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Ecological Modelling 123 (1999) 73-89

ECOLOGICAL MODELLING

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Movement rules for individual-based models of stream fish

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Received 22 September 1998; received in revised form 23 April 1999; accepted 10 May 1999

Abstract

Spatially explicit individual-based models (IBMs) use movement rules to determine when an animal departs its current location and to determine its movement destination; these rules are therefore critical to accurate simulations. Movement rules typically define some measure of how an individual's expected fitness varies among locations, under the assumption that animals make movement decisions at least in part to increase their fitness. Recent research shows that many fish move quickly in response to changes in physical and biological conditions, so movement rules should allow fish to rapidly select the best location that is accessible. The theory that a fish's fitness is maximized by minimizing the ratio of mortality risk to food intake is not applicable to typical IBM movement decisions and can cause serious errors in common situations. Instead, we developed fitness measures from unified foraging theory that are theoretically and computationally compatible with individual-based fish models. One such fitness measure causes a fish to select habitat that maximizes its expected probability of survival over a specified time horizon, considering both starvation and other risks. This fitness measure is dependent on the fish's current state, making fish with low energy reserves more willing to accept risks in exchange for higher food intake. Another new measure represents the expectation of reaching reproductive maturity by multiplying expected survival by a factor indicating how close to the size of first reproduction the fish grows within the time horizon. One of the primary benefits of the individual-based approach is avoiding the need for simplifying assumptions; this benefit is best realized by basing movement decisions on such simple, direct measures of fitness as expected survival and expected reproductive maturity. © 1999 Elsevier Science B.V. All rights reserved.

Keywords: Individual-based model; Fish; Foraging; Growth; Movement; Risk; Survival

1. Introduction

Individual-based models (IBMs) of fish populations are becoming an important tool for research and for supporting environmental management

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PII:S0304-3800(99)00124-6

decisions. Early IBMs of fish generally neglected spatial variation in habitat and fish movement: the eight papers reviewed by Van Winkle et al. (1993) included no spatially explicit models, although Rose and Cowan (1993) identified the need to simulate spatial variation in habitat. More recently, several spatially explicit models have been developed. In the process of developing software for spatially explicit fish IBMs and formulating a model for stream trout (Railsback et al., 1999), approaches for simulating fish movement in spatially and temporally varying habitat were reviewed and developed.

Movement rules are a critical component of spatially explicit IBMs because movement is an essential method used by fish to adapt to changing environmental and competitive conditions. Fish move to improve food intake and growth (Fausch, 1984; Hughes and Dill, 1990; Hughes, 1998), reduce vulnerability to predation risks that vary with fish size and environmental conditions (Harvey, 1991; Milinski, 1993; Tabor and Wurtsbaugh, 1991), seek shelter during high flows and avoid stranding as flows decrease (B.C. Harvey, unpublished data; Pert and Erman, 1994; Matheney and Rabeni, 1995), and avoid competition with dominant fish (Hughes, 1992). Models must be able to simulate these movements accurately if they are to be useful for predicting population responses to changes in habitat, mortality rates, or competition. Verifying that movement rules produce realistic movement decisions is an example of the model evaluation steps needed for IBMs to be accepted for decision-making (Bart, 1995) and research.

Movement rules include departure rules that determine when a fish leaves its current location and destination rules used to select a new location. Departure and destination rules are typically based on some measure of a fish's potential fitness and how this fitness measure varies among potential locations (Clark and Rose, 1997; Van Winkle et al., 1998). These rules are designed to move fish to habitat that provides high fitness, under the assumption that fish select their habitat to maximize fitness. Consequently, the fitness measure's formulation is a very important component of movement rules.

The fish behavior and modeling literature does not provide clear guidance on the design of movement rules, nor does it thoroughly analyze the consequences of using alternative rules. Foraging theory and experiments to test this theory generally include simplifying assumptions that are not met in most fish IBMs (Gilliam and Fraser, 1987; Gotceitas, 1990; Gotceitas and Godin, 1991). Little attention has been given to the assumptions included in movement rules and the likelihood and consequences of violating these assumptions.

The objectives of this paper are to identify the movement rules and fitness measures that have been used in stream fish IBMs; identify the assumptions underlying these rules; and analyze the implications of these assumptions and their violation. This information provides a basis for designing movement rules for future IBMs. Rules used in the models of Clark and Rose (1997) and Van Winkle et al. (1996, 1998) and in a new model (Railsback et al., 1999) are examined. This paper's focus is on IBMs for stream fish with a daily time step, spatial resolution ranging from habitat units (pools, riffles, etc.) to small patches of several square meters, and dynamic habitat conditions. Food intake potential, metabolic costs, and mortality risks vary over space and time in such models. However, the conclusions may be of interest to designers of a variety of IBMs.

2. Methods

We identified the departure and destination rules of all the spatially explicit stream fish models found in the literature (Van Winkle et al., 1996, 1998; Clark and Rose, 1997) and from the model here (Railsback et al. 1999). The expected performance of these rules was evaluated by comparing them to observations of fish movement and habitat selection reported in the literature.

The fitness measures used by Clark and Rose (1997) and Van Winkle et al. (1996, 1998) were also examined, we developed our own measures. These fitness measures are used in movement rules to rate alternative destinations. The theoretical basis of fitness measures and the assumptions used in developing them were identified. How well

these assumptions match those used in typical IBMs and the likelihood and consequences of the assumptions being violated were evaluated. One evaluation method was graphing the value of each fitness measure over wide ranges of growth rate and mortality risk so the broad fitness `field' could be visualized. A number of practical modeling concerns, both positive and negative, with the use of each fitness measure were also identified.

3. Results

3.1. Departure rules

The IBMs of Clark and Rose (1997) and Van Winkle et al. (1998) use departure rules that cause a fish to search for new habitat when its fitness at its current location is less than the average of its fitness over several preceding days. This approach of inducing movement when fitness declines has the drawback of not promoting movement to *improve* fitness: as long as a fish's fitness is not declining, these rules do not cause fish to seek sites with higher fitness even if such sites are nearby.

These departure rules do not reflect the evidence that many fish exhibit awareness of their surrounding environment and readily occupy better habitat when it is available (Gowan et al., 1994; Noda et al., 1994; Young, 1994; Gowan and Fausch, 1996; Young, 1996; see also the literature summary of Matthews, 1998, pp. 448-450). For example, radio tagging studies have shown that northern hog suckers (Matheney and Rabeni, 1995) and cutthroat trout (B.C. Harvey, unpublished data) moved back and forth between mid-channel feeding stations and velocity shelters on the channel margin as flows fluctuated. Under the departure rules of Clark and Rose (1997) or Van Winkle et al. (1998) a fish that was maintaining adequate growth (or steady poor growth) would not attempt to move even if better habitat was available nearby. A sudden decrease in fitness conditions (e.g. due to high flows) would trigger movement (e.g. to velocity refuges), but improvement in conditions would not trigger movement and fish may not find their way to the best habitat available in their immediate vicinity.

