Environ Biol Fish (2014) 97:615–625
DOI 10.1007/s10641-013-0186-7

Feeding modes in stream salmonid population models: is drift feeding the whole story?

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Received: 15 March 2013 / Accepted: 23 September 2013 / Published online: 12 October 2013

Abstract Drift-feeding models are essential components of broader models that link stream habitat to salmonid populations and community dynamics. But is an additional feeding mode needed for understanding and predicting salmonid population responses to streamflow and other environmental factors? We addressed this question by applying two versions of the individual-based model inSTREAM to a field experiment in which streamflow was varied in experimental units that each contained a stream pool and the adjacent upstream riffle. The two model versions differed only in the feeding options available to fish. Both versions of inSTREAM included drift feeding; one also included a search feeding mode to represent feeding in which food availability is largely independent of streamflow, such as feeding from the benthos, or feeding from the water column or the water's surface in low water velocities. We compared the abilities of the two model versions to fit the observed distributions of growth by individual rainbow trout (*Oncorhynchus mykiss*) in the field experiment. The version giving fish the daily choice between drift or search feeding better fit observations than the version in which fish fed only on drift. Values for drift and search food availability from calibration to the individual mass changes of fish in experimental units with unaltered streamflow yielded realistic distributions of individual growth when applied to experimental units in which streamflow was reduced by 80 %. These results correspond with empirical studies that show search feeding can be an important alternative to drift feeding for salmonids in some settings, and indicate that relatively simple formulations of both processes in individual-based population models can be useful in predicting the effects of environmental alterations on fish populations.

Keywords Drift · Search feeding · Foraging mode · Individual-based modeling · Salmonidae

Introduction

One major benefit of drift-feeding models (e.g., Hughes and Dill 1990) is their contribution to the "individual-based ecology" of stream salmonids: theory and models for how populations are affected by, and affect, characteristics and behavior of individuals (Van Winkle et al. 1998; Railsback et al. 2009). Feeding is one of the most important behaviors linking habitat to individual fitness and, therefore, to population ecology. Perhaps in part because it occurs over relatively small and observable areas and times, drift feeding is a relatively well-studied and well-modeled salmonid behavior. Consequently, drift-feeding models are essential components of several models that link, for example, hydraulic habitat to trout habitat selection (e.g., Guensch et al. 2001) and stream

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habitat to trout population and community dynamics (Van Winkle et al. 1998; Railsback et al. 2009).

Models with different objectives often need different representations of the same process. Feeding models for use as components of individual-based population models may be quite different from feeding models intended for other purposes. Drift-feeding models designed to understand in detail how fish physiology, hydraulic conditions, and drift characteristics interact to determine food intake and growth typically include details that are clearly important at the individual level, such as the effects of drift particle size and water velocity on the ability of fish to detect prey (e.g. Hughes et al. 2003; Piccolo et al. 2008a, b). When understanding competition among fish for feeding sites is added as a modeling objective, then modeling of additional processes such as water-column entry, transport and settling of drift organisms and depletion of drift by individual fish may be required (Hughes 1992a; Hayes et al. 2007). However, when a model's objective is to understand and predict long-term population dynamics over substantial lengths of stream (e.g. Harvey and Railsback 2009), a highly detailed representation of feeding may not be feasible or appropriate, because of the challenges in simulating fine-scale, taxon-specific processes such as drift entry and exit over large areas and lengthy timespans, or because the effects on model results do not justify the additional complexity and uncertainty.

This understanding that different representations of feeding may be appropriate for salmonid models with different objectives leaves the question: what is an adequate way to represent feeding in a model designed for a particular purpose? Individual-based population-level models such as inSTREAM (Railsback et al. 2009 describes the model in detail) are designed for large-scale, long-term applications, yet they include simulation of fish feeding on daily or sub-daily time steps. For such models, which mechanisms related to feeding must be retained and which can be left out? One way to answer this question is to develop alternative models and contrast their ability to reproduce empirical observations.

