

Importance of fish behaviour in modelling conservation problems: food limitation as an example

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Simulation experiments using the inSTREAM individual-based brown trout *Salmo trutta* population model explored the role of individual adaptive behaviour in food limitation, as an example of how behaviour can affect managers' understanding of conservation problems. The model includes many natural complexities in habitat (spatial and temporal variation in characteristics such as depth and velocity, temperature, hiding and feeding cover, drift-food supply and predation risk), fish physiology (especially, how food intake and growth vary with hydrodynamics, cover, fish size and temperature) and behaviour. When drift-food concentration was increased over a wide range in 7 year simulations, the simulated population was always food limited. In fact, as food supply increased, the population increased at an increasing rate and consumed a higher percentage of the food supply, apparently because higher food concentrations make more stream area energetically profitable for drift feeders. The behaviour most responsible for this response was activity selection: when food was abundant, fish chose to feed less frequently and more nocturnally, thereby reducing predation mortality so more fish survived longer. These results indicate that the traditional concept of food limitation, that food availability stops limiting population size when it exceeds some threshold level, may not be useful and can be misleading. Results also strongly contradict the concept that a salmonid population is not food limited if the total food supply is greater than the population's consumption. Explicit consideration of adaptive behaviour produced a novel but believable understanding of food effects on salmonid populations. Published 2011. This article is a U.S. Government work and is in the public domain in the USA.

Key words: activity selection; adaptive behaviour; diel; habitat selection; individual-based modelling; salmonid.

INTRODUCTION

The ability to predict population responses to environmental conditions can be valuable in conservation efforts, particularly if that ability extends to novel environmental conditions. For prediction of outcomes under novel conditions, process-based models should be particularly effective. Models centred on the effects of the behaviour of individuals on their survival, growth and reproductive success, from which population-level outcomes emerge, have shown particular promise in predicting consequences of habitat alteration (Goss-Custard *et al.*, 2006). The ability

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to identify key behaviours and represent them in models has become an important problem with relevance to conservation.

Here, an example of this general problem is provided by exploring the significance of different behaviours for food limitation of fish populations, using an individual-based model (IBM) of river salmonids as a virtual laboratory. A conceptual approach to food limitation that ignores the potential influence of behaviour might assume that food limitation occurs only when food availability is less than a given population's potential intake, and when other processes, especially predation, are comparatively unimportant. This assumption has in fact been a foundation of traditional theoretical explorations of food limitation and population regulation (Hairston *et al.*, 1960; Fretwell, 1987; Osenberg & Mittelbach, 1996). Adaptive behaviour, however, is increasingly recognized as complicating the relationship between food availability and predation risk in regulating populations (Werner & Peacor, 2003). Stream fishes may select habitat and patterns of diel behaviour to trade-off food acquisition and the risk of predation, so that higher food availability may be used to reduce risk. For example, Metcalfe *et al.* (1998, 1999) observed juvenile Atlantic salmon *Salmo salar* L. 1758 feeding more in daytime, when risk is presumably higher and when the condition of the fish or food availability was lower. In addition, feedback between food and abundance should be expected: greater food abundance may lead to more reproduction and more fishes and thus perhaps no increase in the amount of food available to individuals. A final problem for the traditional view of food limitation above is that a fish population's potential food intake is far higher than typical availability in natural systems, as illustrated by the densities and growth rates sustained in hatcheries.

These potential complexities are explored here by looking at the relation between food availability and population size in a model that includes foraging behaviours and mechanisms through which the complexities can emerge. The behaviours represented include (1) selecting activity: deciding whether to feed with predation risk or to hide with minimal risk but no food intake, (2) selecting habitat: choosing sites that offer a good trade-off between food intake and predation risk and (3) hierarchical feeding: larger animals dominate feeding sites such that smaller animals have access only to food unused by larger ones. With these behaviours, and mechanisms such as annual reproduction that increases with the number and size of adults, can food supply reach levels where it provides little additional benefit? What proportion of the available food supply does the population consume, and how does that proportion change with food availability? The effects of each behaviour on food and fish population relations are explored by seeing how they change when each behaviour is turned off in the model.

This study's direct relevance to conservation is in questioning whether the traditional concept of food limitation is appropriate for stream-fish management; if not, then managers are likely to underestimate both the amount of food a fish population needs and the benefits of increasing food supply. The study's indirect relevance is in illustrating the extent to which specific behaviours can affect ecological relationships such as food limitation: do management concepts that seem to make sense at a population level (*i.e.* a population only needs so much food) still make sense when the population is thought of as a system of adaptive individuals? If not, then models that include behaviour clearly deserve more consideration in management decisions.

MATERIALS AND METHODS

The general approach was to simulate the effects of food availability on a river salmonid population, using an IBM in which trout have the foraging behaviours discussed above. To ensure that the simulation experiment used realistic habitat complexity over space and time, variable values, fish abundance and size, and food levels, the model was applied to a study site on the Green River, Utah, U.S.A. The population response to food availability, from levels lower to much higher than the level calibrated to produce realistic abundance and growth, was observed over multi-generation simulations.

