WHAT CAN HABITAT PREFERENCE MODELS TELL US? TESTS USING A VIRTUAL TROUT POPULATION

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Abstract. Habitat selection (''preference'') models are widely used to manage fish and wildlife. Their use assumes that (1) habitat with high animal densities (highly selected habitat) is high quality habitat, and low densities indicate low quality habitat; and (2) animal populations respond positively to the availability of highly selected habitat. These assumptions are increasingly questioned but very difficult to test. We evaluated these assumptions in an individual-based model (IBM) of stream trout that reproduces many natural complexities and habitat selection behaviors. Trout in the IBM select habitat to maximize their potential fitness, a function of growth potential (including food competition) and mortality risks. We know each habitat cell's intrinsic habitat quality, the fitness potential a trout in the cell would experience in the absence of competition. There was no strong relation between fitness potential and the density of fish in the IBM; cells where fitness potential was high but density low were common for all age classes, and fitness potential was not proportional to density. This result was consistent at high and low abundance and high and low overall habitat quality. We developed a statistical model of trout density observed in the IBM as a function of the four habitat variables that vary among cells. We then tested the ability of modeled mean density to predict population response to habitat changes resulting from stream flow modification. Modeled density partially explained population response to flow, but only at flows near the flow at which the density model was developed, and not for groups (e.g., juveniles) experiencing strong competition for habitat. Modeled density predicted population response opposite that observed for age-0 trout and incorrectly predicted response of all age classes to major changes in flow. These results make sense if habitat selection is understood as an emergent property of (1) the mechanisms by which habitat affects fitness, (2) habitat availability, (3) population abundance and size structure, and (4) how individuals compete with each other. We identified eight reasons why animal density may not reflect habitat quality and several inherent limitations of habitat selection modeling.

Key words: complexity; habitat modeling; habitat preference; habitat quality; habitat selection; individual-based model; trout; virtual ecology.

INTRODUCTION

Habitat selection models (often referred to as ''preference'' or ''habitat index'' models) are widely used to evaluate habitat quality and predict effects of habitat alteration on animal populations. One habitat selection model for fish, the physical habitat simulation system (PHABSIM; Bovee et al. 1998), has been a basis for management decisions at hundreds of water projects in many countries, and similar approaches (e.g., U.S. Fish and Wildlife Service [USFWS] 1980) are widely used for managing terrestrial wildlife habitat. Habitat selection modeling involves observing the frequency with which animals use various habitat types and the availability of the habitat types; the ratio of habitat use to habitat availability is then transformed into a measure of habitat selection (Manly et al. 2002). Common measures of habitat selection include a habitat selection probability function (the estimated probability that any observation of an animal falls within a specified habitat type, if all types are equally available), animal density (number of animals observed divided by the area of the habitat type), and ''suitability indexes'' scaled between zero and one (used by PHABSIM). The most highly selected habitat types are assumed to be most beneficial, and management activities are then directed towards providing more of the selected habitat.

The popularity of habitat selection modeling likely results from its simplicity and empirical basis. However, the approach is coming under increasing criticism (Scott et al. 2002). For example, Van Horne (1983), Garshelis (2000), and Burgman et al. (2001) have pointed out key problems with using habitat selection models to manage habitat. In addition to a variety of measurement, statistical, and scale issues, Garshelis (2000) identifies two ''fatal flaws.'' First is the as-

sumption that an animal is more likely to use a habitat type if more of that type is available. This assumption could be violated if the habitat type offers abundant or nonlimiting resources (e.g., animals may need habitat for resting and hiding, but a small area of such habitat may be sufficient). The second flaw (also addressed by Van Horne 1983) is the assumption that highly selected habitat provides high fitness potential or carrying capacity. Garshelis (2000) provides five reasons to question this assumption: (1) habitat types used only for short times or in small amounts may still be critical to fitness; (2) if resources are abundant or nonlimiting, the apparent selection for them is likely to be arbitrary; (3) some animals may require a mix of habitat types; (4) competition can exclude all but dominant individuals from the best habitat; and (5) it is possible that none of the observed habitat provides a sustainable level of fitness, or that even rarely used habitat provides adequate fitness. A simple simulation study by Hobbs and Hanley (1990) concluded that habitat selection will reflect carrying capacity only under special circumstances rarely found in nature (e.g., habitat and animals are in a state of long-term, stable equilibrium).

If the most selected habitat does not necessarily offer the highest fitness, then an important question arises: is habitat quality or selection a better predictor of population response to habitat alteration? Will a population be enhanced more by providing habitat where fitness potential is highest, or highly selected habitat? To our knowledge, this difficult question has not previously been addressed by either field or simulation studies.

In this paper, we examine relations between intrinsic habitat quality and observed habitat selection. Whereas Van Horne (1983) suggested that habitat quality be defined as a product of animal density and mean individual fitness, presumably at "carrying capacity," we follow Garshelis (2000) and Tyre et al. (2001) in defining habitat quality as the individual fitness provided by the habitat. We use this definition because, at least in the system we examine, habitat selection is an outcome only of individual decisions made to maximize potential fitness; habitat units have no intrinsic animal density or carrying capacity. Also, in our system, we would have to assume an arbitrary definition of carrying capacity, whereas individual fitness potential is completely known. Our specific measure of habitat quality, FP, is the fitness potential a habitat type provides an average animal in the absence of competition. FP is an intrinsic characteristic of the habitat and can be evaluated even if animals are absent. FP depends on both the growth potential and mortality risks presented by a habitat type. In our virtual population, trout select habitat to maximize a measure that is very similar to FP except for also representing competition among trout. In our analyses, habitat quality is equivalent to one definition of habitat "preference"—the function an individual would use to select among locations varying in physical conditions, in the absence of compet-

itors (e.g., Rosenfeld and Boss 2001). We define habitat selection as density (DEN): The number of individuals observed using a habitat type divided by the area of habitat of that type available to the population (Manly et al. 2002).

This paper's first objective is to examine the assumption that observed habitat selection is a good indicator of habitat quality. This examination is made in a virtual trout population where habitat quality as FP is defined and measurable. Using an individual-based model (IBM) in which trout select habitat to maximize expected fitness while competing for food and habitat, we contrast the characteristics of habitat with highest DEN vs. highest FP. This part of our study is similar in some ways to the work of Tyre et al. (2001), which examined the relationship between habitat occupancy and a single habitat quality variable in a relatively simple IBM. Our study is different in that (1) we use DEN instead of occupancy as the measure of habitat selection, with habitat units large enough to accommodate multiple animals; (2) habitat quality is a complex function of four habitat variables that affect both survival and growth; (3) habitat selection results from individuals continually seeking the best available habitat instead of being a one-time, partially random, dispersal process.

Our second objective is to compare habitat quality and habitat selection as predictors of population response to habitat alteration. We compare FP and DEN as predictors of population response to incremental, then major, habitat alterations.

METHODS

One use of IBMs is as virtual ecosystems in which other ecological models and theories can be evaluated (Grimm 1999, Tyre et al. 2001). In such virtual ecosystems, animal motivations and behaviors, habitat conditions, and population dynamics can be completely known and observable while much of the real system's complexity remains. The virtual ecosystem approach also can avoid errors due to scale (Tyre et al. 2001): In our IBM we observe habitat use by trout at exactly the same spatial and temporal resolution the fish use in selecting habitat, which is not possible in real ecosystems. We take advantage of these benefits of IBMs, using the following four steps. Following Tyre et al. (2001) we use the word "simulated" to refer to IBM results and "modeled" to refer to statistical models of DEN. All the "data" we analyze and model are from the IBM.

1) Adopt an IBM of a stream trout population. In this IBM, each individual fish selects the habitat cell with the highest available fitness potential each day. Fitness potential varies among habitat cells as a function of four habitat variables and the presence of more dominant competitors. The IBM includes three age classes of trout: 0, 1, and 2 yr.