Here we explore the decision of whether to include in individual-based population models a salmonid feeding behavior that has received relatively little attention from modelers: search feeding. While drift feeding is a sit-and-wait form of predation that relies on current to deliver food, search feeding is active searching over the streambed, water column, or surface for food. Drift feeding is clearly a very important and characteristic feeding mode for salmonids, but a variety of salmonids in a variety of lotic systems also use search feeding (e.g., Tippets and Moyle 1978; Grant and Noakes 1987; Nielsen 1992; Fausch et al. 1997; Rosenfeld and Raeburn 2009). Active search feeding may be particularly important during low streamflows, which are often of special interest in instream flow assessments and therefore commonly simulated in trout population models. Is an alternative to drift feeding essential for understanding and predicting trout population responses to flow under conditions often of interest in management decision support? We address this question by comparing the performances of two versions of inSTREAM: one that allows fish to feed only on drift and one that allows feeding via both drift and search feeding. In particular, we contrast the ability of these two model versions to reproduce observed effects of flow reductions on growth of rainbow trout (*Oncorhynchus mykiss*) in a field experiment.

Methods

A field experiment on the effects of streamflow on rainbow trout growth and survival in a small California stream (Harvey et al. 2006) provided the observations used to test the two versions of inSTREAM. The experiment spanned 48 d during the dry season (19 July to 4 September 2003), when streamflow declined steadily from 30 to 15 l/s and turbidity was negligible. The experiment included 8 experimental units in a natural stream, four with unaltered flow and four with flow reduced by about 80 % by diverting water around the units in plastic pipes. Each experimental unit included one pool and all or part of the adjacent upstream riffle, enclosed with plastic mesh fencing; units ranged 9.0–15.3 m in total length (mean 11.7 m). Riffle sections within experimental units averaged 3.5 m long, 2.1 m wide and 8 cm deep. Pools within units averaged 8.2 m long, 3.5 m wide and 26 cm deep. Units initially contained 10 to 20 fish (mean 13) ranging 9.5 – 17.0 cm fork length (mean 12.0 cm). Fish numbers and size distributions varied among experimental units because we used naturally occurring individuals. Field measurements included: the mass of individual trout in the enclosures at the beginning and end of the experiment (with individuals identified by PIT tagging), multiple measurements of invertebrate drift in all experimental units, unit-specific temperature records, delineation and characterization of habitat cells appropriate for the model and measurements of hydraulic conditions within those cells on three dates during the experiment (Fig. 1). In the research at hand, we used the unit-specific field measurements to separately model all 8 experimental units. We also obtained diet samples from all fish captured at the end of the experiment using gastric lavage and later computed taxon-specific biomass composition of the gut contents using length-mass regressions (Harvey et al. 2006).

In previous studies, inSTREAM has reproduced a wide range of observed habitat selection patterns, including shifts in habitat use in response to floods, competition, predation risk, change in season, and reduced food availability (Railsback and Harvey 2002). The model has also reproduced a number of observed population-level phenomena (Railsback et al. 2002). The model is designed to cover multiple generations and has been used in simulations of up to 78 years, but the simulations offered here cover only the time period of the field experiment and not the entire lifecycle. We used version 5.0 of inSTREAM, which uses a 1-d time step, with stream habitat represented as sets of polygonal cells. Habitat cells were delineated such that (1) hydraulic conditions were relatively uniform within a cell, while (2) the full range of natural hydraulics was captured among cells and (3) cell length and width were > 1 m, the approximate scale over which trout select feeding habitat. The habitat variables that affect trout food intake, growth, and survival in the model are: water depth, velocity, temperature, and turbidity; fraction of the cell containing velocity shelters that reduce the swimming energy needed to capture drifting food; distance to hiding cover; the concentration of invertebrate drift (g/cm^3); and the production rate of search food (g/cm^2/h). Depth, velocity, velocity shelter and distance to hiding cover vary among cells; temperature, turbidity, and the two food variables do not. The model assumes that distance to hiding cover and fraction velocity shelter are constant over time, but streamflow, temperature and turbidity vary daily. While habitat-cell-specific depths and velocities are usually calculated from streamflow via hydraulic modeling, in this case modest changes in hydraulic conditions during the experiment allowed us to simply apply the three sets of empirical measurements to three blocks of dates.