MODEL DESCRIPTION

Simulation experiments used one of the inSTREAM family of stream salmonid IBMs (www.humboldt.edu/ecomodel/instream.htm). The version used here is identical to that described by Railsback *et al.* (2005, 2006) with one exception: instead of habitat being represented as transects of rectangular cells and hydrodynamics simulated *via* a one-dimensional model, this version uses a two-dimensional (horizontal) representation of habitat as a network of irregular polygons, with hydrodynamics simulated *via* a finite-element hydrodynamic model. Here, a summary of the model and details especially relevant to this study are presented.

Overview and schedule

The model represents, in simplified ways, many complexities of the real river it represents (Fig. 1): many habitat characteristics vary over both time and space, and population dynamics emerge from the fate and behaviours of individuals. The model operates at a semi-daily time scale, updating at the start of each daytime (at the hour preceding sunrise) and night (at the hour after sunset). The spatial resolution was chosen considering the most important fish activity represented: feeding on invertebrate drift. Each cell is at least as large as the feeding territory of an adult fish and larger if the habitat is relatively homogeneous; multiple fish can occupy the same cell.

This summary of its schedule of actions provides an overview of the model; processes especially important to this experiment are explained in more detail. (1) At the start of each daytime period, daily values of time-varying habitat characteristics are read from input developed from on-site observations. These inputs include river flow, temperature and drift-food



FIG. 1. The Green River study site, as depicted in the model. The site is 1000 m in length along its thalweg and depicted as 2204 polygonal cells, though some cells (■) are dry at typical flows. Cells are shaded by velocity, with redder cells faster. Each cell also has variables that represent its depth, area of velocity shelter for drift feeding and availability of hiding cover. Circles in a cell indicate the presence of one or more fishes.

concentration. The concentration of drift food (g food m^{-3}) is assumed constant over space but varies daily in proportion to temperature, as indicated by measurements made upstream of the study site (Filbert & Hawkins, 1995). The depth and velocity of each habitat cell is updated from the flow. (2) Each day, female fish determine whether to spawn. Fish can spawn once per year, and when they do depends on the date, and on thresholds for fish age, fork length (L_F) and mass. Fecundity increases with spawner L_F . The representation of spawning and redds is simple but allows the model to simulate the full life cycle and long-term population dynamics. (3) At the start of each daytime and night period, all fish update their selection of activity and feeding v , hiding and habitat cell, using methods described below to identify the best combination of activity and cell. This action is executed in descending order of L_F , with larger fish depleting the food available for smaller fish to simulate a size-based hierarchy. (4) After selecting habitat and activity, the resulting semi-daily growth (or mass loss if metabolic costs exceed energy intake) is calculated. (5) Whether each fish survives or dies is determined for each of several sources of mortality, especially predation, and starvation and disease. Because activity and habitat selection trade-off the risks of starvation and predation, small or starving fish often die of predation. A fish's semi-daily probability of survival is a function of L_F and mass, and its choice of habitat and activity. (6) Each day, the developmental state of any redds is calculated; when a redd is fully developed its eggs become new individual fish.

Food and feeding

The model represents two kinds of food: drift (food items entrained in the flow) and search (food that fish must actively seek from the benthos). Search food, however, is far less important, typically used only by very young fish. At realistic food levels, the simulated production of search food is 10–20% of the total food supply and its consumption is c , one tenth that of drift. The simulations included search food and its consumption, but experimental manipulations of food supply alter only drift food. The total drift food available in a cell varies with daily drift-food concentration and flow, being proportional to cell area, depth and velocity.

The rate of drift intake by a fish is modelled using a conventional drift-feeding approach, adapted from the models of Hughes (1992) and Hill & Grossman (1993). A fish is assumed to capture food within a 'reactive distance' that increases with L_F but decreases with water velocity, while the amount of food passing within the reactive distance increases with velocity and drift concentration. As a consequence, drift-food intake peaks at an intermediate velocity that increases with fish size [Fig. 2(a)]. Fish growth is modelled as net energy intake, the difference between energy intake from food and metabolic costs. Metabolic costs increase with L_F , swimming speed and temperature. As a consequence of these processes, growth peaks at an optimal velocity that delivers sufficient food while not requiring excessive energy for swimming. The reactive distance is assumed to be reduced by half at night; hence, at night optimal feeding velocities are lower and a smaller range of velocities provides opportunity for growth [Fig. 2(b)].

Competition for food is modelled explicitly, at the cell scale. Each time a fish chooses to feed in a habitat cell, its food consumption is subtracted from that remaining for smaller fish. The intake of any fish cannot exceed the amount remaining unconsumed by larger fish in the same cell.

These feeding processes are executed by those fish using the feeding activity. Fish can alternatively select a hiding activity, during which food intake and swimming speed are assumed to be zero, so slight mass loss occurs.