A simple departure rule was developed that reflects a fish's knowledge of its surroundings. On each day, each fish examines all the habitat within a specified maximum movement distance (this distance is discussed in Section 3.2). If any of this habitat provides a better value of the model's fitness measure, then the fish moves. Under this rule, each fish finds the best available habitat each day, whether conditions in the stream are improving or declining. One practical drawback of this departure rule is that it is more computationally intensive, requiring each fish to evaluate its potential fitness in each of the locations within the maximum movement distance, at each daily time step. This departure rule assumes fish have no behavioral site fidelity, so the rule may not be appropriate for fish that clearly demonstrate such behavior.

3.2. Destination rules

In the IBMs of Clark and Rose (1997) and Van Winkle et al. (1998), destination habitat is selected using combinations of chance, exclusion of destinations that do not meet some habitat requirements, and optimization of some variables.

The model of Clark and Rose (1997) assumes that a fish randomly picks a movement direction (upstream or downstream) and then examines locations that are accessible considering barriers (due to high velocity or cascades), a minimum depth requirement, a maximum slope limit, and a maximum movement distance. The fish then chooses the accessible location that has the fewest fish bigger than itself. In this model, food intake is dependent on competition with larger fish within a habitat location, as well as on depth and velocity. (The Clark and Rose model uses food intake as the fitness measure in its departure rule.) Therefore, this destination rule optimizes one variable affecting food intake (competition with other trout) but does not consider the other variables affecting intake. (This destination rule may inadvertently tend to send fish to poor habitat: fish should be more dense where food availability is high, so moving to where fish densities are

lowest may send fish to sites where food availability is low.)

The model of Van Winkle et al. originally was formulated with random selection of destinations, under the assumption that a sequence of random moves would eventually lead a fish to good habitat (Van Winkle et al., 1996). When a fish moved in this model, its destination was the first location, selected randomly from among nearby locations, where depth and velocity fell within specified tolerance ranges. However, tests of the model showed that these random destination rules did not allow fish to keep up with rapidly changing stream habitat. In combination with a departure rule that uses a fitness measure averaged over several days, random destination selection did not give fish the ability to find good habitat in streams where the spatial distribution of food intake potential, risks, and competing fish could have major changes in as little as one time step. Therefore, Van Winkle et al. reduced the degree of randomness in the destination rule by letting fish repeat the movement process several times to simulate a within-day search for good habitat (Van Winkle et al., 1998).

Two concerns with these approaches were identified. First, random selection of movement destinations does not reflect the evidence (cited above) that fish are aware of their environment over a significant area and are, therefore, unlikely to move randomly within the area they are familiar with. Instead, it seems more realistic to assume fish are capable of making informed choices among locations within at least a limited distance.

Second, random (or partially random) destination rules require several iterative moves before a fish can be expected to find the best available habitat. For models with dynamic habitat, and especially when combined with a departure rule based on multiple-day average fitness, such destination rules can unrealistically prevent fish from making good habitat choices for long time periods. With random destination rules, it is quite possible for a fish to move to a location where conditions are worse than those at its previous location. The within-day search approach of Van Winkle et al. (1998) is a way of addressing this problem by essentially using a smaller time step for movement than for habitat variation

In the model we are developing, a nonrandom destination rule is used: it is assumed fish thoroughly explore the habitat known to them and select the location within it that offers highest fitness. (In this model, fitness depends on food intake and metabolic costs, which are affected by competition with more dominant fish at the same site; otherwise the presence of other fish in the destination rule is not considered.) It is assumed fish select destinations that maximize the model's full definition of fitness, compared to the Clark and Rose (1997) approach of selecting destinations that optimize only one component of fitness (competition with other fish). This approach may overestimate a fish's ability to explore its vicinity and select the best location, but giving fish the ability to actively seek out good habitat is in better agreement with the available evidence than is partially random selection of destination. This rule also avoids the possibility of fish moving to a destination that is less suitable than their original location.

A key aspect of this approach is modeling how much habitat is known to each fish and therefore provides potential movement destinations. Given the authors' incomplete understanding of how trout search habitat, the first departure rule being tested simply lets each fish consider all the habitat within a specified maximum movement distance. This maximum movement distance increases with fish length and can be estimated from the literature on fish movement. The evidence that some trout periodically explore long distances (Gowan et al., 1994) could be simulated by making the maximum movement distance a stochastic function, with the probability of considering distant locations on any day lower than the probability of considering closer locations. The evidence that movement tendencies vary among individuals (Gowan and Fausch, 1996) could be simulated by making maximum movement distance partially dependent on a `genetic' trait of individuals. However, some variation in movement tendencies is expected to emerge from our movement rules naturally (e.g. large fish are likely to move longer distances to find sites with food intake sufficient

to maintain their fitness); such variation should not be forced into the model unless it: (a) is clearly important; and (b) does not result from the processes already simulated in the model.

3.3. Fitness measures

Fitness measures are the variables used in departure and destination rules to represent the quality of specific locations. The fitness measures used in fish IBMs and related studies have generally been adapted from the optimal foraging literature (Giske et al., 1998). These measures vary by how many components of fitness (food intake, growth, survival, reproduction) they consider and how these components are combined.

3.3.1. Foraging intake or growth

Following the lead of early optimal foraging literature, the model of Clark and Rose (1997) uses growth rate (G) as a fitness measure. In all published IBMs of fish, growth is assumed proportional to net energy intake, the difference between gross energy intake from food (F) and metabolic costs of swimming. Use of G or net energy intake as the fitness measure, as opposed to using the gross intake (F), has the advantage of considering metabolic costs of swimming as well food intake; trout appear to base habitat selection on both of these factors (Fausch, 1984; Hughes and Dill, 1990).

Growth as a fitness measure does not cause fish to move to avoid predation risks, while the literature indicates that predator avoidance can be an important factor in habitat selection (Fraser and Huntingford, 1986; Gilliam and Fraser, 1987; Gotceitas, 1990; Harvey, 1991; Tabor and Wurtsbaugh, 1991; Milinski, 1993). Net energy intake or growth has been shown to be a good predictor of trout habitat selection (Fausch, 1984; Hughes and Dill, 1990; Hughes, 1998); however, this observation may have resulted in part from studying situations where the same habitat that offers high food intake also offers low predation risk (deep, fast water with cover nearby). It does not seem appropriate to assume that habitat with high food availability always provides low risk of predation, especially for smaller fish vulnerable to predation by other fish. In models where mortality risks do not vary over space (Clark and Rose, 1997), including risk in the fitness measure will not change movement decisions. Energy intake or growth by itself would be a questionable fitness measure, however, for any model with spatially explicit mortality risks.