2) On a single simulation day, observe fish density in each cell of the IBM. Using these data, build statistical models of how DEN varies with the four habitat variables.

3) Contrast the statistically modeled DEN with the known FP, examining how well DEN predicts FP.

4) Contrast the ability of FP and DEN to explain population response, by simulating a range of stream flows and evaluating at each the following: (1) area-averaged FP, (2) area-averaged DEN, and (3) the virtual population's response over 90 d.

Virtual trout population

We conducted our experiment using an IBM of a stream population of coastal cutthroat trout (*Oncorhynchus clarki clarki*). The IBM predicts how stream flow affects habitat availability, trout habitat choice, and population dynamics. Railsback and Harvey (2001, 2002) describe the IBM's assumptions, equations, parameter values, and their bases. Here we summarize how the IBM simulates habitat, growth, survival, FP, and habitat selection.

The trout IBM uses a one-day time step, with stream habitat represented as rectangular cells. At the study site, cells were placed so that (1) hydraulic conditions were relatively uniform within a cell, while (2) the full range of natural hydraulics was captured among cells and (3) cell length and width were greater than a minimum resolution of 1 m, the approximate scale over which trout select feeding habitat. The habitat variables that affect trout food intake, growth, and survival are water depth, velocity, temperature, and turbidity; fraction of the cell containing velocity shelters (FVS) that reduce the swimming energy needed to capture drifting food; distance to hiding cover (DHC); production rate of stationary food (e.g., benthic invertebrates); and concentration and production rate of drifting food. Depth, velocity, FVS, and DHC vary among cells; temperature, turbidity, and the three food variables do not. The IBM assumes that FVS and DHC are constant over time, but depth and velocity vary with stream flow, as determined by a hydraulic model.

The daily growth of each trout is a function of food production rates, the trout's ability to catch food, competition among trout, and the energetic cost of swimming. The availability of stationary food (e.g., invertebrates eaten off the stream bottom) is independent of stream flow. The availability of drifting food increases with flow because the volume of food passing through a cell increases with both velocity and depth, but the distance over which a fish can detect and capture drifting food decreases as velocity increases. Swimming costs increase with velocity, but if a trout has access to velocity shelter, its swimming costs are reduced by 70%. As a consequence of these processes, growth rate increases with velocity up to a peak velocity, after which growth declines; the peak velocity for growth increases with trout size and is higher for trout using

velocity shelters. The virtual trout compete for food and velocity shelters in a size-based hierarchy. Each cell contains, each day, a fixed amount of food and velocity shelter; trout move in descending order of size and the food and shelter area used by larger fish are not available to smaller fish in the same cell.

Trout survival is partially stochastic. The daily probability of surviving each of several mortality sources is a deterministic function of habitat and fish conditions, but whether a trout survives each mortality source, each day, is determined by drawing a random number and comparing it to the survival probability. The probability of surviving cannibalism by large trout is higher at shallow depths and increases with fish length. Survival of avian and mammalian predators (e.g., mergansers, otters) increases with increasing depth and velocity, and is higher for small fish. The probability of surviving predators also increases as the cell's DHC decreases. Starvation risk is a function of the fraction a fish is of "healthy" weight for its length. Velocities higher than a fish's maximum sustainable swim speed reduce survival, as do depths much less than a fish's length (which subject a fish to stranding and excess predation risk).

The virtual trout move daily to the cell (within a radius they are assumed to know growth and risk conditions in, equal to 20 times the square of the fish's length) that offers the highest value of a fitness indicator "expected maturity" (EM; Railsback et al. 1999). The value of EM is a fish's estimated probability of surviving both starvation and nonstarvation risks over a future time horizon. For immature fish, EM also includes a term equal to the expected fraction of reproductive size (12 cm length) achieved at the end of the time horizon; this term encourages small fish to select habitat that also provides growth toward reproductive maturity. We use 90 d for the time horizon as it produces adult habitat choice nearly identical to an infinite horizon while encouraging immature fish to achieve reproductive maturity in a realistic time. The starvation survival and growth to reproductive size components of EM depend on growth rate, and the nonstarvation survival component depends on predation and other mortality risks. Fish are not excluded from any cell, but the value of EM a fish expects from a cell is reduced if the consumption by larger fish of food or velocity shelter is sufficient to limit growth. Under "normal" conditions, this approach produces habitat selection behavior closely resembling territoriality (Railsback and Harvey 2002: see Appendix A), but it also allows model trout to respond realistically to short-term events like floods and to spatial variation in food availability.

The trout IBM has reproduced a wide range of observed habitat selection patterns, including shifts in habitat use with flood flows, competition, predation risk, change in season, and reduced food availability (Railsback and Harvey 2002); and a number of ob-

TABLE 1. Initial characteristics of the virtual trout population.

Age	Abundance	Mean length (cm)	Standard deviation in length (cm)
0	300	6.1	0.94
1	100	11.6	1.1
2	30	17.1	2.4

Notes: Three age classes are used: age 0 (young-of-year), age 1, and age 2. For each age class, the model was initialized with the specified abundance. The length of each fish was drawn randomly from a normal distribution with the specified mean and standard deviation.

served population-level phenomena (Railsback et al. 2002).

Habitat input for the IBM was taken from a study site on Little Jones Creek, Smith River basin, Del Norte County, California. This site, described by Harvey (1998) and Railsback and Harvey (2001), is 184 m in length with widths typically 8–15 m, and contains a variety of riffles and pools created by bedrock and logs. To increase the number of fish in our analysis we made the simulated habitat twice the length of the study site by simply repeating the entire reach.

The virtual trout population's initial abundance (Table 1) approximates the highest midsummer population typically observed at the site. The IBM was initialized for 1 July 2000, using typical early July conditions for the study site: flow of 0.44 m³/s, temperature of 12°C, and negligible turbidity.

Evaluation of habitat quality

We defined a habitat cell's FP to be the potential fitness an average trout would experience in the absence of competition. FP values for each cell were calculated separately for each age class of trout. The value of FP for a cell (and trout age class) is the EM that a trout of the age class's mean length would obtain in the cell, assuming (1) the trout is in good condition; (2) food intake is not reduced by competition; and (3) the trout has access to velocity shelter for feeding if the cell has a nonzero FVS.

Evaluation of habitat selection

Statistical models of DEN were generated from simulated habitat and fish location observed from the virtual trout population for 5 July 2000 (Table 2). We verified that there was little change in habitat selection by the virtual trout in the surrounding days. Each age class was modeled separately. The author who developed the statistical models (H. B. Stauffer) was unfamiliar with how habitat selection is simulated in the virtual trout population.

The dependent variable was trout density, the number of fish in a cell divided by cell area. The habitat variables that vary among cells—depth, velocity, DHC, and FVS—were evaluated for inclusion in the density model as independent variables. To accommodate non-

linearities, the natural logarithm and square of the habitat variables were also included as potential independent variables. Some independent variables had zero values, so we added 0.5 before taking their logarithm. To accommodate interactions among habitat variables, we included the products of pairs of habitat variables (depth × velocity, depth × DHC, etc.) as potential independent variables. Cells with zero fish were included in the model-fitting input.

Best-subsets multiple regression was used to identify the best models of fish density. Akaike's information criterion (AIC) was used to select the best-fitting parsimonious model (Burnham and Anderson 1998). These analyses used PROC REG (SAS Institute 1999). For all three age classes, there were many combinations of independent variables that provided nearly equally good models of DEN, having values of AIC within two units of the minimum. We verified that the "best-fitting" (lowest AIC) model included the same habitat variables (but different transformations) and the same interaction terms as most of the other good models, then used this best-fitting model to represent DEN.