Mortality

Mortality is modelled by calculating the daily probability of each individual fish's survival, then stochastically determining if it dies. Predation risks to feeding fish vary among cells in ways that represent the study site's actual mix of bird and mammal (especially, river otter *Lontra canadensis*) predators. Risk decreases with increasing depth and velocity, which make fish harder for birds to see. Risk is assumed 70% lower at night, a diel difference lower than that estimated by Metcalfe *et al.* (1999) from the literature. This assumption reflects that

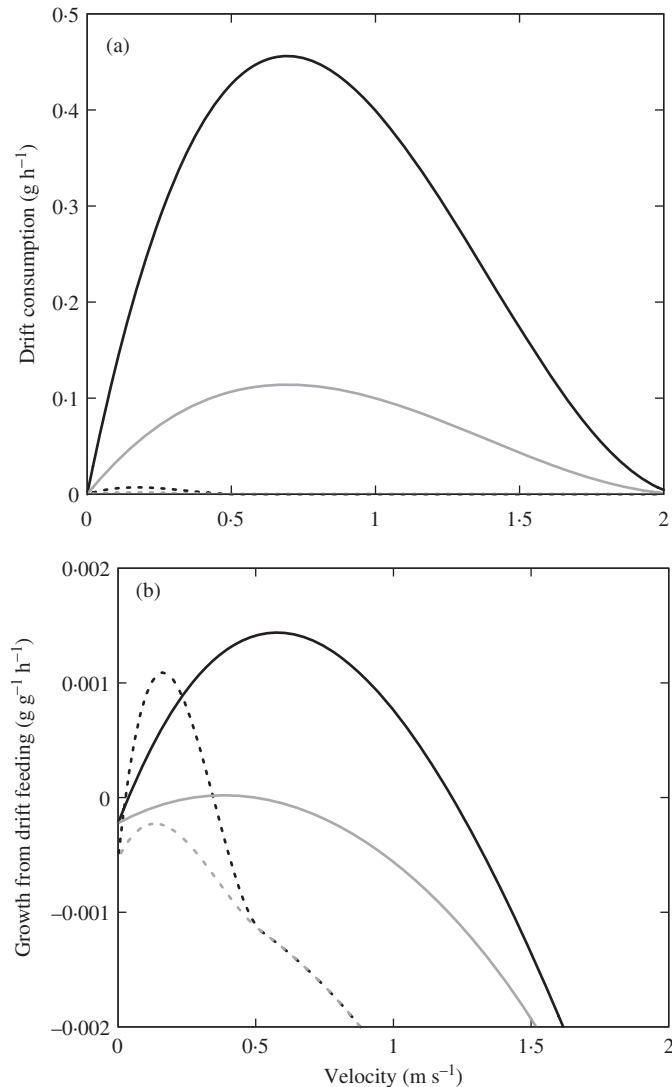


FIG. 2. Hourly (a) drift consumption (mass of food captured) and (b) growth rates (mass of growth per mass of fish) of simulated salmonids, as a function of water velocity under typical conditions: temperature of 15°C , drift concentration of $2.0 \times 10^{-4} \text{ g m}^{-3}$, and fish using velocity shelter that reduces swimming speed by 50%. —, —, a 200 mm fork length (L_F) fish; - - - - , - - - - , 50 mm L_F fish; ·····, —, daytime; - - - - , —, night.

visibility is lower and the avian predators observed at the site are inactive at night, while nocturnal predators such as *L. canadensis* are relatively abundant at the site. Very small fish, however, are assumed vulnerable to predation by large fish and hence are safer in shallow habitat. Fish are assumed to have accurate knowledge of predation risks and how they vary with habitat. Fish using the hiding activity are assumed almost completely safe.

The model does not assume that an individual's predation risk is directly affected by fish abundance. It does not, for example, represent risk dilution: if three identical fish are in the same cell, they each experience the same daily survival probability as would a lone fish. (This

assumption is made simply because effects of risk dilution are uncertain and their importance to the model's purpose is not clear.) Therefore, higher fish abundance inevitably results in higher numbers of fish killed by predation. Competition for safe and energetically profitable habitat is a mechanism causing often-strong indirect feedback of fish abundance on risk: as fish density increases, more fish are forced to feed in daytime or in riskier habitat and hence the per-individual mortality rate can increase.

Habitat and activity selection behaviour

The model fish make two contingent decisions each semi-daily time step: activity selection and habitat selection. Activity selection is the decision whether to feed or hide for the current day or night period. Habitat selection is the choice of which cell to occupy for feeding or hiding, within a radius (increasing with L_F) that fish are assumed to explore and be familiar with. Each time they make their decision, fish consider both feeding and hiding for each potential habitat cell, by evaluating a fitness measure; they select the combination of activity and cell that offers the highest value of the fitness measure. The fitness measure depends on both the habitat characteristics of the cell and the number of larger fish already occupying it: model fish cannot use food or hiding space occupied by larger fish.

The fitness measure is conceptually simple (though its implementing algorithm is quite complex; Railsback *et al.*, 2005). The fitness benefits of an alternative are represented as the expected probability of surviving both predation and starvation over a sliding time horizon, the next 90 days, multiplied by a term representing how growth affects fitness. Basing the fitness measure on survival of both predation and starvation causes individuals to balance growth and risk. The growth term represents the fitness benefits of reaching reproductive size (growth has the greatest importance for fish below spawning size) and of continued growth for adults (*e.g.* higher fecundity and ability to compete for feeding and spawning habitat; growth decreases in importance as a fish approaches the size of its largest competitor).

To evaluate the fitness measure for a behaviour alternative, model fish must predict the growth and survival probability they would experience over the 90 day time horizon. They do so by simply assuming that habitat and competitive conditions occurring at the current time step, and thus the predation risk and growth rate they would experience under the behaviour alternative, will persist over the time horizon. Therefore, survival of predation over the 90 days is S^{90} , where S is the probability of surviving predation for the current day, under the behaviour being considered. Starvation survival and growth over the time horizon depend on the individual's current L_F , mass and net energy intake rate; starvation is more likely if the individual is currently underweight or if its net energy intake is negative (Railsback *et al.*, 1999). The sliding time horizon of 90 days was chosen because it is long enough for starvation to become a severe risk for fish if they choose not to feed (Simpkins *et al.*, 2003), yet not too long for the prediction that current conditions persist over the time horizon to be useful.