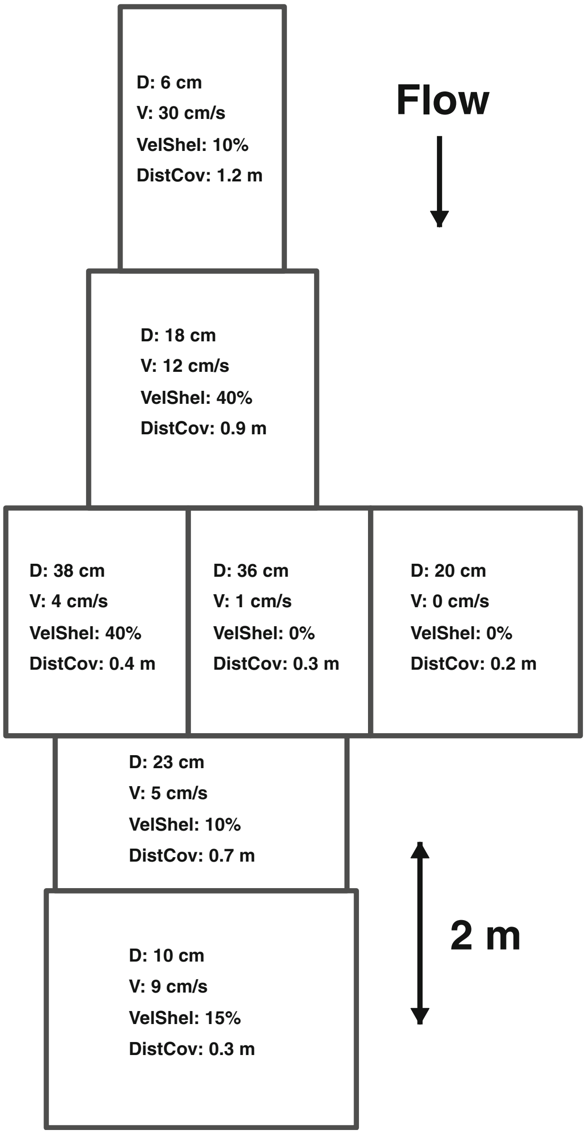

Fig. 1 Habitat cell delineation within one of the 8 experimental units in a small California stream simulated using a spatially explicit individual-based model. The diagram depicts one of the four control units in which streamflow was not altered. The habitat cells contain their cell-specific characteristics: depths (D) and water velocities (V) quantified by averaging measurements at three points along a transect through each cell (in this example from measurements taken near the middle of the experiment); Vel Shel describes the % of each cell where fish might hold position at a water velocity <30 % of the main flow in the cell. The use of velocity shelters reduces the energetic cost of drift feeding; Dist Cov describes a characteristic distance to cover, which influences predation risk