3.3.2. Ratio of risk to intake

The IBM of Van Winkle et al. (1996) used the ratio of mortality risk (μ) to G as a fitness measure. The ratio of μ to G was adapted from the optimal foraging literature: μ/F was originally derived as a surrogate measure of fitness where fitness is defined as minimizing the risk of death by predation while achieving some minimum net foraging rate (Gilliam and Fraser, 1987). As a fitness measure, μ/F or μG has the apparent advantage of considering both growth and survival, two important aspects of fitness. However, there are both theoretical and practical concerns with use of μ/F or μ/G as the fitness measure in fish IBMs.

The theoretical concern with μ/F or μ/G as the fitness measure is that the theory that minimizing μ/F maximizes fitness was derived using assumptions that are likely to be violated in fish IBMs in the following ways.

(1) The μ/F measure was derived by Gilliam and Fraser (1987), who used minimizing μ/F as a rule for fish deciding which patch to forage in when they were not hiding in a refuge, with the time spent in the refuge (where food intake and mortality risk are both zero) also a variable (Gilliam, 1990). This is a significantly different decision than the movement decision made in any of the published IBMs for fish; the IBM decision is typically to select a patch where the fish must remain (without a refuge) for at least one time step. This IBM formulation is used because: (a) fish IBMs typically use relatively large spatial scales, with each habitat location possibly containing both foraging and hiding habitat; and (b) at least for salmonids, fish apparently feed throughout a day (Hill and Grossman, 1993). In the IBMs, fish cannot offset higher risks by spending less time foraging and more time in a refuge as they can in the mathematical derivation

and laboratory test by Gilliam and Fraser (1987). (This is especially true for risks other than predation, such as stranding at low depths, which are also simulated in fish IBMs.) Minimizing μ/F does not maximize fitness in IBMs because fish do not control the time they spend in a refuge and because refuges do not provide protection from all risks.

(2) The μ/F measure was intended to apply only when some threshold minimum level of food intake can be met in all habitat patches (Gilliam, 1990), an assumption that is routinely violated in fish IBMs. This minimum intake is not clearly defined, and it is common in stream simulations for none of the available locations to provide sufficient intake to maintain positive growth (discussed further below).

(3) As originally derived, the μ/F measure uses gross foraging intake in the denominator, assuming that metabolic costs do not vary significantly over space (Gilliam, 1990); this assumption is violated in streams with high and variable velocities (Hughes and Dill, 1990; Hill and Grossman, 1993). This limitation has been dealt with by using net energy intake or G in the denominator.

(4) Other assumptions behind the theory that fish should select habitat to minimize μ/F (or μ/G) include that population sizes are stable and individuals are not in reproductive life stages (Leonardsson, 1991; Werner and Anholt, 1993; Giske et al., 1998); these assumptions are also commonly violated in fish IBMs.

The primary practical drawback to using μ/G (or its inverse G/μ, or the related $S \times G$, where S is survival, $1 - \mu$) as a fitness measure in fish IBMs is that it can result in erroneous or ambiguous decisions when comparing locations where G is negative. Negative net energy intake and growth is a common phenomenon for stream fish. It is especially common in juveniles, few of which grow large enough to survive their first winter in many species (Elliott, 1994), and negative growth sometimes persists for several months even in older fish (Railsback and Rose, 1999). Consequently, IBMs must allow fish to make good habitat selection decisions when some potential destinations provide negative net energy intake. If G is negative at one or both of two sites being compared, movement to minimize μ/G will often lead to illogical decisions with severe consequences; for example, if two sites have equal risk this rule would cause a fish to select the one offering the more negative growth potential.

The problems arising from negative G values are not readily circumvented by logical algorithms, for example by maximizing instead of minimizing μ/G when G is negative. Instead, the μ/G fitness measure becomes ambiguous when G is negative: increasing fitness by decreasing risk causes μ/G to *increase* (become less negative); increasing fitness by making growth less negative causes μ/G to *decrease* (become more negative); yet increasing fitness by making growth positive instead of negative causes μ/G to *increase.* It is possible, for example, for two sites to have the same value of μ/G even when one site has both lower risk and higher growth (e.g. Site A with $\mu/G = 0.01/-0.1 = -0.1$; and Site B with $\mu/G = 0.001/-0.01 = -0.1$).

This problem can be addressed by using gross intake, F, instead of net intake or G. Gross intake can be zero but never negative; but using F prevents fish from selecting sites with low metabolic costs over similar sites with higher costs.

Van Winkle et al. (1998) addressed this problem by adding an arbitrary constant (C) to G to keep the denominator from being negative. This $\mu/(G + C)$ decision rule makes movement decisions partially dependent on the value of C. The value of C is arbitrary except that: (a) C must be large enough to ensure that $(G + C)$ is never negative; and (b) the influence of G on movement decisions is reduced as C increases.

A second practical concern with the μ/G measure is that, even when restricted to positive values of G, this measure induces a strong preference for movement to increase growth (vs reduction of predation risk) that does not seem to match observed, or reasonably expected, fish behavior. This is shown in Fig. 1, a surface plot of the value of μ/G over wide ranges of risk and growth; fish minimizing μ/G prefer lower points on the surface. This preference is strong when G is close to zero (e.g. in the back corner of Fig. 1). Movement to minimize μ/G would cause fish with low but positive growth rates to assume much higher pre-

dation risk to further increase their growth rate, which does not concur with literature documenting the avoidance of habitat with high intake but high risks (Tabor and Wurtsbaugh, 1991). This problem likely reflects the difference between the original purpose of μ/G (selecting foraging habitat to use when not hiding in a refuge, when higher risks during foraging can be offset by lower foraging times) and its use in a fish IBM when the measure is applied to daily foraging with no refuge. The $\mu/(G + C)$ variant of this fitness measure results in a fitness surface with a stronger preference for reducing predation risk and a lower preference for increasing growth, because the effect of G on decisions is damped by adding C (Fig. 2). Even so, the preference for increasing growth remains unrealistic; e.g. in the back of Fig. 2, minimizing $\mu/(G + C)$ could cause fish to move downslope toward higher growth even at mortality risks as high as 0.1/day. Such high risks essentially guarantee death within a few days; realistically, fish should move away from such high risks at any cost to food intake unless they are near starvation.