Generally, the fitness measure causes individuals to choose behaviours that avoid mass loss if possible and provide growth if the additional predation risk is small. Although the simulated prediction that today's conditions will persist for 90 days is simplistic and often very wrong, it provides a useful model of adaptive behaviour. In previous studies, the fish IBM has reproduced a variety of ways that real fish adapt their choice of habitat and activity, *e.g.* in response to changes in temperature, life-history status, competition, food availability and habitat characteristics (Railsback *et al.*, 2005). The model also reproduced a variety of ways fish adapt their choice of habitat to episodic and seasonal changes in environment, changes in competition and predation, and food availability (Railsback & Harvey, 2002).

BEHAVIOUR SCENARIOS

Four scenarios of fish behaviour were used. The standard scenario is the full IBM as described above. The fixed-activity scenario has the choice of when to feed *v.* hide disabled: model fish always feed during the day and hide at night, though they still choose the best

available cell for these activities. Feeding during day was chosen for this scenario (instead of always feeding at night) somewhat arbitrarily, but reflects that salmonid populations have traditionally been observed most often during the day.

The weak-habitat-selection scenario disables the ability to identify the best available cell. The model fish still evaluate the fitness measure used to rank the cells they could move to, but the fitness measure is then multiplied by a random number between zero and one. Hence, fish are still very unlikely to select an extremely bad cell (which have fitness measure values near zero), but are unable to distinguish among the relatively good cells. (A preliminary experiment making the choice of cell completely random, from among all cells with non-zero depth, resulted in rapid extinction at all food levels. Model fish too often chose cells with high predation risk or extremely negative net energy intake.) Model fish still choose the best activity (feeding *v.* hiding) for the selected cell.

Finally, the no-hierarchy scenario disables the size-based feeding hierarchy. The order in which fish select habitat and consume the available food is randomized each time step instead of being ordered from the largest to the smallest fish.

STUDY SITE

The study site is a 1 km reach of the Green River in Daggett County, Utah, U.S.A., c. 37 km downstream of Flaming Gorge Dam. Physical habitat data for modelling channel shape, hydrodynamics and cover availability were collected in extensive field studies conducted in July 2007. Flow and temperature data were available from nearby long-term gauging stations. Over the simulated period, this large river had flows ranging from 13 to 193 m³ s⁻¹ and averaging 32 m³ s⁻¹. At the median flow of 24 m³ s⁻¹, the mean channel width is 71 m, mean depth is 0.70 m and mean velocity is 0.31 m s⁻¹. The modelled site includes a main channel with generally uniform habitat offering little hiding or feeding cover, plus a more variable and complex side channel (Fig. 1). Monthly mean water temperatures range from 2° C in January to 19° C in July.

The site's salmonid community is dominated by a naturally reproducing population of brown trout *Salmo trutta* L. 1758, but also includes hatchery-produced rainbow trout *Oncorhynchus mykiss* (Walbaum 1792) stocked upstream and small numbers of other salmonid species. The simulated fish use parameters for *S. trutta* but represent the entire community and hence are referred to generically as salmonids. To correspond with empirical observations, the model was initialized with a typical population of 440 adult salmonids ranging in L_F from c. 250 to 500 mm and 125 juveniles with mean L_F of 130 mm.

inSTREAM is typically calibrated by varying both the drift-food concentration and the parameter controlling risk of predation by terrestrial animals to find a combination of values that reasonably reproduces observed salmonid abundance and size. This process could not be used at the study site because no fish censuses are conducted there. Instead, the predation risk parameter value was adopted from another, similar, study site several km upstream where the same model was calibrated to site-specific fish data. Drift-food concentration was varied in the experiments instead of calibrated.

EXPERIMENT DESIGN

Simulation experiments were designed to address the question: what happens to the population as food availability is increased? Does the population reach a level where it is no longer limited by food availability? For each of the behaviour scenarios described above, the model was executed eight times, varying only drift-food concentration. These eight food scenarios varied the factor multiplied by each day's temperature to obtain its drift concentration. The food scenarios produce drift concentrations averaging, over the entire simulation, from 5.0×10^{-5} to 8.0×10^{-4} g m⁻³. For comparison, the model was roughly calibrated to observed fish sizes and densities at a mean drift concentration of 1.2×10^{-4} g m⁻³. Hence, all but the first and second food scenarios represent levels above those actually occurring at the study site. Drift-concentration scenarios higher than these proved computationally infeasible because they produced extremely high abundances of simulated salmonids.

Simulations used historic flow and temperature input representing October 2000 through to September 2007. Results from the first 3 years were not included in the analyses to give populations time to respond to the food and behaviour scenarios.

The results examined include the abundance and biomass of adult (age ≥ 1 years) salmonids, as the average of notional annual census values taken on 30 September of simulated years 2004 to 2007. Food production and consumption results, though, are reported as totals (including drift and search food) over all fishes on all days of the 2004 to 2007 period.