Evaluation of habitat selection as an indicator of habitat quality

To evaluate the assumption that DEN is a good indicator of habitat quality, we first used contour plots to compared how FP and DEN vary with depth and velocity. These plots identify differences in peaks and trends between FP and DEN.

The second comparison was made by plotting the value of FP vs. the value of DEN in each cell, using the same observations used to model DEN. These plots provide a direct examination of the relation between observed DEN and known FP in the virtual trout population. We used three criteria for whether observed DEN was a good indicator of FP: (1) whether cells with low densities consistently had low FP, (2) whether cells with high DEN consistently had high FP, and (3) whether there was a significant, positive relation between DEN and FP.

TABLE 2. Summary of data used to model habitat selection.

Cell characteristic	Mean	Minimum	Maximum
Trout density (fish/m²)			
Age 0	0.17	0.0	1.3
Age 1	0.053	0.0	0.60
Age 2	0.015	0.0	0.27
Area (m²)	15.1	4.0	42.0
Depth (cm)	35	4	141
Velocity (cm/s)	28	1	148
DHC (cm)	250	0	900
FVS	0.21	0.0	1.0

Notes: Observations were made from 174 habitat cells. The number of cells with zero fish is 97 for age 0, 136 for age 1, and 159 for age 2.

We repeated this cellwise comparison of FP and DEN to test two common assumptions about the relationship between observed habitat selection and habitat quality: That observed habitat selection better reflects habitat quality when (1) population density is high (so more of the ''usable'' habitat is occupied), and (2) habitat quality is generally low (so the population is more ''habitat limited''). The first assumption was tested by examining FP vs. DEN with one-third of the fish abundance shown in Table 1. The second assumption was tested by examining FP vs. DEN from simulations in which the best habitat for adult trout (deep pools) was replaced by shallower, faster habitat. Railsback et al. (2002) showed (using the same IBM) that this ''no pools'' habitat produced substantially lower growth and abundance of adult trout.

Comparison of habitat quality and selection as predictors of population response

We conducted simulation experiments to contrast how well FP and DEN predict population response to changes in habitat. The experiments used a sensitivity analysis approach, simulating population response over a range of stream flows. The first (''low-flow'') experiment examined flows over a range including the flow (0.44 m³/s) used to model DEN, but the second (''high-flow'') experiment examined higher flows.

For the low-flow experiment, we simulated the virtual trout population at stream flows from 0.3 to 1.0 m³/s at increments of 0.1 m³/s. As flow increases, cell depths and velocities generally increase and additional cells become available as the stream widens. We evaluated the response of each age class over a 90-d period of steady flow and temperature.

We examined a measure of trout population response chosen to match the objective trout use in selecting habitat, making this measure as directly related to habitat choice as possible. The virtual trout select habitat with the objective of maximizing EM, which for trout near and above the minimum size of reproductive maturity (our age-1 and age-2 trout) is essentially the trout's expected probability of survival over a time horizon. Therefore, for age-1 and age-2 trout, we used survival rate over the 90-d simulation (number of trout alive at the end of the simulation divided by the initial number) as the population response variable. For age 0, EM encourages trout to seek habitat providing growth as well as survival, so for age-0 trout we used production (change in total biomass of the age class) as the response variable. Because survival is partially stochastic, we compared the flow scenarios using 20 replicate simulation runs that differed only in the random numbers used in mortality simulations.

At each flow rate, we evaluated the FP in each habitat cell for an average fish of each age class and evaluated the density of each age class from our statistical models of DEN. Overall DEN and FP for the total simulated stream is the area-weighted mean over all cells. If the density model predicted a cell to have negative density, we set the cell's DEN to zero.

Some of the simulated population responses to flow may occur because stream area increases with flow. To eliminate this effect, we (1) adjusted the initial trout abundance so all simulations started with the same trout density (number per total stream area), and (2) divided production of age-0 trout by stream area before analysis.

The high-flow experiment was identical to the low-flow experiment except that flows ranged from 2.0 to 6.0 m³/s at intervals of 1.0 m³/s. This experiment was designed to determine whether the habitat selection model is less successful at predicting population response under conditions less similar to those occurring when the data used to fit the statistical model of DEN were observed. (This experiment also typifies a common application of PHABSIM: using a model developed at low flow to assess the need for higher flow releases from existing dams.)

RESULTS

Relation between habitat quality and habitat selection

DEN models.—The statistical models of DEN included all four habitat variables as predictors of age-0 and age-1 trout density (Table 3), and had more nonlinear than linear terms. The model for age 0 included four interaction terms, but the age-1 model included only one (depth × FVS). For age-2 trout density, DHC and FVS appeared only in the interaction terms. The statistical models explained about half the variation in observed trout density, with r^2 between 0.45 and 0.54.

Variation in FP and DEN over depth and velocity.— Contour plots for each age class (Fig. 1) compare how FP and DEN vary over wide ranges of depth and velocity, for trout with access to nearby hiding cover and velocity shelter for feeding. For each age class, there are qualitative differences between FP and modeled DEN. For age-0 trout, FP is highest at high depths, yet DEN is greatest at low depths and zero in the range where FP is highest. For age-1 trout, FP is highest at low to intermediate velocity and high depth, while DEN peaks at intermediate depth and increases continuously with velocity. Similarly, FP for age-2 trout is highest at low to intermediate velocity and high depth, but DEN increases continuously with velocity and depth. (These plots are not comparable to PHABSIM ''preference criteria'' because of differences between our habitat modeling methods and those typically used in PHABSIM. Especially, we use cell-average velocity and treat velocity shelter as a separate variable, whereas PHABSIM criteria use velocities observed at the fish's exact location.)

Habitat selection as an indicator of habitat quality.—The fish densities observed from IBM habitat cells have little relation to FP in the same cell (Fig. 2).

TABLE 3. Habitat selection models.

Parameter	Parameter values		
	Age 0	Age 1	Age 2
Intercept	4.58	0.212	0.00431
Depth	0.00606	0.0115	−0.000585
ln(Depth + 0.5)		−0.152	
(Depth)^2	−0.0000218	0.0000586	0.0000138
Velocity	−0.00661	0.000408	
(Velocity)^2	0.0000425		3.96×10^{-6}
DHC	−0.00154	−0.000445	
(DHC)^2	1.10×10^{-6}	4.75×10^{-6}	
FVS	−10.4		
ln(FVS + 0.5)	6.13	−0.156	
(FVS)^2	4.13		
Depth × velocity	−0.0000993		
Depth × DHC	9.77×10^{-6}		
Depth × FVS	−0.0105	0.00493	−0.000789
Velocity × DHC	7.82×10^{-6}		$−9.82 \times 10^{-7}$
Velocity × FVS			0.00168
Model statistics			
r^2	0.54	0.45	0.46
Adjusted r^2	0.50	0.42	0.44
Root MSE	0.19	0.09	0.04

Our first criterion for whether DEN is a good indicator of FP—whether cells with low densities consistently have low FP—is clearly not met. For all age classes, there are a number of cells with low or zero trout density but higher FP than many of the occupied cells. Our second criterion for DEN as an indicator of FP—whether cells with high observed densities consistently have high FP—is partially met. In general, cells with high DEN have high FP. However, for ages 0 and 1 many of the cells with highest density have FP well below the maximum. Finally, for none of the age classes is there a strong, positive relation between observed density and FP. Fig. 2 indicates that it would be risky to assume, for example, that habitat cells with highest density clearly have higher FP than cells with half (or even one third) the maximum density. For cells with nonzero density, the slope of FP with DEN is significant only for age-0 trout ($P > 0.5$ for age 1 and 2). However, age-0 density explains only 24% of the variation in FP and the slope is low.