A third practical concern with the μ/F or μ/G fitness measures is that it does not reflect how the importance of a unit of food intake or growth to a fish varies with fish size and maturity. For example, if F is evaluated as intake in g of food/day, a daily F value of one g/day would represent high intake for a small fish and low intake for a large fish. If instead we evaluate F as g of food/g of fish body weight per day, then one value of F (e.g. 0.002 g/g per day) could represent low intake for small fish and relatively high intake for large fish, because small fish need food intake equal to a larger percent of their body weight/day. Similarly, the value of a unit of growth changes with fish size: immature fish must grow if they are to survive and reproduce, but mature fish need not grow rapidly. These changes in the value of food with fish size should be reflected in the fish's movement rule as it makes the tradeoff between food intake and mortality risk. However, whether

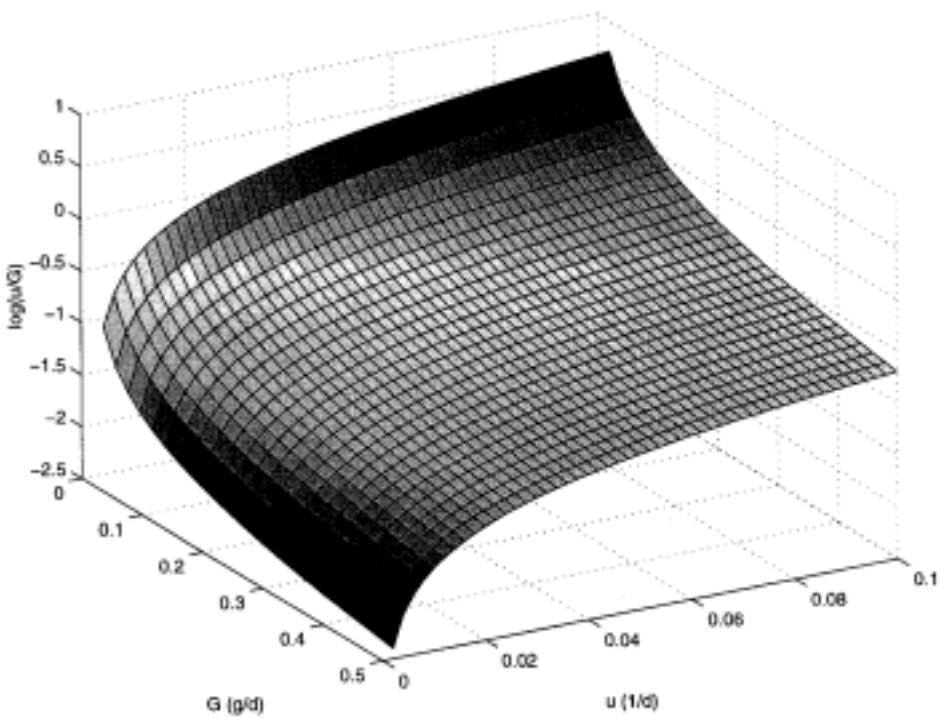

Fig. 1. Value of the μ/G fitness measure as the daily risk of non-starvation mortality μ varies from 0.002 to 0.1/day and growth rate G varies from 0.02 to 0.5 g/day. Fish are assumed to prefer lower values of μ/G. The μ/G axis uses a logarithmic scale.

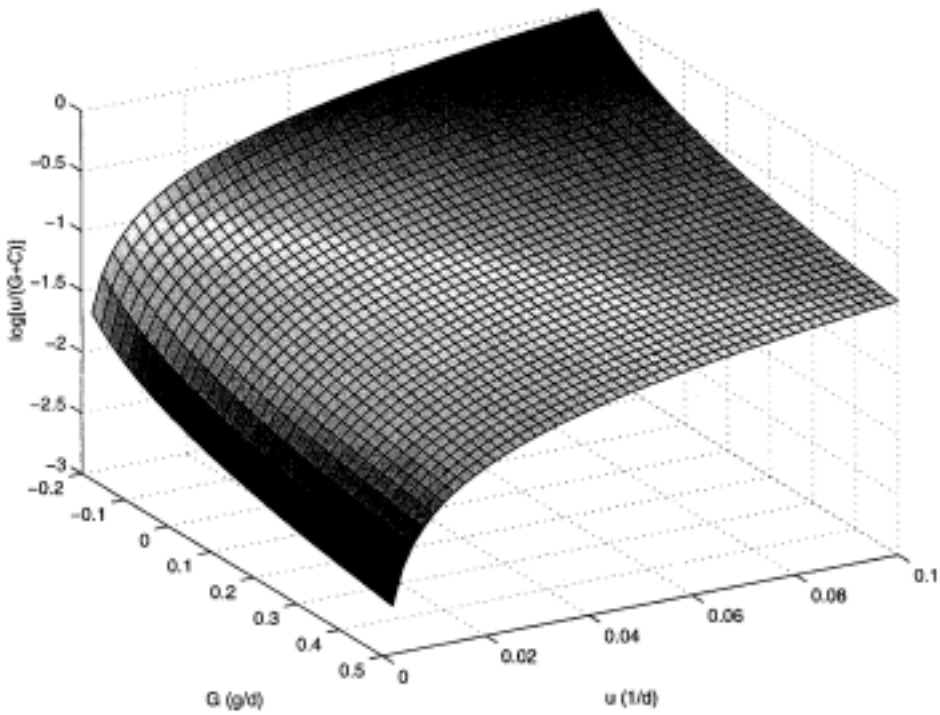

Fig. 2. Value of the μ /(G+ C) fitness measure as daily risk μ varies from 0.002 to 0.1/day and growth G varies from - 0.2 to + 0.5 g/day, with *C* equal to 0.3. Fish are assumed to prefer lower values of μ /(*G*+*C*). The μ /(*G*+*C*) axis uses a logarithmic scale.

F or *G* are evaluated as absolute or as body weight-specific measures, movement rules based on the μ /*F* or μ /*G* fitness measure do not account for the influence of fish size on the importance of a unit of food or growth.

The μ /*F* fitness measure and its variants also have numerical problems when *F* (or *G*) is zero. The value of μ /*F* is indeterminate when *F* is zero; if the inverse is used *(F/*μ *)*, then two sites that have zero intake but varying risk cannot be compared because the value of *F/*μ is zero for both. In most models, *G* is unlikely to often be exactly equal to zero, but *F* will often be zero because such habitat conditions as high flows or low temperature can preclude feeding.

3.3.3. Expected Survival over time T

A new fitness measure was developed, 'Expected Survival' of a fish over a specified decision time horizon (*T* time steps), considering risks from predation, physical habitat, and starvation (which depends on food intake). The basis of this measure is the assumption that the most important component of a fish's fitness is survival over some upcoming period *T* and that fish will move to maximize survival. Expected Survival can readily be modeled using methods adopted from the 'unified foraging theory' of Mangel and Clark (1986) and variables commonly included in IBMs. This fitness measure is described to illustrate how approaches from unified foraging theory can be used to build fitness measures for IBMs; the model actually uses an extension of Expected Survival described below.

Unified foraging theory was developed as a way of predicting how animals choose over time among habitat patches. The theory presented by Mangel and Clark (1986) is not directly applicable to IBMs because it assumes mortality risk and food conditions are constant over time, whereas in an IBM risks and food availability vary over time in ways not known to the animals being modeled. A close adaptation of this theory to IBMs would be to: (a) assume a method that

animals use to predict future conditions in each potential location; and (b) use the dynamic programming method of Mangel and Clark (1986) to identify the optimal location for the current day. As these calculations would be made for each individual on each day, this close adaptation of unified foraging theory would be computationally demanding. Instead, Expected Survival was determined simply by: (a) assuming fish use the simplest possible prediction of risk and food conditions over the decision time horizon *T*, which is that they do not change from the current day's conditions; and (b) assuming fish move to the location with the highest resulting probability of survival over time *T*.