RESULTS

STANDARD BEHAVIOUR SCENARIO

With all fish behaviours activated, food limited the simulated population across the entire range of food availabilities: more food always produced more fishes and more fish biomass (Fig. 3). The rate at which population abundance increased with food availability also increased as food availability increased. At the highest drift concentration simulated, $8.0 \times 10^{-4} \text{ g m}^{-3}$, the mean adult fish density at median flow was 0.24 fish m^{-2} . The fraction of total available drift food consumed by salmonids also increased with food availability, at an increasing rate (except between 6.0×10^{-4} and $8.0 \times 10^{-4} \text{ g m}^{-3}$; Fig. 4).

The simulated fishes adapted to variation in food availability by changing the amount of time spent feeding and by switching between feeding during day *v.* night (Fig. 5). At the lowest food availability, feeding during both day and night was common. As food availability increased, fishes switched to almost exclusively night feeding and decreased the total frequency of feeding. At the highest food availability levels, the population became so abundant (Fig. 3) that competition forced some individuals to use daytime feeding.

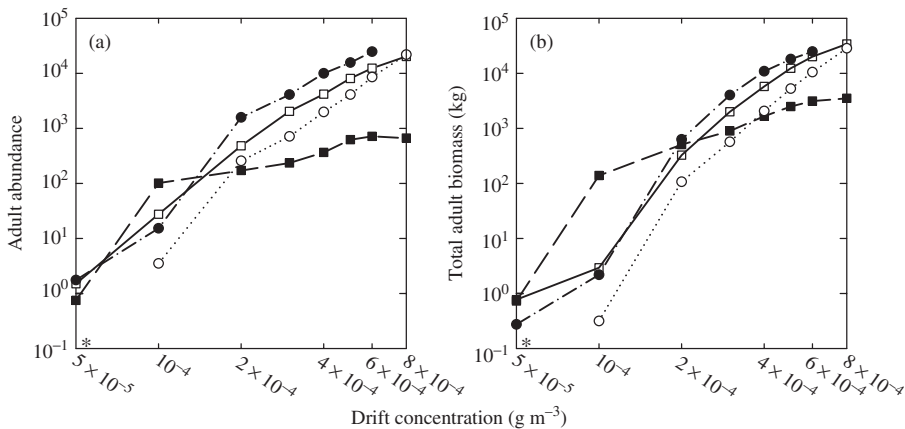


FIG. 3. Simulation results for (a) adult abundance and (b) population biomass in the standard (□), fixed activity (■), weak habitat selection (○) and no-hierarchy (●) scenarios. Note that both axes are logarithmic. *, abundance and biomass were zero at the lowest drift-food concentration in the weak-habitat-selection scenario. Because of their low and hence more variable values, results for the first three food availability scenarios (drift concentrations 0.5 , 1.0 and $2.0 \times 10^{-4} \text{ g m}^{-3}$) are means of five replicate simulations differing only in the model's random number sequence.

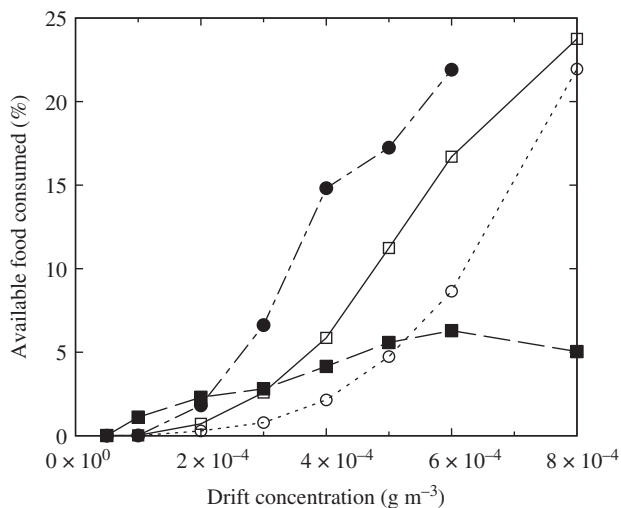


FIG. 4. Per cent of available food consumed by salmonids in the standard (□), fixed activity (■), weak habitat selection (○) and no-hierarchy (●) scenarios. Values are means over all days except the first 3 years simulated.

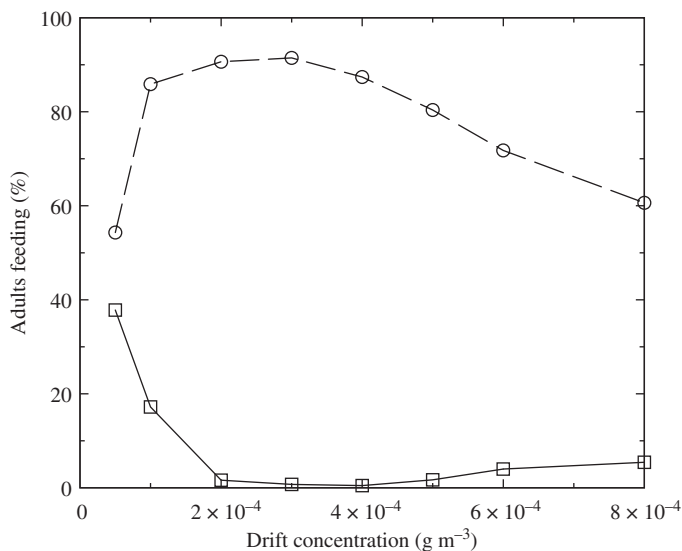


FIG. 5. Diel feeding patterns in the standard-behaviour scenario: per cent of all adult salmonids feeding during day (□) and night (○). Values are means over all days except the first 3 years simulated.

