. Our EM simulations of trout under non-starvation conditions indicate they often use habitat with near-optimal growth but higher survival than the cell with optimal growth. In the competition and predation tests, age-0 trout maximizing EM had a velocity distribution very similar to fish maximizing growth, but used depths more similar to those of trout maximizing survival. Movement to maximize both MG and MS produced observed responses to floods. These results indicate that, when we consider only depth and velocity, there may often be only subtle differences between habitat that maximizes growth vs. provides a good trade-off between growth and survival. To some extent, the choice between high growth and low risk may be a false dichotomy for stream salmonids because the trade-off can be small. However, consideration of other habitat variables may reveal stronger trade-offs between growth and short-term risk. For example, use of cover can increase survival but reduce food intake (Wilzbach 1985, Keith et al. 1998).

The simulation experiments presented here show that our IBM is capable of reproducing a variety of representative patterns of habitat selection by individual stream salmonids. We believe this ability is due to three novel characteristics of the model. First, we avoid imposing behaviors that are not always appropriate, e.g., requiring trout to maintain territories. Instead, we let fish select whatever habitat maximizes their fitness-based objective. This approach requires providing simple models of how the habitat-selection objective varies spatially. Among these simple models, simulation of how competition for food affects energy intake appears essential for reproducing some patterns. This approach produces habitat-selection behavior resembling territoriality in some cases (in relatively uniform habitat during moderate flows), but also reproduces critical non-territorial behaviors like use of refuges during extreme flows. Failure to reproduce such critical short-term behaviors can cause IBMs to mistakenly predict mortality events that have major and persistent effects. Second, we assume trout have sufficient knowledge of their habitat to make good foraging decisions within the daily time step instead of forcing movement to be partly random. Finally, the EM habitat-selection objective appears to be a useful representation of how trout select habitat among alternatives that vary in energy intake and mortality risk.

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Literature Cited

Auyang, S. Y. 1998. Foundations of complex-system theories in economics, evolutionary biology, and statistical physics. Cambridge University Press, New York, New York, USA.

Bart, J. 1995. Acceptance criteria for using individual-based models to make management decisions. Ecological Applications **5**:411–420.

Bennett, A. T. D., and A. I. Houston. 1989. When to change habitat. Trends in Ecology and Evolution **4**:3–4.

Bowen, M. D. 1996. Habitat selection and movement of a stream-resident salmonid in a regulated river and tests of four bioenergetic optimization models. Dissertation. Utah State University, Logan, Utah, USA.

Brown, L. R., and P. B. Moyle. 1991. Changes in habitat and microhabitat partitioning within an assemblage of stream fishes in response to predation by Sacramento squawfish (*Ptychocheilus grandis*). Canadian Journal of Fisheries and Aquatic Sciences **48**:849–856.

Bugert, R. M., and T. C. Bjornn. 1991. Habitat use by steelhead and coho salmon and their responses to predators and cover in laboratory streams. Transactions of the American Fisheries Society **120**:486–493.

Bull, C. D., N. B. Metcalfe, and M. Mangel. 1996. Seasonal matching of foraging to anticipated energy requirements in anorexic juvenile salmon. Proceedings of the Royal Society of London **B 263**:13–18.

Campbell, E. A. 1998. Influence of streamflow and predators on habitat choice by trout. Dissertation. University of California, Davis, California, USA.

Everest, F. H., and D. W. Chapman. 1972. Habitat selection and spatial interaction by juvenile chinook salmon and steelhead trout in two Idaho streams. Journal of the Fisheries Research Board of Canada **29**:91–100.

Fausch, K. D. 1984. Profitable stream positions for salmonids: relating specific growth rate to net energy gain. Canadian Journal of Zoology **62**:441–451.

Fausch, K. D., and R. J. White. 1986. Competition among juveniles of coho salmon, brook trout, and brown trout in a laboratory stream, and implications for Great Lakes tributaries. Transactions of the American Fisheries Society **115**:363–381.

Gatz, A. J. J., M. J. Sale, and J. M. Loar. 1987. Habitat shifts in rainbow trout: competitive influences of brown trout. Oecologia **74**:7–19.

Gilliam, J. F., and D. F. Fraser. 1987. Habitat selection under predation hazard: test of a model with foraging minnows. Ecology **68**:1856–1862.

Grimm, V. 1999. Ten years of individual-based modelling in ecology: What have we learned and what could we learn in the future? Ecological Modelling **115**:129–148.

Grimm, V., K. Frank, F. Jeltsch, R. Brandl, J. Uchmanski, and C. Wissel. 1996. Pattern-oriented modelling in population ecology. The Science of the Total Environment **183**: 151–166.

Hanson, P., T. Johnson, J. Kitchell, and D. E. Schindler. 1997. Fish bioenergetics [version] 3.0. University of Wisconsin Sea Grant Institute, Madison, Wisconsin, USA.

Harvey, B. C., R. J. Nakamoto, and J. L. White. 1999. The influence of large woody debris and a bankfull flood on movement of resident coastal cutthroat trout during fall and winter. Canadian Journal of Fisheries and Aquatic Sciences **56**:2161–2166.

Hill, J., and G. D. Grossman. 1993. An energetic model of

microhabitat use for rainbow trout and rosyside dace. Ecology **74**:685–698.

Hughes, N. F. 1992*a*. Selection of positions by drift-feeding salmonids in dominance hierarchies: model and test for arctic grayling (*Thymallus arcticus*) in subarctic mountain streams, interior Alaska. Canadian Journal of Fisheries and Aquatic Sciences **49**:1999–2008.