It should be noted that this fitness measure is still intended to be updated each time step; basing Expected Survival on the decision time horizon *T* does not inhibit the movement of fish each day in response to changing conditions. In fact, basing the fitness measure for each day on the assumption that the current risk and food conditions will prevail into the future causes movement to respond very strongly to the current conditions.

From a theoretical standpoint the Expected Survival fitness measure has the advantages that its biological meaning is clear, that it is a direct measure of a primary component of fitness (survival) instead of a derived surrogate for fitness, and that its formulation does not make assumptions about population stability, life history parameters, or reproductive state that are commonly violated in a fish IBM. Different values of *T* alter the relative importance of starvation versus other risks (higher values of *T* giving more importance to food intake in movement decisions), in some ways similar to the effect of the constant in the $\mu/(G + C)$ fitness measure. However, the decision time horizon *T*, unlike *C*, has a clear meaning.

Movement to maximize this survival fitness measure implements the foraging theory that fish in poorer condition (having lower energy reserves) are more willing to take risks in return for higher food intake. Fish in poor condition are more likely to die of starvation, so movement to maximize survival will cause them to prefer sites with higher intake. Maximizing Expected Survival also provides good tradeoffs between long- and short-term risks: short-term high risks almost always dominate Expected Survival but in the absence of such risks movement will favor long-term survival. For example, exposure to high water velocities during a flood poses a sudden high risk. Under these conditions, maximizing survival causes a fish to move to refuge habitat where it is protected from high velocities, even if food intake there is low. If the flood persists long enough to deplete the fish's energy reserves, Expected Survival becomes dominated by starvation so the fish then selects relatively high risk, high intake habitat until its energy reserves are restored. After that, the fish resumes a balance between maintaining its reserves and minimizing non-starvation risks.

The Expected Survival fitness measure is evaluated by: (a) calculating the probability of surviving mortality risks other than starvation over the time horizon *T*; (b) calculating how energy reserves change over *T* and the subsequent probability of surviving starvation risk, then (c) multiplying these two survival probabilities together. Our trout model uses the following approach.

Non-starvation mortality risks are typically a function of both the habitat conditions and the fish. Expected Survival is evaluated using the same survival probability estimation methods used by the model to determine whether the fish dies of any cause except starvation on day *t* (P_t); the non-starvation survival probability over time *T* is then projected simply to be $(P_t)^T$.

In IBMs, the survival factor representing starvation is typically related to a state variable that represents the fish's energy reserves; the condition factor of Van Winkle et al. (1998) was used in our model. This condition factor *(K)* is equal to the fraction a fish is of ‘normal’ weight for its length; ‘normal’ weight is determined from a length-weight relationship developed from field data. Using the assumption that a fish bases its movement decision on day *t* on the expectation that food intake will be constant over the next *T* days, the fish’s potential weight and *K* at time $t + T$ can be projected for each potential movement destination. For example, if on the current day a site

provides a fish with growth of 0.1 g/day and we use a decision time horizon T value of 30 days, then it is projected the fish's weight will increase by 3.0 g by time $t + T$. Starvation mortality can then be estimated as a function of K as K changes from its value at time t to its value at time $t + T$.

The assumed relation between an animal's condition (energy reserves) and daily survival probability is typically nonlinear; in our stream trout formulation a logistic function is used to relate the probability of surviving starvation on day t (S_t) to K (Fig. 3):

$$S_t = \frac{e^{(ak+b)}}{1+e^{(aK+b)}} \tag{1}$$

where a and b are constants. The cumulative starvation survival probability over the decision time horizon T can be calculated by determining S_t for each day between day t and $t + T$ and multiplying these daily survival values together.

The computational requirement for this method may be a problem when evaluating a number of potential movement destinations for each of many fish. Starvation survival over the decision time horizon T can be approximated without calculating survival for each day by assuming there is an average daily survival $\bar{S}$ from which survival over the time horizon can be estimated as $\bar{S}^T$. (This assumption is not generally true but it is still useful, as discussed below.) There are several ways to evaluate the average daily survival ($\bar{S}$).

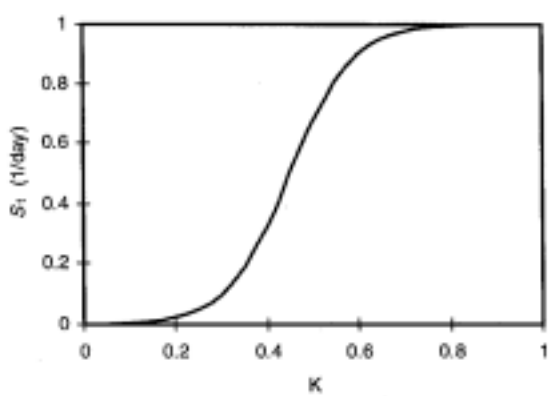

Fig. 3. Logistic relation between fish condition K and daily survival probability for starvation (S_t).

(1) $\bar{S}$ can be assumed equal to the mean starvation survival between times t and t + T, which can be calculated from the first moment of the survival-K curve. Using the logistic survival curve (Eq. (1)) as an example:

$$\bar{S} = \int_{K_t}^{K_{t+T}} \frac{e^{(aK+b)}}{1+e^{(aK+b)}} dK \Big/ (K_{t+T} - K_t)$$

$$= \frac{1}{a} \ln\left(\frac{1+e^{(aK_{t+T}+b)}}{1+e^{(aK_t+b)}}\right) \Big/ (K_{t+T} - K_t) \tag{2}$$

where K_t is the fish's condition at the movement decision time, t; and K_{t+T} is condition at time $t + T$. (This equation will give a divide-by-zero error if K_t equals K_{t+T}, which will happen for any fish starting with K of 1.0 and maintaining 'normal' growth. This problem can easily be fixed by setting $\bar{S}$ equal to S_t in such cases.)

(2) The survival probabilities resulting from K at time t and from K at time $t + T$ can both be determined, then averaged to approximate $\bar{S}$.

(3) $\bar{S}$ can be assumed equal to the daily survival resulting from the value of K at time $t + T/2$.

These approximations were tested against the exact survival calculation (using Eq. (1) and T= 30) and found that $\bar{S}^T$ using $\bar{S}$ from Eq. (2) provided a good estimate of exact survival, within 0.01 over most reasonable ranges of starting and ending K. Using the value of S at time $t + T/2$ to represent $\bar{S}$ did not provide a good approximation of survival in the nonlinear part of the condition-survival curve. Using the average of daily starvation survival probabilities at times t and $t + T$ produced an even poorer approximation of overall survival.

The following practical considerations were identified for using Expected Survival in fish IBM movement rules.