To support the assumption that FP is proportional to DEN (e.g., that a 50% increase in DEN indicates a 50% increase in FP), there must be a linear relation between FP and density and FP must be zero when density is zero. Our results do not support such an assumption.

Our comparison of FP vs. DEN with trout abundance reduced by two-thirds (Fig. 3, left column) does not consistently confirm the assumption that habitat selection better reflects habitat quality at high densities. For age-2 trout, the relation between FP and DEN appears stronger at higher fish density (Fig. 2 vs. Fig. 3). At the reduced abundance, all age-2 trout occupied cells of equally high FP. However, for age-0 and age-1 trout, the relation between FP and DEN was, if anything, clearer at low abundance.

Similarly, we found little support for the assumption that habitat selection better reflects habitat quality when overall habitat quality is low (Fig. 3, right column). With high-quality pools removed, the relation between FP and DEN may be slightly stronger for age-2 trout (Fig. 3 vs. Fig. 2), but there was little qualitative change in this relation for other age classes.

Comparison of habitat quality and selection as predictors of population response

Low-flow experiment.—These experiments tested whether the areal mean FP and DEN could predict population response over a range of flows. The low-flow experiment examined flows near the flow at which DEN was modeled. Over these flows, age-0 trout production actually declines as FP and DEN increase (Fig. 4A, B). For age-1 and age-2 trout, there are strong, positive relations between survival and both FP and DEN (Fig. 4C–F). For both FP and DEN, the intercept of the relation is large (>0.6) for age-1 and age-2 fish, indicating that survival was not proportional to FP or DEN. Logically, we expect survival to approach zero as FP or DEN approaches zero, which would not occur if the relations in Fig. 4C–F were extrapolated linearly back toward zero—evidence that population response is not linear with respect to these habitat measures over wide ranges.

High-flow experiment.—The second experiment produced qualitatively different results. When stream flow was varied from 2.0 to 6.0 m³/s, population response was positive with respect to FP for age-0 and age-2 trout (Fig. 5A, E). However, population response was negative with respect to DEN for these two age classes (Fig. 5B, 5F). For age-1 trout, population survival was not clearly related to either FP or DEN (Fig. 5B).
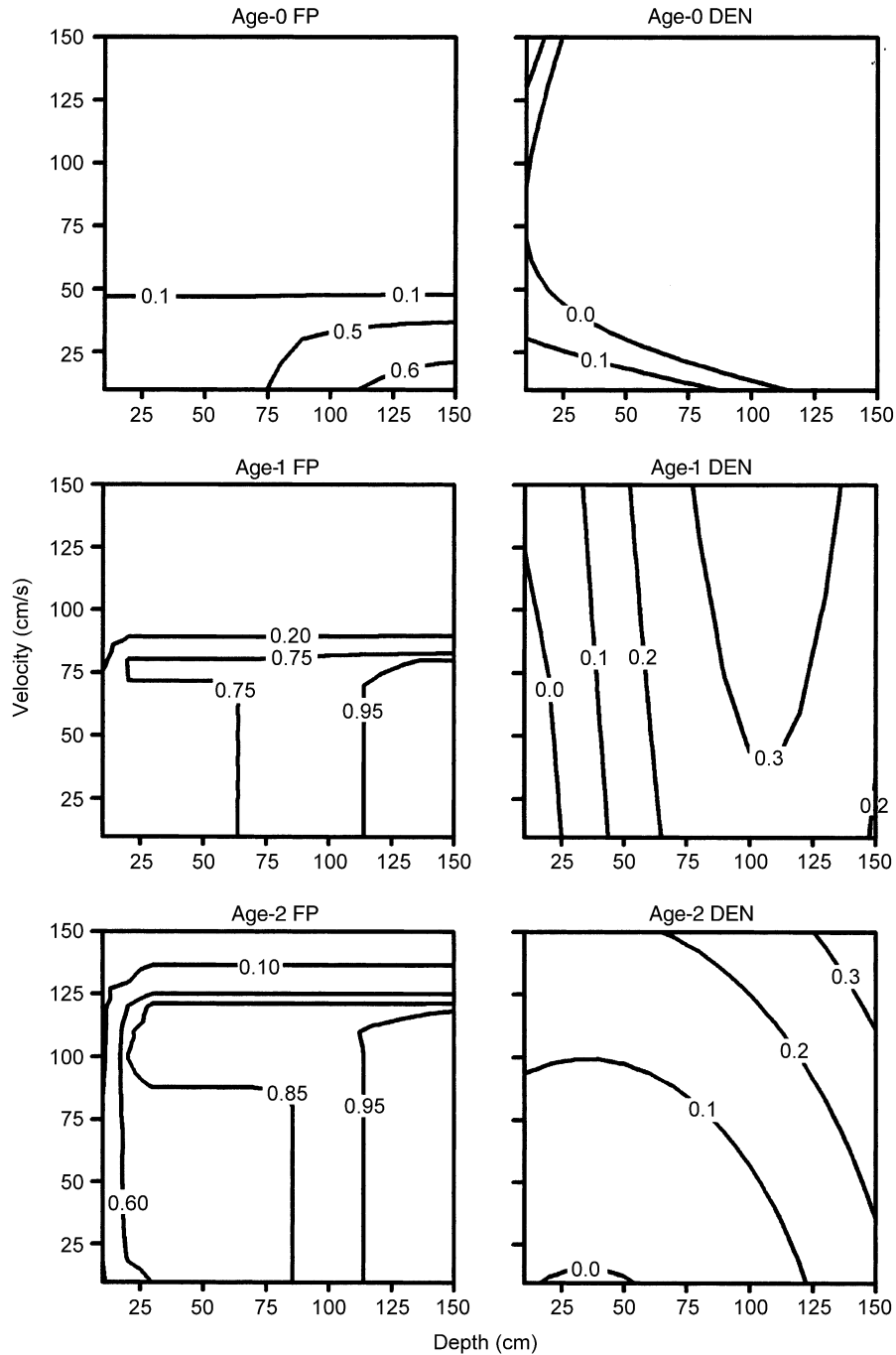
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FIG. 1. Variation in FP (left column) and DEN (right column) over depth and velocity for average age-0, age-1, and age-2 virtual trout. The value of DHC is 100 cm, and trout have access to velocity shelters (FVS = 0.5).