FIXED ACTIVITY SCENARIO

Forcing the simulated fishes to feed in daytime and hide at night produced a qualitatively different population response to food availability (Fig. 3). The rate of population increase with increasing food availability was much lower than under the standard scenario, and both abundance and biomass peaked at an intermediate food

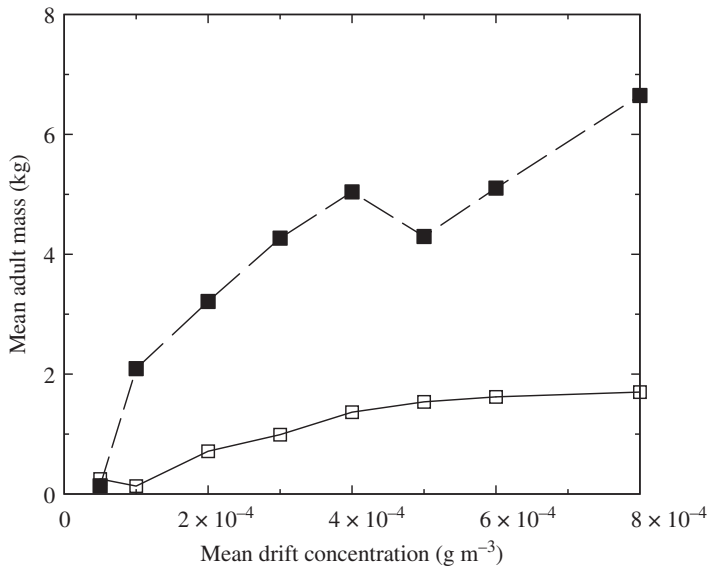


FIG. 6. Mean individual mass of fishes in the standard (\square) and fixed-activity (\blacksquare) behaviour scenarios. Values are from annual 30 September censuses. Results for the lowest three food scenarios are means of five replicate simulations.

level and actually decreased as food availability increased further. At intermediate and high drift concentrations, populations were much smaller than in the standard scenario. Predictably, these small populations used a relatively small proportion of available food (Fig. 4).

When forced to feed each day, the simulated salmonids became much larger than in the standard-behaviour scenario (Fig. 6). This result is not surprising because fishes in the standard scenario adapted to increasing food availability by switching almost exclusively to night feeding (Fig. 5), which is safer but greatly reduces intake (Fig. 2), and by not feeding at all on some days. The high abundance and competition which presumably caused some daytime feeding at the highest food levels (Fig. 5) probably also contributed to the lower mean size in the standard-behaviour scenario. The simulated salmonids in the fixed-activity scenario were larger despite a shorter average lifespan: the salmonids at least 3 years old, observed at the end of each simulation, were no more than 1% of all adults (age ≥ 1 years) in all the food scenarios. With the standard behaviour, this number always exceeded 24%.

WEAK HABITAT SELECTION

When simulated salmonids were unable to reliably identify the best habitat cell, the population response to food availability was similar in shape to that in the standard scenario (Fig. 3). At low drift concentrations, the population was much smaller with weak habitat selection, but the difference grew smaller as drift concentration increased and disappeared at $8.0 \times 10^{-4} \text{ g m}^{-3}$. As in the standard scenario, the fraction of food consumed by the simulated salmonid population increased sharply as food availability increased (Fig. 4).

NO HIERARCHY

When the size-based feeding hierarchy was disabled, the population's response to increasing food availability was even stronger than in the standard scenario (Fig. 3). At middle and high food levels, simulated abundance and biomass were roughly twice as high without the feeding hierarchy. Without larger individuals dominating the choicest feeding locations and times, the population was much more efficient at capturing the available food: at drift-food concentrations of 2.0×10^{-4} to $5.0 \times 10^{-4} \text{ g m}^{-3}$ the population consumed much more food without the feeding hierarchy than with it (Fig. 4).

DISCUSSION

The inSTREAM model used here is complex and, in this application, not extensively calibrated. Because it includes simple representations of important habitat dynamics and key adaptive behaviours, however, it is useful for exploring the role of behaviour in fish population responses to habitat change. The model's ability to reproduce observed patterns of behaviour-mediated population response to diverse changes (Railsback & Harvey, 2002; Railsback *et al.*, 2005) provides some confidence in these kinds of results. The ability to execute long-term, completely controlled experiments is a major advantage of such simulation models. The experiment simulated here would be impossible to conduct on real stream-fish populations.

UBIQUITY OF FOOD LIMITATION

The simulation experiments indicated that food limitation, defined as a strong positive effect of increased food on population size, is ubiquitous. With the exception of only one behaviour scenario, with the ability to adaptively select feeding *v.* hiding activity turned off, more food always produced larger populations, even at drift-food concentrations much higher than those producing realistic salmonid abundances. In fact, one basic concept in the traditional understanding of food limitation, that food becomes less important as it becomes more available, was contradicted. In sharp contrast, the simulated population increased, at an increasing rate, as food supply increased. Fishes consumed a higher, not lower, percentage of the available food as drift-food concentration increased. Further simulations at even higher drift concentrations might find food levels where the population becomes so dense that a lack of space prevents further population growth. It is worth considering, however, that very dense fish populations accumulate biomass rapidly in hatcheries, where food is virtually unlimited.