Hughes, N. F. 1992*b*. Ranking of feeding positions by drift-feeding arctic grayling (*Thymallus arcticus*) in dominance hierarchies. Canadian Journal of Fisheries and Aquatic Sciences **49**:1994–1998.

Hughes, N. F. 1998. A model of habitat selection by drift-feeding stream salmonids at different scales. Ecology **79**: 281–294.

Huston, M., D. DeAngelis, and W. Post. 1988. New computer models unify ecological theory. BioScience **38**:682–691.

Jowett, I. G., and J. Richardson. 1994. Comparison of habitat use by fish in normal and flooded river conditions. New Zealand Journal of Marine and Freshwater Research **28**: 409–416.

Keith, R. M., T. C. Bjornn, W. R. Meehan, N. J. Hetrick, and M. A. Brusven. 1998. Response of juvenile salmonids to riparian and instream cover modifications in small streams flowing through second-growth forests of southeast Alaska. Transactions of the American Fisheries Society **127**:889–907.

Leonardsson, K. 1991. Predicting risk-taking behaviour from life-history theory using static optimization technique. Oikos **60**:149–154.

Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology **68**:619–640.

Mangel, M. 1994. Life history variation and salmonid conservation. Conservation Biology **8**:879–880.

Mangel, M., and C. W. Clark. 1986. Toward a unified foraging theory. Ecology **67**:1127–1138.

Matheney, M. P., IV, and C. F. Rabeni. 1995. Patterns of movement and habitat use by northern hog suckers in an Ozark stream. Transactions of the American Fisheries Society **124**:886–897.

Metcalfe, N. B., and J. E. Thorpe. 1992. Anorexia and defended energy levels in over-wintering juvenile salmon. Journal of Animal Ecology **61**:175–181.

Minar, N., R. Burkhart, C. Langton, and M. Askenazi. 1996. The Swarm simulation system: a toolkit for building multiagent simulations. Working Paper 96-06-042. Santa Fe Institute, Santa Fe, New Mexico, USA.

Moyle, P. B., and B. Vondracek. 1985. Persistence and structure of the fish assemblage in a small California stream. Ecology **66**:1–13.

Nielsen, J. L. 1992. Microhabitat-specific foraging behavior, diet, and growth of juvenile coho salmon. Transactions of the American Fisheries Society **121**:617–634.

Nislow, K. H., C. L. Folt, and D. L. Parrish. 1999. Favorable foraging locations for young Atlantic salmon: application to habitat and population restoration. Ecological Applications **9**:1085–1099.

Nislow, K., C. Folt, and M. Seandel. 1998. Food and foraging behavior in relation to microhabitat use and survival of age-0 Atlantic salmon. Canadian Journal of Fisheries and Aquatic Sciences **55**:116–127.

Railsback, S. F. 2001. Getting ''results'': the pattern-oriented approach to analyzing natural systems with individual-based models. Natural Resource Modeling **14**:465–474.

Railsback, S. F., R. H. Lamberson, B. C. Harvey, and W. E. Duffy. 1999. Movement rules for spatially explicit individual-based models of stream fish. Ecological Modelling **123**:73–89.

Ross, S. T., and J. A. Baker. 1983. The response of fishes to periodic spring floods in a southeastern stream. American Midland Naturalist **109**:1–14.

Roussel, J.-M., and A. Bardonnet. 1999. Ontogeny of diel pattern of stream-margin habitat use by emerging brown trout, *Salmo trutta*, in experimental channels: influence of food and predator presence. Environmental Biology of Fishes **56**:253–262.

Strange, E. M., P. B. Moyle, and T. C. Foin. 1992. Interactions between stochastic and deterministic processes in stream fish community assembly. Environmental Biology of Fishes **36**:1–15.

Tabor, R. A., and W. A. Wurtsbaugh. 1991. Predation risk and the importance of cover for juvenile rainbow trout in lentic systems. Transactions of the American Fisheries Society **120**:728–738.

Thorpe, J. E., M. Mangel, N. B. Metcalfe, and F. A. Huntingford. 1998. Modelling the proximate basis of salmonid life-history variation, with application to Atlantic salmon, *Salmo salar* L. Evolutionary Ecology **12**:581–599.

Van Winkle, W., H. I. Jager, S. F. Railsback, B. D. Holcomb, T. K. Studley, and J. E. Baldrige. 1998. Individual-based model of sympatric populations of brown and rainbow trout for instream flow assessment: model description and calibration. Ecological Modelling **110**:175–207.

Vondracek, B., and D. R. Longanecker. 1993. Habitat selection by rainbow trout *Oncorhynchus mykiss* in a California stream: implications for the Instream Flow Incremental Methodology. Ecology of Freshwater Fish **2**:173–186.

Werner, E. E., and B. R. Anholt. 1993. Ecological consequences of the trade-off between growth and mortality rates mediated by foraging activity. American Naturalist **142**: 242–272.

Wilzbach, M. A. 1985. Relative roles of food abundance and cover in determining the habitat distribution of stream-dwelling cutthroat trout (*Salmo clarki*). Canadian Journal of Fisheries and Aquatic Sciences **42**:1668–1672.

APPENDIX A

A complete description of the individual-based trout model, including justification of assumptions and parameter values, calibration methods, and software implementation is available in ESA's Electronic Data Archive: *Ecological Archives* E083-031-A1.

APPENDIX B

Animations of the hierarchical feeding, high flow, and food availability simulations are available in ESA's Electronic Data Archive: *Ecological Archives* E083-031-A2.