DISCUSSION

Relation between habitat selection and habitat quality

Our analyses confirm the two "fatal flaws" of habitat selection modeling identified by Garshelis (2000), especially the riskiness of assuming that observed habitat selection reflects the intrinsic quality of habitat. With habitat quality defined as the fitness potential a habitat cell offers an individual in the absence of competition (FP), and fish actively selecting the habitat that offers highest available fitness potential, we found no strong relation between FP and DEN. When we used trout density observed from the virtual population to fit statistical models of DEN, we found substantial differences in how modeled DEN and FP vary over habitat
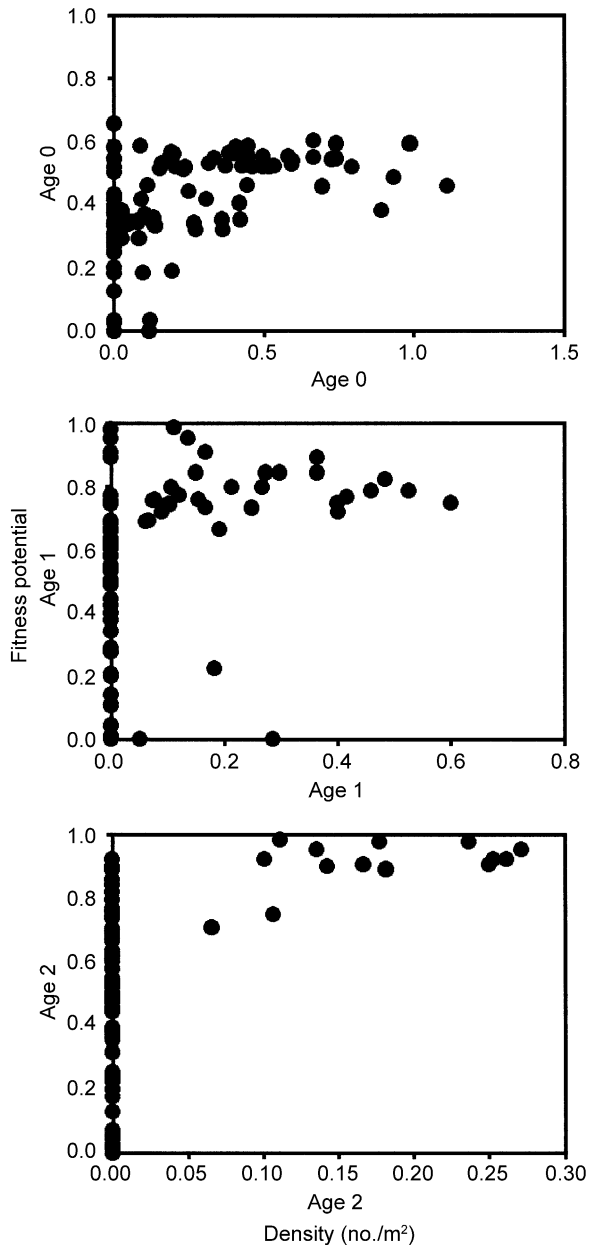
FIG. 2. Relation between FP and DEN observed in the IBM on one day, for age-0, age-1, and age-2 trout. Each point represents one cell, with DEN equal to the number of fish in the cell divided by cell area.

gradients (Fig. 1). In a direct comparison of FP and observed fish density in each habitat cell (Fig. 2), cells with highest densities generally had relatively high FP, but for none of the age classes was there a strong, positive relationship supporting the assumption that an increase in DEN reflects an increase in FP. These results were consistent even when fish abundance and overall habitat quality were strongly altered. These differences between FP and modeled DEN occurred despite com-

plete knowledge of the scales and variables driving habitat selection.

The simplest explanation for the lack of close, positive relations between FP and DEN is competition for food and velocity shelters. A cell offering high FP in the absence of competition may actually offer low fitness potential after larger fish have consumed the cell's food or velocity shelter space. Most fish are forced to use cells with lower quality than they would in the absence of competitors (as observed in real trout by Gowan and Fausch 2002). Because the largest fish are the best competitors and use the most resources per individual, competition tends to produce low densities of large fish in the highest quality habitat.

However, competition does not explain the weak relation between DEN and FP observed even among age-2 trout, the dominant competitors. We also identified the following seven reasons why density was sometimes low in habitat with high fitness potential, yet habitat with relatively low fitness was sometimes occupied; and why there was no positive linear relation between FP and DEN. These reasons also apply to real animal populations in which habitat selection is driven by spatial variation in growth potential and mortality risk and individuals compete via dominance hierarchies.

Unused habitat.—The number of age-2 trout appears too small to use all the available high quality habitat. This effect (also noted by Tyre et al. 2001) can explain why some patches of high quality habitat have low animal density. Factors other than habitat may commonly keep abundance too low for all high quality habitat to be occupied.

Individual variability.—The fitness value of habitat can vary sharply with animal size (compare among ages in Fig. 1). Individual variation in size and, therefore, the fitness benefits of various habitat types, undoubtedly introduces variability in the relation between density and fitness potential.

Discontinuous nature of habitat selection.—Animals do not necessarily have a continuous gradient of habitat quality to select from. Once a high quality patch is fully occupied by dominant individuals, the next-most-dominant individuals are forced to occupy the patch with next-best quality, whether that patch offers fitness 5% less or 50% less than that of the best patch.

Nonlinear relations between habitat quality and resource availability.—Habitat with highest food availability does not necessarily provide highest fitness. An individual can use only a limited amount of food, so increasing food availability does not necessarily result in higher fitness, but it can increase the density of animals a patch can support. Consider two patches, the first with low mortality risks but food sufficient only for one individual, and the second with higher mortality risks but much more food. The first patch provides higher fitness for the first individual, offering sufficient food and lower risks. However, additional individuals
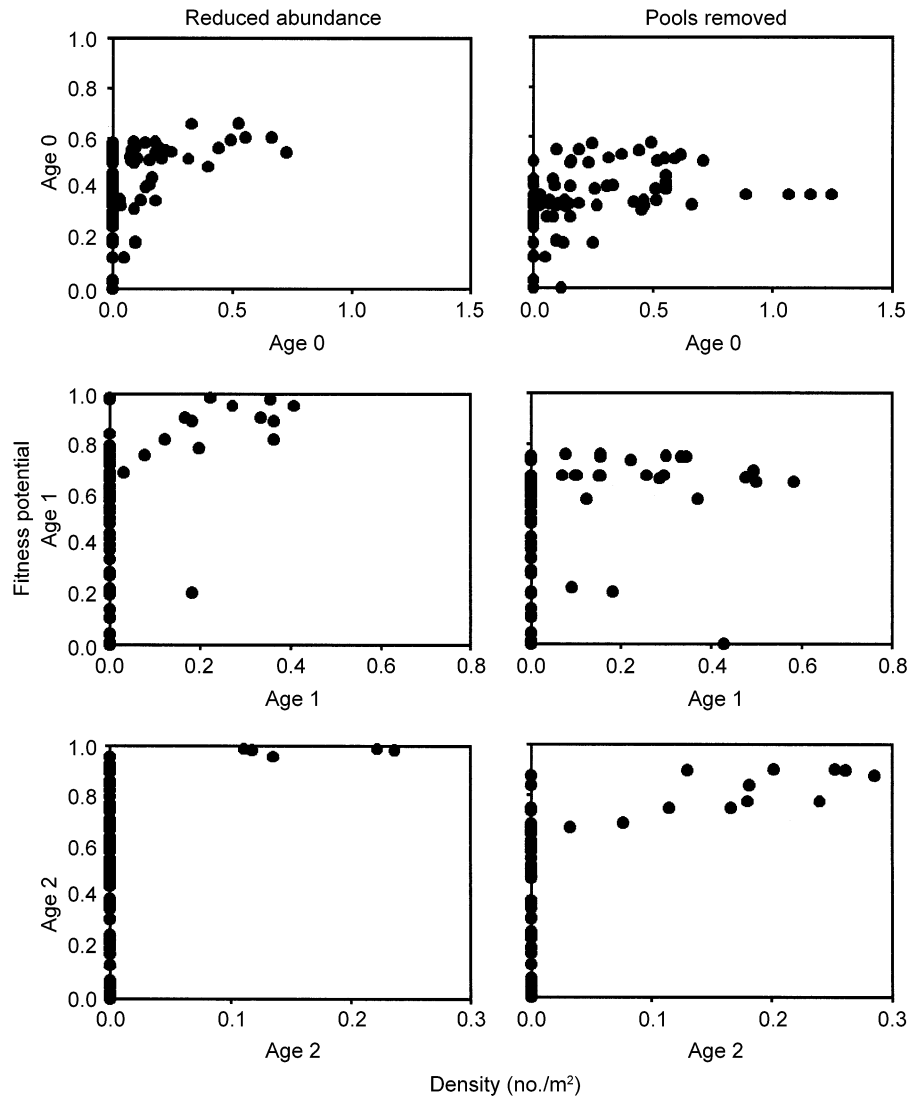
Fig. 3. Relation between FP and DEN observed in each cell, with virtual trout abundance reduced by two-thirds (left column) and with deep pools removed from the modeled habitat (right column).

will use the second patch (because no food remains in the first), and at higher densities than in the first patch (because food is available for more animals). Such non-linear relations between resource availability and fitness potential can cause density to vary widely even over narrow ranges of habitat quality.