(1) The movement decision is a function of a fish's current condition. This dependence is illustrated in Fig. 4 with plots of Expected Survival over wide ranges in non-starvation mortality risk and growth rate; fish maximizing survival prefer higher locations on the plot. Fish in good condition (Fig. 4a) tend to move only toward lower non-starvation risks, except for a fitness gradient causing movement away from locations where

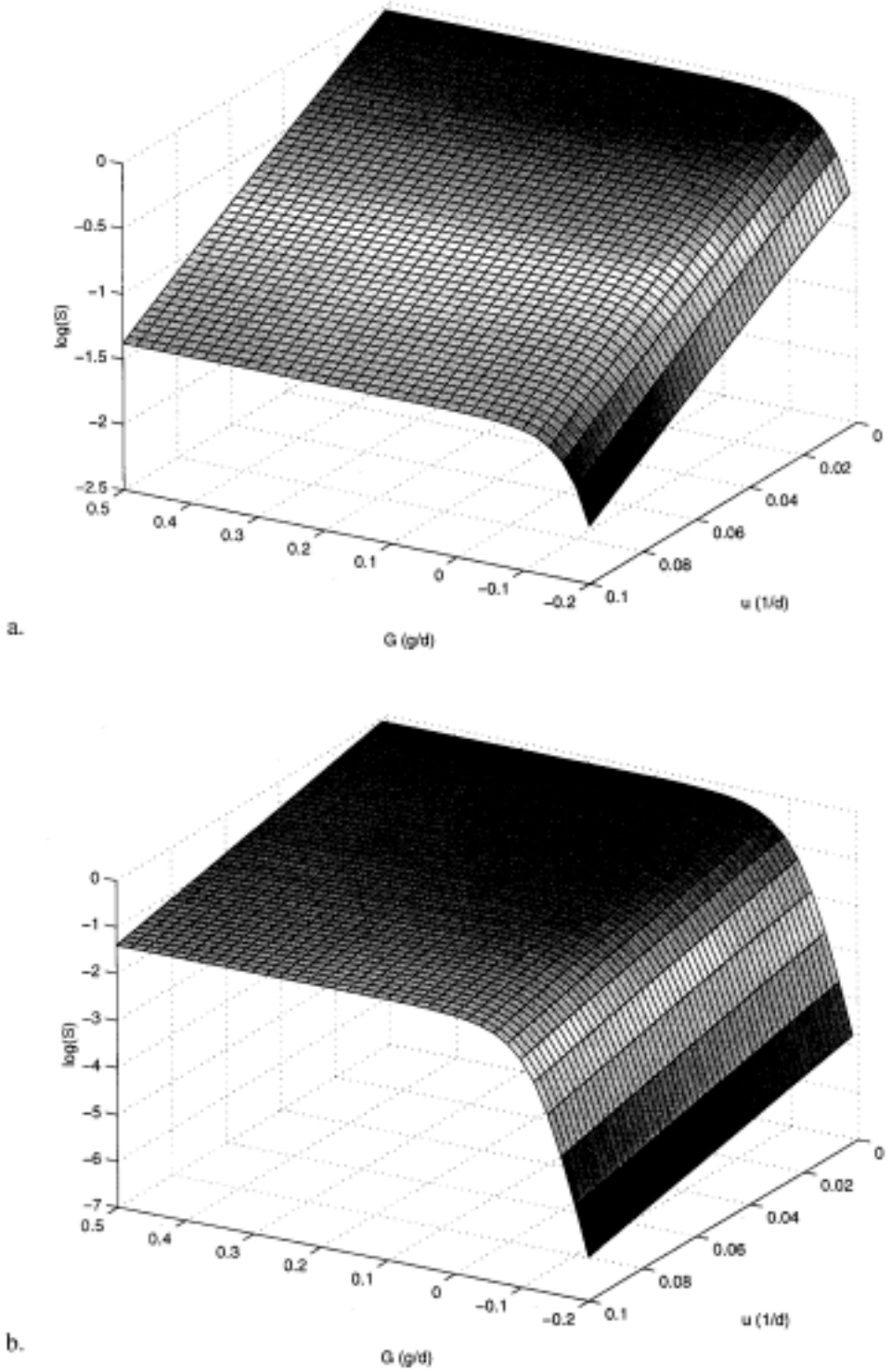

Fig. 4. Value of the Expected Survival fitness measure (*S*) as non-starvation risk p varies from 0.002 to 0.1/day and growth *G* varies from - 0.2 to + 0.5 g/day, with *T* equal to 30 days, for fish with starting length of 10 cm and (a) a condition factor of 1.0 and (b) a condition factor of 0.8. Fish are assumed to prefer locations with higher values of *S*. The *S* axis uses a logarithmic scale.

growth is insufficient to maintain good condition. Fish in poor condition (Fig. 4b) have a strong gradient toward higher growth over a wider range of growth rates because their probability of starving is high over a wider range of growth.

(2) Reducing the decision time horizon T puts more emphasis on non-starvation risks in movement decisions; increasing T put more emphasis on food intake. This is because energy reserves make starvation less likely to occur over shorter time periods.

(3) Expected Survival provides a good basis for comparison among sites even if growth is negative or food intake is zero at some or all sites.

(4) Movement to maximize Expected Survival reflects how the value of a unit of food intake or growth varies with fish size, because the fitness measure considers not just the raw intake or growth rate but how the expected growth affects a fish's condition and survival.

(5) Unified foraging theory assumes a threshold level of energy reserves below which mortality occurs (Mangel and Clark, 1986). This assumption is not useful for IBM movement rules because it does not allow fish to pick the best among sites which would all result in starvation within T time steps; all sites where condition would fall below the threshold would have the same potential fitness value of zero, even if one would provide longer survival than the other. It seems more realistic to design the fitness measure (as has been done here) to let fish select sites that offer the best opportunity to survive until conditions improve or until a better site becomes available when a more dominant fish dies or moves.

(6) Maximizing Expected Survival does not provide incentive for fish of any size to grow, only to maintain high enough energy reserves to avoid starvation. Movement to maximize this measure would not cause a fish in good condition to move from a site where its weight is only maintained to a site offering equal risks and positive growth; both such sites have no risk of starvation so the expected survival values for the sites would be equal.

3.3.4. Expected Reproductive Maturity over time T

Reproductive success is also a key component of an animal's fitness. A simple way was developed to incorporate reproduction in the movement fitness measure, modifying expected survival to consider how close a fish comes to the size of reproductive maturity within the decision horizon T. In our stream trout model an 'Expected Reproductive Maturity' measure was used equal to the expected survival between time t and $t + T$ multiplied by M_{t+T}, the percent of sexually mature size the fish is projected to be at time $t + T$. Movement to maximize Expected Reproductive Maturity gives fish an incentive to grow until they are large enough to spawn, which the expected survival fitness measure does not. Like Expected Survival, the factor M_{t+T} is state-dependent: the values of M_{t+T} for alternative locations are expected to get larger but less variable as a fish grows.