Why did the percentage of food consumed increase instead of decrease as food concentration increased? Much more of the total habitat area becomes energetically profitable for more fishes at higher food concentrations. In inSTREAM fishes avoid habitat with negative net energy intake: where velocities or depths are too low to provide much drift, or where velocities are so high that swimming costs exceed energy intake. Especially at night, moderate drift concentrations yield relatively little energetically profitable habitat (Fig. 2). But increasing the drift concentration moves the curves in Fig. 2 upwards, so a wider range of velocities provides the opportunity for growth. At high drift concentrations, fishes can feed in much more

of the stream area and consume much more of the available food, resulting in greater abundance.

EFFECTS OF BEHAVIOUR ON THE POPULATION RESPONSE TO FOOD AVAILABILITY

The experiments identified activity selection as the behaviour largely responsible for the population's ability to continually grow as more food was provided. This behaviour lets fishes segregate temporally (between night and day) in addition to spatially: multiple fishes can feed at the same spot if they feed at different times of day. More importantly, activity selection is a way to convert higher food resources to lower predation risk: when food levels were higher, the model fishes could avoid starvation and still grow while feeding less during daytime when predation risks are higher. Model fishes could even hide for whole days between feeding bouts while still maintaining growth. These kinds of adaptive shifts in activity and feeding times have been convincingly demonstrated in real salmonids (Metcalf *et al.*, 1998; Alanärä *et al.*, 2001; Orpwood *et al.*, 2006). The importance of this behaviour to simulated population responses is in accord with the current understanding of trophic interactions as potentially affected strongly by individual behaviour (Abrams, 1995; Werner & Peacor, 2003).

When activity selection was turned off, the population not only was much smaller at middle and high food concentrations, it became limited by something other than food. The limitation appears to have been the availability of safe and profitable habitat for large individuals. When forced to feed during daytime, the simulated fishes that survived became very large, which makes it difficult to maintain sufficient intake during times of low food availability (*e.g.* during low temperatures) or high metabolic demands (*e.g.* during high temperatures). In the simulations, there appeared to be relatively little habitat where very large individuals could consistently obtain sufficient food without also incurring high predation risk.

Habitat selection had less effect on the population's response to food availability. Some ability to select safe and profitable habitat is clearly essential, as shown in the preliminary experiment with completely random habitat selection that always produced extinction. In the weak-habitat-selection scenario, the population was much lower than in the standard scenario at low and middle food availability levels. But the difference between these two scenarios got smaller as drift concentrations increased; when food was extremely abundant, the ability to identify good habitat became less and less important.

Hierarchical feeding, in which larger fishes exclude smaller ones from their preferred feeding sites, appears to reduce the population's ability to use high food resources. With the feeding hierarchy turned off, fish abundance and biomass were far higher at middle and high drift-food concentrations. This result was not surprising: preventing the largest fishes from dominating feeding sites when food is abundant would be expected to allow more fishes to feed profitably and persist.

CONSEQUENCES FOR STREAM FISH CONSERVATION

These simulation results imply that food limitation may not be a very useful concept for stream fish conservation: they indicate that food availability can have a

strong effect on population size even when the food supply is large. The experiment did not find a threshold above which additional food availability is unimportant, and it found food and predation effects to be highly interdependent.

Activity selection has the potential to make effects of food availability on population size difficult to detect *via* daytime observations. Less diurnal feeding when food supply and fish condition are high is well documented in stream salmonids (Metcalf *et al.*, 1998, 1999). In the standard scenario simulations, the mean abundance of adult fishes increased by >150 times when drift concentration increased from 1.0×10^{-4} to $4.0 \times 10^{-4} \text{ g m}^{-3}$, but the number of fishes feeding during daytime increased only by a factor of four. Most of the increase in population would not be detected via daytime observations of feeding fishes.

The result that the per cent of food consumed by the fish population went up, not down, as food supply increased is also potentially important for conservation. It is tempting to assume that food should not be important if a population is consuming only a small fraction of the available supply. The weakness of this assumption has already been shown for shorebirds using a food resource more spatially homogeneous than drift food is for fishes. Goss-Custard *et al.* (2003), also using an IBM, concluded that leaving 100% of a shorebird population's energy demands available as food still caused a serious reduction in survival: even though enough food was available, its reduced density combined with the limited rate at which birds can find and harvest food led to starvation. Goss-Custard *et al.* (2003) found that food availability eight times the population's consumption was needed to prevent starvation. This problem is even more pronounced in the fish simulations reported here, because much of the river habitat is not energetically profitable at low to moderate drift concentrations. At such concentrations, most of the total food availability occurred in habitat where fishes could not maintain a positive net energy balance. At drift densities producing simulated fish abundance close to observed levels (1.0×10^{-4} to $2.0 \times 10^{-4} \text{ g m}^{-3}$), the simulated population consumed <1% of the food available, yet the population increased very sharply with increasing food availability.

Because inSTREAM's depiction of drift-food availability is very simple, these results should not be taken literally. The model does not represent the influence of neighbouring habitat cells on food availability (food not captured in one cell does not contribute to food availability in downstream cells), so it may underestimate the proportion of drift captured by fish at the population level. The results do suggest, however, that the ratio of food availability to fish consumption is a risky basis for conservation decisions. The amount of food needed to sustain a population may be much higher than expected because many locations in a stream are not energetically profitable or safe from predators.