Variation in food "catchability" or quality.—Habitat conditions that make food easy to catch can offer higher fitness to the first individuals while supporting lower densities. For example, a cell of low velocity allows a drift-feeding trout to catch food over a large area. A few trout may consume all the food, providing them with high fitness. In contrast, a cell with the same amount of food but with higher water velocity limits each fish to feeding over a smaller area. The high-velocity cell provides lower fitness to each fish because the difficulty of catching food limits food intake, but

fish density can be higher because each fish uses up less of the available food. Similar effects have been observed in mammals. Hobbs and Swift (1985) found that deer habitat with small amounts of high quality food provided higher fitness but supported lower densities than other habitat. Powell (1994) found that fishers spent little time in the habitat where they caught their primary prey, the easily caught porcupine, and more time in habitat where they hunted hare, which is less important to fisher diet but more difficult to catch. Consequently, the fishers were more likely to be observed in the lower-quality hare habitat.

Uncontested resources.—Relations between habitat quality and selection can be confounded by resources that are abundant and therefore have little effect on density (Garshelis 2000). In the virtual trout population, velocity shelters for feeding and hiding cover have
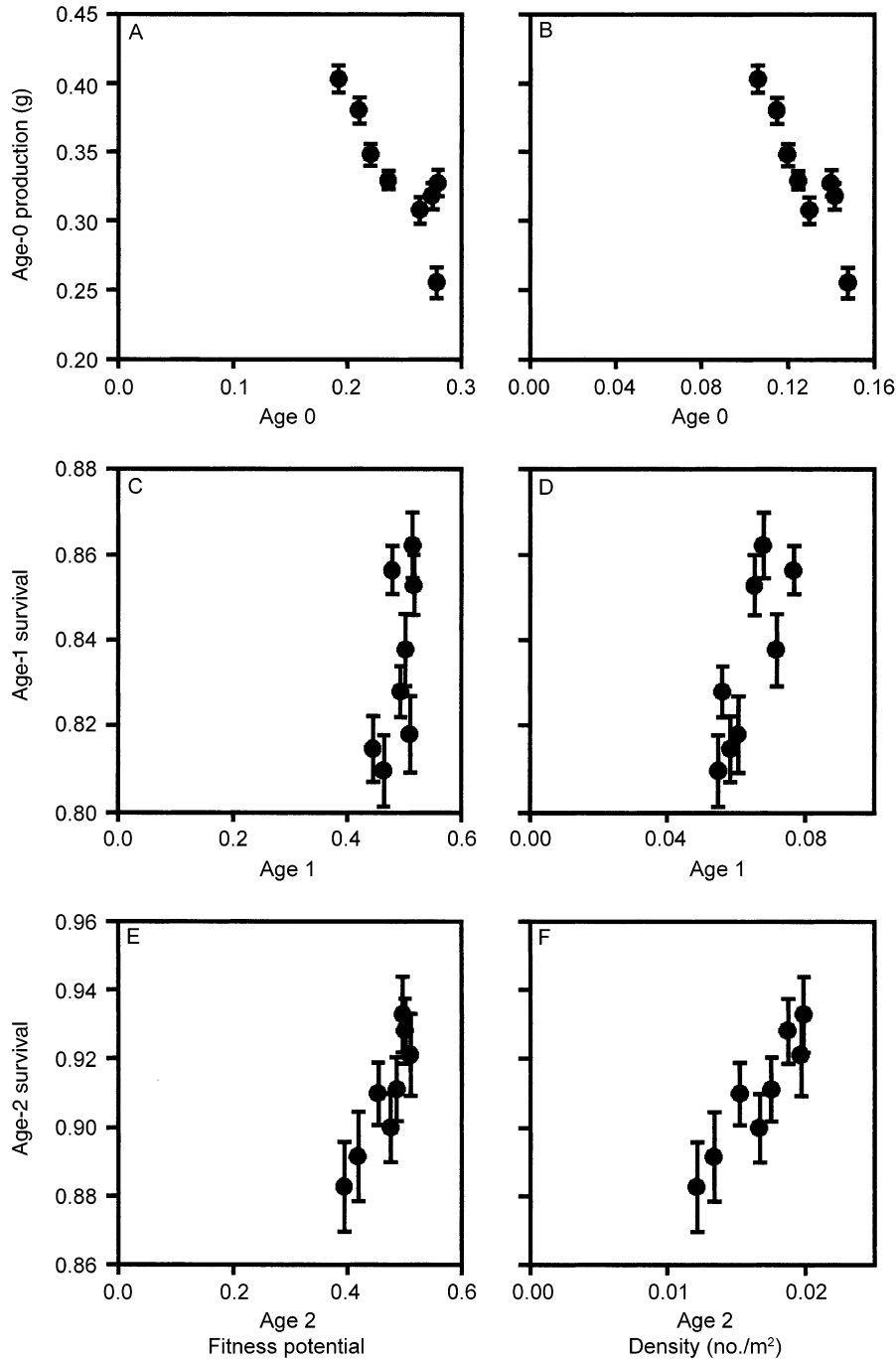
FIG. 4. Relation between habitat and virtual population response over 90 d in the low-flow sensitivity experiment. Habitat variables are areal average FP (left column) and areal average DEN (right column). The population response variable for age-0 trout (A and B) is biomass production per area (g/m^2). For age-1 (C and D) and age-2 (E and F) trout, the population response variable is the survival rate. Population response is mean of 20 replicate runs; error bars represent ± 1 SE.

strong effects on fitness. However, velocity shelter space is relatively abundant and there is no competition for hiding cover, so fish density is much more likely to be limited by food availability. Uncontested resources may have important effects on fitness benefits offered by a habitat patch, but animal density in the patch is more likely limited by resources like food that individuals deplete.