Expected Reproductive Maturity is similar to the expected progeny measure of Mangel and Clark (1986), which is the survival probability multiplied by the expected number of progeny. Unlike the expected progeny measure, which assumes that the probability of reproduction (and, therefore, fitness) is zero if reproductive size is not reached, Expected Reproductive Maturity allows movement decisions to be made even if no potential destinations are projected to allow a fish to reach maturity. This measure is also similar in some ways to the survival times growth rate fitness measure derived by Leonardsson (1991), although Leonardsson derived this measure from life-history theory using assumptions that are not valid in typical IBMs (e.g. that life-history parameters are constant and growth is always positive).

From a practical perspective, Expected Reproductive Maturity is a way to incorporate reproduction in fitness with minimal increase in model complexity. The factor M_{t+T} is simple to compute from the projected growth and an assumed size of sexual maturity. Compared to expected survival, Expected Reproductive Maturity adds a fitness gradient toward sites providing higher growth, even for fish with high energy reserves.

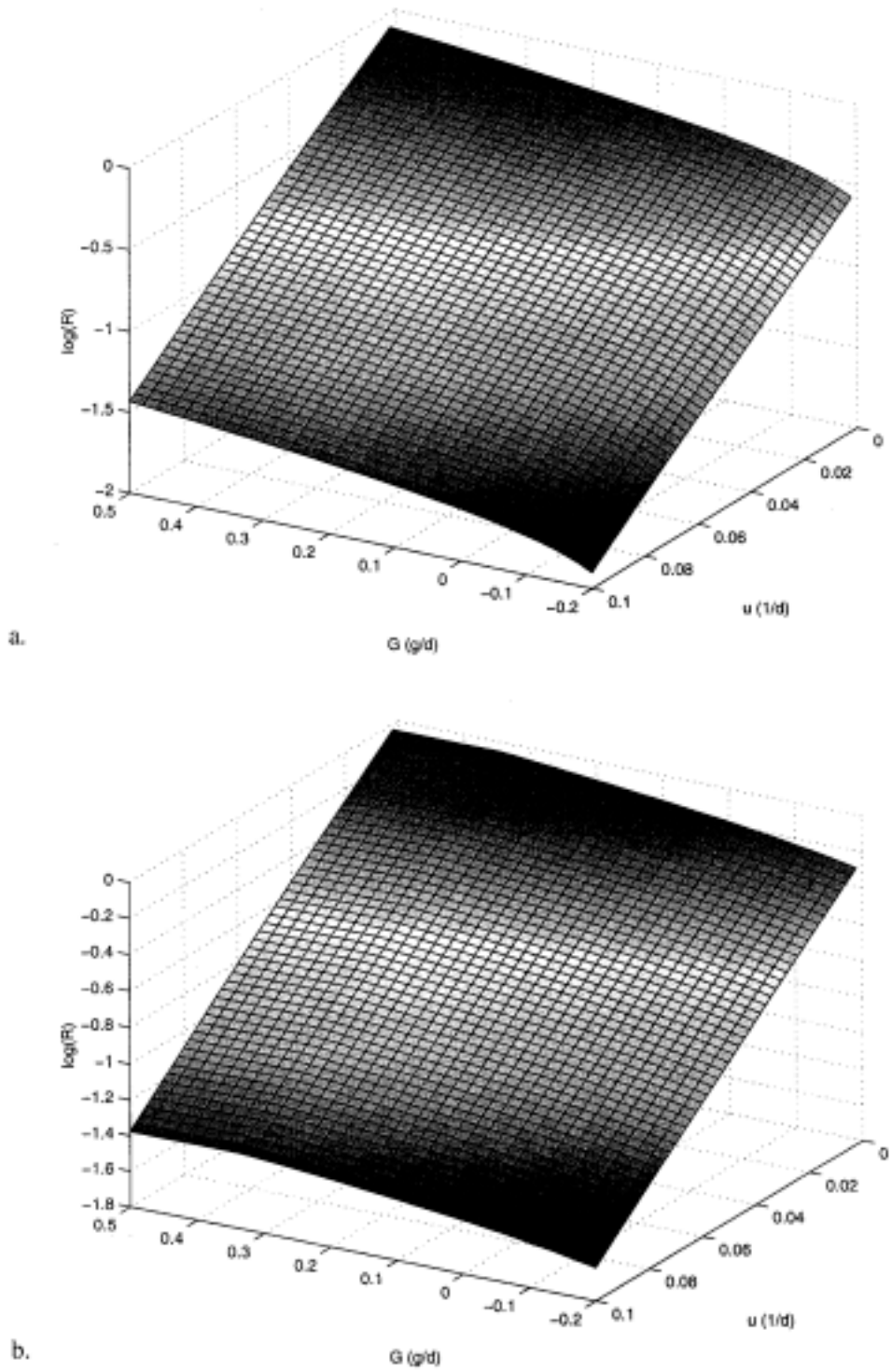

Fig. 5. Value of the Expected Reproductive Maturity fitness measure (*R*) as non-starvation risk μ varies from 0.002 to 0.1/day and growth *G* varies from - 0.2 to + 0.5 g/day, with *T* equal to 30 days, for fish with a condition of 1.0 and sizes of (a) 20 g and (b) 30 g. The size of reproductive maturity is assumed to be 40 g. Fish are assumed to prefer locations with higher values of *R*. The *R* axis uses a logarithmic scale.

This difference is illustrated by comparing Fig. 5 (plots of Expected Reproductive Maturity over wide ranges of risk and growth) to the similar Fig. 4; in Fig. 5 there is a gradient toward higher growth rate even when food intake is sufficient to avoid starvation mortality. This gradient is higher for fish that are much smaller than reproductive size (Fig. 5a) than it is for fish close to reproductive size (Fig. 5b). The back corner of Fig. 5b shows that when growth rates are sufficient for the fish to attain size of reproductive maturity by the end of the decision time horizon (growth greater than about 0.3 g/day in this example) there is no fitness benefit to additional growth. Unlike the μ/G and $\mu/(G+C)$ fitness measures, Expected Reproductive Maturity does not cause movement to increase growth unless it involves very little increase in risk.

More detailed consideration of reproductive success could be added to this fitness measure if desirable for some IBMs. For example, how the number and viability of offspring varies with fish size could be included in the fitness measure. Different fitness measures, with and without reproductive components, could be used for fish in and not in reproductive cycles (Mangel and Clark, 1986). For example, female adult fish could spend part of the year simply maximizing survival and then switch to maximizing the expected number and size of eggs during the pre-spawning period. Different values of the decision time horizon T may also be appropriate when fish are in reproductive cycles.

4. Conclusions

Spatially explicit IBMs use movement rules to determine when individuals depart their current locations and how they select destinations. These rules generally compare locations using some measure of an individual's expected fitness. Movement rules are critical to realistic simulation of how individuals, and therefore populations, respond to changes in habitat and population density: IBMs that do not accurately reproduce individual habitat selection have little hope of accurately modeling such spatially explicit processes as feeding, growth, and mortality.