How general are these results? The main mechanism identified as the way fish can convert higher food availability to higher survival and larger populations, activity selection, can be effective only if there is cover where fish can hide from predators when not feeding. The relation between food supply and population size is therefore expected to be different at sites where inadequate hiding cover makes activity selection ineffective. Likewise, a different relation would be expected at sites where mortality is dominated by causes that are not easy to hide from, such as winter ice or acute thermal stress. Nothing about the modelled site, however, suggests that this study's conclusions would not be applicable to other populations of fish able to utilize hiding cover.

This study illustrates how models representing individual adaptive behaviour can produce results that contradict traditional ways of thinking about and modelling conservation problems. These models also allowed experiments to be conducted that would be impossible in the field (*e.g.* by turning off some behaviours) and, sometimes, to arrive at explanations that are unexpected but believable once discovered.

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References

- Abrams, P. A. (1995). Implications of dynamically variable traits for identifying, classifying, and measuring direct and indirect effects in ecological communities. *American Naturalist* **146**, 112–134.
- Alanärä, A., Burns, M. D. & Metcalfe, N. B. (2001). Intraspecific resource partitioning in brown trout: the temporal distribution of foraging is determined by social rank. *Journal of Animal Ecology* **70**, 980–986.
- Filbert, R. B. & Hawkins, C. P. (1995). Variation in condition of rainbow trout in relation to food, temperature, and individual length in the Green River, Utah. *Transactions of the American Fisheries Society* **124**, 824–835.
- Fretwell, S. D. (1987). Food chain dynamics: the central theory of ecology? *Oikos* **50**, 291–301.
- Goss-Custard, J. D., Stillman, R. A., West, A. D., Caldow, R. W. G., Triplet, P., Durell, S. E. A. I. V. d. & McGrorty, S. (2003). When enough is not enough: shorebirds and shellfishing. *Proceedings of the Royal Society B* **271**, 233–237.
- Goss-Custard, J., Burton, N. H. K., Clark, N. A., Ferns, P. N., McGrorty, S., Reading, C. J., Rehfish, M. M., Stillman, R. A., Townend, I., West, A. D. & Worrall, D. H. (2006). Test of a behavior-based individual-based model: response of shorebird mortality to habitat loss. *Ecological Applications* **16**, 2215–2222.
- Hairston, N. G., Smith, F. E. & Slobodkin, L. B. (1960). Community structure, population control, and competition. *American Naturalist* **94**, 421–425.
- Hill, J. & Grossman, G. D. (1993). An energetic model of microhabitat use for rainbow trout and rosyside dace. *Ecology* **74**, 685–698.
- Hughes, N. F. (1992). Selection of positions by drift-feeding salmonids in dominance hierarchies: model and test for Arctic grayling (*Thymallus arcticus*) in subarctic mountain streams, interior Alaska. *Canadian Journal of Fisheries and Aquatic Sciences* **49**, 1999–2008.
- Metcalfe, N. B., Fraser, N. H. C. & Burns, M. D. (1998). State-dependent shifts between nocturnal and diurnal activity in salmon. *Proceedings of the Royal Society B* **265**, 1503–1507.
- Metcalfe, N. B., Fraser, N. H. C. & Burns, M. D. (1999). Food availability and the nocturnal vs. diurnal foraging trade-off in juvenile salmon. *Journal of Animal Ecology* **68**, 371–381.
- Orpwood, J. E., Griffiths, S. W. & Armstrong, J. D. (2006). Effects of food availability on temporal activity patterns and growth of Atlantic salmon. *Journal of Animal Ecology* **75**, 677–685.
- Osenberg, C. W. & Mittelbach, G. G. (1996). The relative importance of resource limitation and predator limitation in food chains. In *Food Webs: Integration of Patterns and Dynamics* (Polis, G. A. & Winemiller, K. O., eds), pp. 134–148. New York, NY: Chapman & Hall.
- Railsback, S. F. & Harvey, B. C. (2002). Analysis of habitat selection rules using an individual-based model. *Ecology* **83**, 1817–1830.

- Railsback, S. F., Lamberson, R. H., Harvey, B. C. & Duffy, W. E. (1999). Movement rules for spatially explicit individual-based models of stream fish. *Ecological Modelling* **123**, 73–89.
- Railsback, S. F., Harvey, B. C., Hayse, J. W. & LaGory, K. E. (2005). Tests of theory for diel variation in salmonid feeding activity and habitat use. *Ecology* **86**, 947–959.
- Simpkins, D. G., Hubert, W. A., Martinez Del Rio, C. & Rule, D. C. (2003). Physiological responses of juvenile rainbow trout to fasting and swimming activity: effect of body composition and condition indices. *Transactions of the American Fisheries Society* **132**, 576–589.
- Werner, E. E. & Peacor, S. D. (2003). A review of trait-mediated indirect interactions in ecological communities. *Ecology* **84**, 1083–1100.

Electronic Reference

- Railsback, S. F., Hayes, J. W. & LaGory, K. E. (2006). Simulation analysis of within-day flow fluctuations on trout below Flaming Gorge Dam. *Technical Memorandum ANL/EVS/TM/06-01*. Argonne, IL: Argonne National Laboratory. Available at www.osti.gov/bridge