Limited knowledge of the habitat.—While mobile animals may explore large areas over their lifetime, they have limited knowledge of current conditions in surrounding habitat, especially for short-term habitat se-
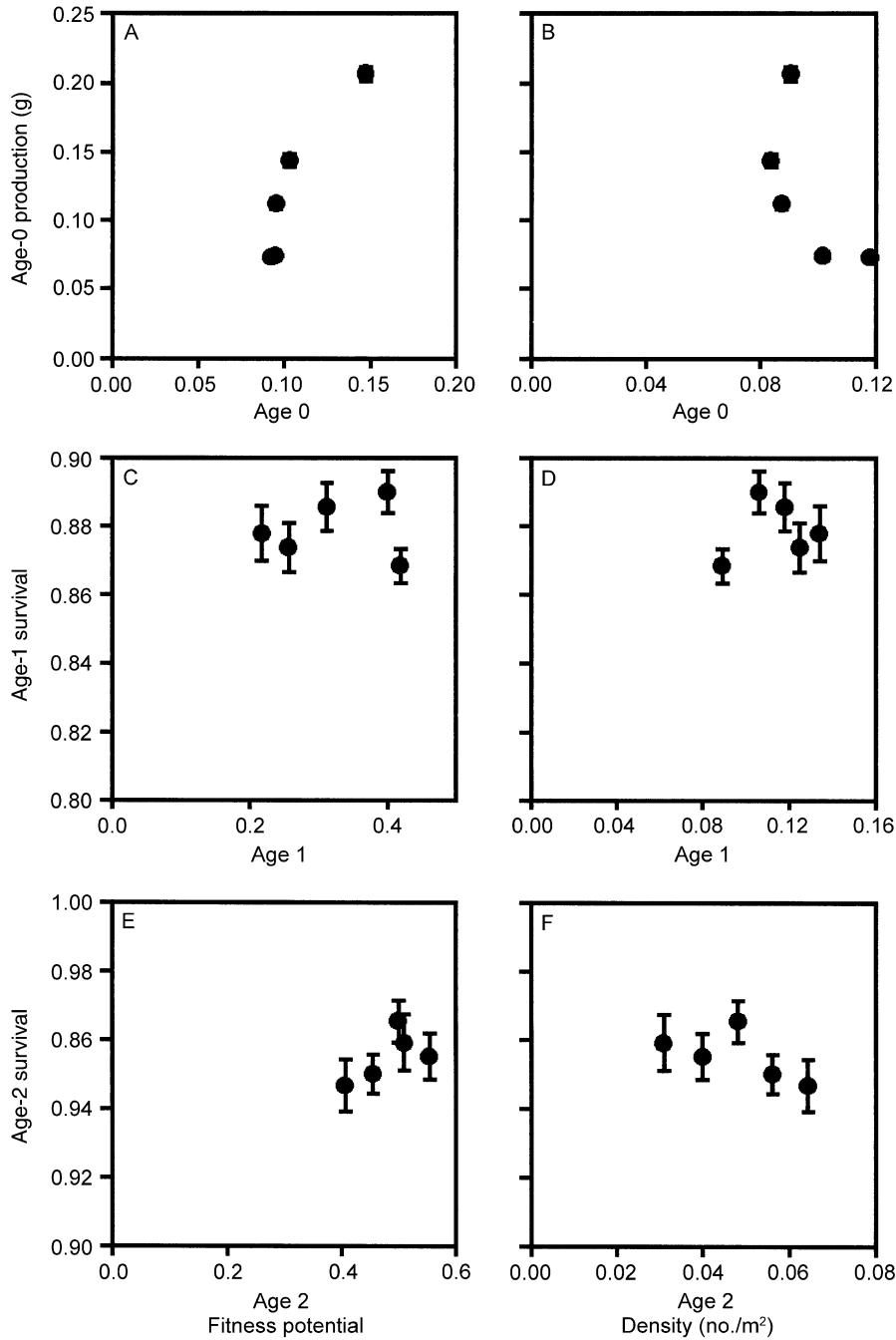
FIG. 5.   Relation between habitat and virtual population response in the high-flow sensitivity experiment. Figure format is identical to that of Fig. 4.

lection decisions. Therefore, it is possible that an an- imal may not use habitat offering higher quality simply because the habitat is too far away to know about with adequate certainty.

In addition to the above ecological explanations, the different trends in FP and DEN over habitat variables observed in Fig. 1 may result in part from statistical uncertainty in our models of DEN. Uncertainty is es-

pecially a concern in modeling DEN at high depth and velocity: in our virtual population (as in real streams), fewer observations are available at habitat extremes.

Artifacts of cell size are a potential confounding fac- tor in the relation between FP and DEN that appear not to be important in this study. Consider two cells in which conditions are such that 2 m² of cell area is needed to support each trout. If one cell has an area of

3.5 m^2, it can support only one trout, with a resulting density of 0.3 fish/m^2. If the second cell has an area of 4.1 m^2, it can support two trout, at a density of 0.5 fish/m^2. The apparent difference in density is an artifact of cell area. Such artifacts could induce noise in the relation between FP and DEN, and tend to make density of large fish lower in smaller cells. To determine whether cell size has an important effect on this relation, we included cell size as well as observed density in stepwise regressions of FP. These analyses used the data presented in Fig. 2, including only cells with non-zero densities. Cell size did not enter the stepwise regression as a significant covariate for any of the three age classes, indicating that artifacts of cell size are not an important cause of the weak relation between trout density and FP.

We expect that the relationship between habitat quality and selection varies with the scale used in the comparison. In our study, DEN and FP were evaluated at the same scale that individual animals use in selecting habitat, so competition among individuals is an important complicating factor. At much larger scales, animal density may be more closely related to changes in habitat quality (e.g., to large-scale variation in availability of food and hiding cover; Morris 1987).

Ability of FP and DEN to predict population responses

One important result of the low-flow sensitivity experiment, in which we simulated small changes in habitat by varying stream flow, is that the response of age-0 trout was opposite that predicted by both FP and DEN. There is sufficient overlap in habitat between age-0 and older trout that providing higher average FP (or DEN) for age-0 trout actually reduced their production by increasing competition with larger trout. This result suggests that for animals with low ability to compete for habitat, habitat selection models such as PHABSIM can be misleading predictors of responses to habitat alteration.

For age-1 and age-2 trout in the low-flow sensitivity experiment, population response was positively related to both FP and DEN, with DEN explaining more variation in population response than FP. However, the high-flow experiment showed that DEN can be a misleading predictor of population response to more than minor changes in habitat availability: the age-2 survival rate followed the trends indicated by FP, not DEN. This result indicates that the common practice of using habitat models (such as PHABSIM ''suitability criteria'') at different sites or over wide flow ranges can incorrectly predict even the direction in which population responds to habitat change.

That DEN more closely correlated to population response than FP in the low-flow experiment yet incorrectly predicted population trends in the high-flow experiment is not surprising. In the virtual trout population and, presumably, in populations of real animals

that are good at finding habitat that provides high fitness, habitat selection is an emergent property of the habitat quality function (how the fitness potential of an individual animal varies with habitat characteristics), habitat availability (the characteristics of the available habitat patches), the number and characteristics of the individual animals, and how the animals compete. In the low-flow experiment, we held all these factors constant except for making small changes in habitat availability, so it is not surprising that the DEN observed at a flow of $0.44 \text{ m}^3/\text{s}$ was a good predictor of habitat use and trout production over flows of $0.1\text{–}1.0 \text{ m}^3/\text{s}$. The high-flow experiment, however, made larger changes in habitat availability. At least three factors explain why modeled DEN was a poor predictor of population response under different habitat conditions.

First, we extrapolated the DEN models beyond the data ranges used to fit them. Extrapolation error was especially likely for age-1 and age-2 fish, for which DEN increases with velocity (Fig. 1).

Second, if we consider habitat selection as emerging from habitat availability and other factors, we expect the relation between DEN and habitat variables to change as habitat availability is altered. In fact, when we model DEN from habitat selection observed in the virtual trout at a high flow ($4.0 \text{ m}^3/\text{s}$), we find it differs from the original DEN model (Fig. 6; compare to Fig. 1). Compared to density modeled at $0.44 \text{ m}^3/\text{s}$, age-0 density at the higher flow peaked at greater depth. This shift in peak density occurs simply because more deep habitat is available: fitness for age-0 trout increases with depth (Fig. 1), and at higher flow there is not only more deep habitat, but more deep habitat unoccupied by larger trout. Density of other age classes changed but retained similar general trends over depth and velocity.

Third, the importance of habitat as a factor determining population response can change as habitat availability changes. Age-1 and age-2 survival varied over a much smaller range in the high-flow experiment, indicating that habitat had less effect at the higher flows. A simple mechanism provides a likely explanation: at higher flows, more food is available in most cells, so more fish can inhabit the cells offering lowest mortality risk. With fewer fish inhabiting marginal cells, the population is less subject to habitat effects. In fact, we observed that the density of fish in occupied cells was higher at higher flows, especially for age-1 trout.