Departure and destination rules for IBMs should reflect the ability of real fish to select habitat over the temporal and spatial scales used in the model. The evidence for many stream fishes indicates they are familiar with their surroundings over substantial distances and are able to find good habitat quickly. Rules that include randomness in selection of locations within the area that fish are familiar with seem unlikely to be appropriate in models where habitat variation occurs at the same temporal scale as fish movement. Such rules can unrealistically prevent fish from avoiding high risks or low food intake during unsteady conditions. (This conclusion does not mean that models should exclude occasional long-distance, apparently random, exploratory movement that could increase the area with which a fish is familiar.) Likewise, movement rules that cause fish to move only when fitness declines seem inappropriate because they do not let fish take advantage of nearby habitat with higher fitness potential. It is concluded that IBMs should assume fish are familiar with their surroundings over an area greater than their current location. Models should let fish move any time that better habitat is available within the area they are familiar with. It is also concluded that models should let fish select the best habitat available instead of moving randomly. If routine, non-exploratory movement is simulated as partially random, it should occur over a substantially smaller time scale than habitat variation. More restricted departure or destination rules may be appropriate for species with clearly demonstrated limits on movement.

Fitness measures used as the basis of movement rules should be carefully evaluated. Fitness measures that are initially appealing may have significant theoretical and practical problems. The gross food intake F has been used as a fitness indicator, even though it does not reflect the importance of metabolic costs of swimming and mortality risks. Using F as a fitness measure may be appropriate in models where metabolic costs and risks are not spatially variable.

The μ/F fitness measure of Gilliam and Fraser (1987) and its variants (μ/G, G/μ, $S \times G$) do not provide an appropriate basis for movement in fish IBMs. Their use in IBMs with a daily time step

violates key assumptions made in deriving the μ/F measure from optimal foraging theory. Important practical problems with these fitness measures include: (a) the value of μ/F is indeterminate when F is zero, a common situation; (b) movement to minimize μ/G causes erroneous or ambiguous decisions when G is negative, also a common situation; and (c) minimizing μ/F or μ/G can cause well-fed fish to assume high mortality risks to obtain even more food, an unrealistic result.

Erroneous movement decisions resulting from negative values of G can be avoided by using $\mu/(G+C)$ as a fitness measure. This is a simple, computationally efficient measure, though it lacks theoretical justification and C has no biological meaning. Movement to minimize $\mu/(G+C)$ generally puts more emphasis on reducing predation risk than on increasing growth, but still imposes a willingness to accept high mortality risks that is unrealistic under most situations. This measure does not vary with a fish's energy reserves.

Fitness measures representing expected survival over a selected time horizon, or Expected Reproductive Maturity, are readily derived from the unified foraging theory of Mangel and Clark (1986). Such fitness measures consider effects of food intake and mortality risks, and have both theoretical and practical advantages. They are simple and clearly defined representations of important aspects of an organism's fitness, and are theoretically and computationally compatible with IBMs. Compared to the $\mu/(G+C)$ fitness measure, our Expected Reproductive Maturity measure has the advantages of inducing realistic changes in habitat selection priorities with fish condition (giving avoidance of predation risks very high priority for healthy fish, but giving fish with low energy reserves more emphasis on food intake) and fish size (giving larger fish less emphasis on growth and more emphasis on avoiding mortality). The primary disadvantage of these fitness measures is a modest increase in computations.

The IBM for stream trout we are developing and testing (Railsback et al., 1999) uses a daily time step, a spatial resolution of several square meters, and spatial variation in food intake, predation risks, and habitat-related risks. Stream reaches of several hundreds to thousands of meters are typically modeled. For each fish at each time step, the model conducts the following calculations.

- Potential movement destinations are identified. It is simply assumed all locations within a maximum movement distance are potential destinations. This maximum distance is a function of fish length.
- The daily probability of surviving non-starvation risks (P) is calculated for each potential movement destination.
- The average daily probability of starvation-related survival ($\bar{S}$) is calculated for each potential movement destination, using the fish's current condition factor and the condition factor projected to occur after T days. The condition factor at time $t + T$ (K_{t+T}) is determined by: (a) assuming that the current day's growth rate would continue for T additional days; and (b) projecting the fish's resulting length and weight at time $t + T$. Growth rate is a function of the food availability and competing fish at the potential destination.
- The fraction of sexually mature size the fish will be at time $t + T$ (M_{t+T}) is calculated by dividing its projected length at time $t + T$ by the minimum length of sexual maturity (an input parameter). (Values of M_{t+T} are not allowed to exceed one.)
- Expected Reproductive Maturity for each potential destination is calculated as $P^T \times \bar{S}^T \times M_{t+T}$. The fish moves to the destination with the highest Expected Reproductive Maturity.

One of the primary advantages of the individual-based modelling approach is that it does not require many of the simplifying assumptions and mathematical derivations typically needed in more aggregated models (Huston et al., 1988). Therefore, using fitness measures like μ/G that were derived under limiting assumptions seems contradictory to the IBM approach. Such measures can impose behaviors that are neither realistic nor truly fitness-maximizing under many conditions. Instead, the advantages of the IBM approach can best be realized by using simple,

direct measures of an animal's fitness as the basis for movement (and other decisions). Expected Survival and Expected Reproductive Maturity are two such simple, direct fitness measures.

Tests of fitness measures and movement rules that use spatial and temporal scales relevant to fish IBMs are a critical research need. These models typically use a spatial resolution of at least several square meters and a daily time step; published studies of fish habitat selection among locations varying in risk and food intake (Fraser and Huntingford, 1986; Gotceitas, 1990; Gotceitas and Godin, 1991; Angradi, 1992) have used much smaller spatial and time scales. Challenges in testing movement rules include measuring and controlling food availability; measuring and controlling mortality risks and determining how these risks are perceived by fish; and observing fish over relatively large time and space scales. Those studies in which observed habitat selection appeared to support the 'minimize μ / G' rule (Gilliam and Fraser, 1987; Gotceitas, 1990) may also support the 'maximize Expected Survival' and 'maximize Expected Reproductive Maturity' rules proposed here.

Acknowledgements

This research was partially funded by a research grant to the Humboldt State University Foundation provided by Pacific Gas & Electric (PG&E) and Southern California Edison (SCE), and co-sponsored by EPRI, Electric Power Research Institute under agreement W06953-02 with Lang, Railsback & Assoc. Glen Ropella and Chris Langton (Santa Fe Institute and The Swarm Corporation) and other members of the Swarm community provided the intellectual seeds of this research. Many ideas were derived from the *Compensation Mechanisms in Fish Populations* project conducted by the Environmental Sciences Division of Oak Ridge National Laboratory with funding from EPRI, PG&E, and SCE. We appreciate the very helpful comments provided by Dr Kurt Fausch and the anonymous reviewers.

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