Even though population response was correlated with DEN in the low-flow sensitivity experiment, DEN models are not often useful for predicting population response to habitat alteration. In no case was population response proportional to DEN (or FP), which means that the slope and intercept of the relation between average DEN and population response must be known to predict population response from a change in the availability of selected habitat. However, the slope and
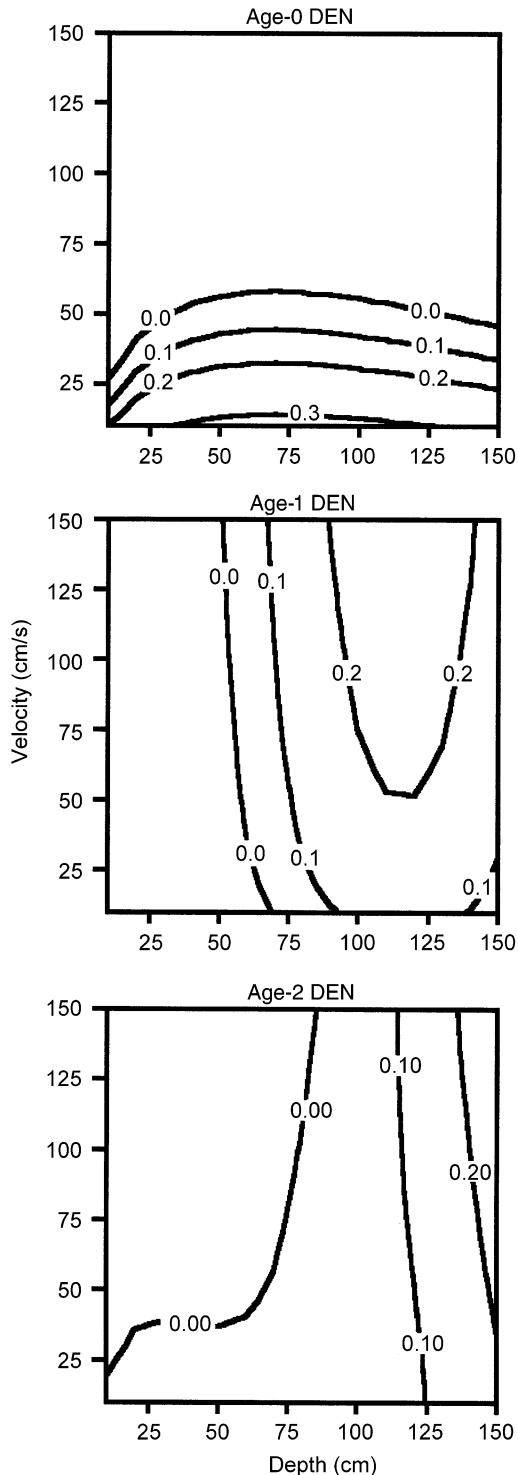
FIG. 6. Habitat selection in the virtual trout population at high flow. This figure is identical to the right column of Fig. 1, except that DEN was modeled from observations taken at a flow of 4.0 m³/s. Mean density (fish/m²) is constant between Fig. 1 and this figure.

intercept can only be known by manipulating habitat and observing population response, which makes habitat modeling unnecessary.

Limitations of habitat modeling

In our experiments, we encountered the following problems that appear to be inherent limitations of habitat modeling as a way to predict consequences of habitat alteration.

1) Relations between habitat selection and habitat variables can be too complex to model well statistically. Even with uncertainties eliminated by using a virtual population, we could explain only half the variation in density (Table 3). Similarly, Hirzel et al. (2001) and Tyre et al. (2001) found high levels of unexplained variation in statistical models of habitat occupancy fit to synthetic data with no measurement error. One cause of this complexity is that cells with very different habitat characteristics can provide equal fitness (Fig. 1).

2) Factors other than habitat have important effects on population response. Competition among individuals can strongly affect population response, and competition can create complex secondary effects of habitat alteration such as the negative relation between DEN and age-0 trout production observed in our sensitivity experiment. In our high-flow sensitivity experiment, FP and DEN had little or no effect on survival of some age classes.

3) Observing habitat selection over sufficient ranges and combinations of habitat variables is difficult, and extrapolating habitat selection models is difficult to avoid. Hundreds of unique observations are needed to capture all combinations of even a few variables. Typically a habitat model is fit to data collected under one set of conditions (e.g., one stream flow), making extrapolation unavoidable when applying the model to any other conditions.

4) The most dominant animals are often of greatest interest and, because they have high fitness, their habitat selection may be important to model. However, the most dominant animals are observed least often and in the smallest range of habitat because they are rare and occupy only the best habitat.

5) Habitat selection (and the fitness value of habitat to individuals) varies over time, yet habitat selection models do not consider time. For example, habitat selection by trout varies with such factors as temperature and day length (Vondracek and Longanecker 1993), food availability (Wilzbach 1985), fish size (Everest and Chapman 1972), and the density of competitors and predators (Fausch and White 1986, Brown and Moyle 1991, Rosenfeld and Boss 2001). The dependence of habitat selection on factors that change over time makes habitat selection models difficult to use or test. We also do not know the time scale over which observed density–habitat relations are appropriate—does density vary with habitat over days, months, or

years? The typical approach to using these models is the one we were forced to use in the sensitivity experiments: unrealistically assuming that all factors affecting habitat selection are constant.

6) Habitat selection models typically predict response variables of limited or unclear meaning. Our DEN model predicts the density of trout in each habitat cell; for comparison to population-level responses, we had to aggregate the predicted density in each cell into a predicted response over the entire stream reach. We encountered such issues as (1) whether to assume there is an integer number of fish in each cell or whether to assume, for example, that two cells that each are predicted to contain 0.5 fish total to contain one fish; and (2) whether negative predicted densities should be treated as zero fish per cell. Likewise, we assumed the spatial mean of FP as an aggregate measure of habitat quality, whereas other measures (e.g., the total area of cells having high fitness potential) might be more appropriate. These kinds of unsupported assumptions are required to obtain testable predictions from habitat models. Furthermore, density predicted from a DEN model provides no information on important variables like population production, sustainable harvest rate, or probability of extinction.

Conclusions

Our experiments evaluated the potential usefulness of habitat selection modeling for assessing the fitness potential provided by habitat and for predicting population responses to habitat alteration. In our virtual trout population, only two habitat selection modeling assumptions were supported:

1) Highly selected habitat usually has relatively high individual fitness value; and

2) Population response varies positively with the availability of selected habitat *if* the assessment involves only small changes in conditions (e.g., habitat availability, animal density) from those used to model habitat selection *and if* the animals are not subject to strong competition for their selected habitat.

A number of habitat modeling assumptions were contradicted by our experiments. We conclude that:

1) Unoccupied habitat with low selection cannot be assumed to provide low fitness potential.

2) The fitness potential of habitat cannot be assumed to vary with habitat selection—a gradient in observed density does not necessarily indicate a gradient in habitat quality.

3) The ability of habitat selection to represent fitness potential cannot be assumed to improve when animal density is high or when overall habitat quality is low.

4) Population response cannot be assumed to vary positively with the availability of selected habitat for animals that are subject to strong competition for habitat (e.g., juveniles).

5) Population response cannot be assumed to vary positively with the availability of selected habitat when conditions (habitat availability, population density, competitive conditions) are substantially different from those used to model habitat selection.

6) Population response to habitat alteration cannot be quantitatively predicted by habitat selection modeling, even if population response is linear with the availability of selected habitat. The slope and intercept of population response with respect to availability of selected habitat varies unpredictably among sites.

Given our conclusion that little can be inferred about the fitness value of habitat from observed habitat selection, we join previous authors (e.g., Hobbs and Hanley 1990) in recommending that habitat selection studies be supplemented with mechanistic approaches to understanding the fitness value of habitat. Learning how key fitness elements like growth, survival, and reproductive success depend on habitat characteristics seems more likely to produce general and reliable results than is habitat selection modeling alone.

However, we also conclude that there are inherent limitations to the overall approach of predicting population changes from habitat alone. This study illustrates that even complete and accurate knowledge of how individual fitness varies with habitat characteristics is inadequate for predicting population response in many situations. Models like IBMs that represent individual variation and competition in addition to habitat effects, and consider temporal variation, may be necessary to capture the key mechanisms driving population response to major changes in habitat. For stream salmonids, neither habitat-based nor individual fitness-based models have been tested convincingly, with predicted population responses to habitat alteration being developed and then tested against field data.

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