The daily growth of each trout is a function of food availability, the trout's ability to catch food, competition among trout, energetic costs including swimming, and water temperature. Both drift and search feeding are represented (except in the version used here with search feeding turned off); individuals evaluate the net energy intake of both feeding modes when selecting habitat cells. Drift feeding is modeled using a simplified interpretation of standard drift-feeding assumptions. Drift concentration is treated as a constant over space and time, and variation in prey size is neglected. Fish are assumed to detect all drift that passes through a rectangle, perpendicular to flow, with width equal to two times the detection distance and height equal to the minimum of detection distance or depth. Detection distance increases linearly with fish length. The fraction of detected drift that is actually captured and consumed decreases logistically as the ratio of water velocity to fish swimming speed increases, reaching about 50 % capture success when velocity equals the fish's maximum sustainable swimming speed (which depends on fish length and temperature). These assumptions and the parameters implementing them were based primarily on data reported by Hill and Grossman (1993), which have been generally supported by subsequent research (e.g. Piccolo et al. 2008a). Search feeding is modeled extremely simply because it is less well-defined and studied. The basic assumptions are that search food intake rate: 1) is relatively independent of fish size: larger fish may see food better but smaller fish may be better able to feed on small or less-accessible food; and 2) decreases as velocity increases, relative to fish swimming ability, due to reduced maneuverability and detection probability. Search food availability is a constant density (prey mass per stream area) produced daily, independent of flow. Search food intake is equal to search food availability times a parameter representing the area one fish consumes food from per day times a function that decreases intake linearly to zero as cell velocity approaches the fish's maximum sustainable swimming speed. Swimming costs increase with cell velocity, but habitat cells with velocity shelters allow some fish to swim at 30 % of the cell's water velocity, to reflect observations of habitat selection by drift feeding fish (Fausch 1984). Fish using search feeding are assumed not to use velocity shelter.

The virtual trout compete for food and velocity shelters in a size-based hierarchy, following Hughes (1992a, b) and Nakano (1995). Each cell contains, each day, a fixed amount of food and velocity shelter; trout select their habitat cell and feeding mode in descending order of size and deplete the food and shelter area in their selected cell. Food and shelter used by larger fish are not available to smaller fish in the same cell. This representation of asymmetric competition coincides with laboratory observations of filtering interference of subordinates by Atlantic salmon (*Salmo salar*) (Nilsson et al. 2004).

The model's fish are subject to both starvation and and non-starvation risks. The daily probability of surviving each of several mortality sources is a deterministic function of habitat and fish conditions, but whether a trout survives each mortality source, each day, is determined by drawing a random number and comparing it to the survival probability. Survival of avian and mammalian predators increases with increasing depth and is higher for small fish (Harvey and Stewart 1991). The model also includes the assumption that survival of avian and mammalian predators increases with increasing water velocity. The probability of surviving predators also increases as distance to hiding cover decreases. Survival of starvation decreases as the fish's mass falls below the "healthy" mass for its length. Velocities higher than a fish's maximum sustainable swim speed reduce survival, as do depths much less than a fish's length (which subject a fish to stranding and high predation risk).

Habitat selection is the key behavior of model trout. The virtual trout daily select the cell (within a radius they are assumed to know growth and risk conditions in, equal to 20 times the square of the fish's length [in cm]), that offers the highest value of a fitness indicator, "Expected Maturity" (EM; Railsback et al. 1999). In the simulations presented here, all individuals always had access to all of their experimental unit's habitat cells. The value of EM is a fish's estimated probability of surviving both starvation and non-starvation risks over a future time horizon. For immature fish, EM also includes a term equal to the expected fraction of reproductive size achieved at the end of the time horizon; this term encourages small fish to select habitat that provides growth opportunities. We use 90 d for the time horizon as it produces adult habitat choice nearly identical to an infinite horizon while encouraging immature fish to achieve reproductive maturity in a realistic time. This approach, combined with inSTREAMS's feeding, growth, competition and survival assumptions, produces habitat selection behavior closely resembling territoriality under typical conditions (Railsback and Harvey 2002).

Because this study addresses feeding models and because fish enjoyed high survival during the field experiment (98 of 106 fish were collected at the end of the experiment), we focused on fish growth in evaluating the simulation results. To give some emphasis to the growth of larger individuals, we evaluated simulations by quantifying the unit-specific mean squared differences in absolute growth rates for all surviving fish. Each simulation of each experimental unit started with unit-specific numbers and sizes of fish captured at the beginning of the experiment. To account for the loss of fish during the experiment (one fish each from four experimental units, two fish each from two units), these individuals were removed mid-way through the 48-d simulations. (The model software includes a graphical interface that allows individuals to be identified and removed at any point during a simulation.) Also, although individual fish considered predation risks in selecting habitat cells during the simulations, we prevented mortality to provide exact correspondence between the actual and simulated sets of surviving individuals. We set predation risk parameters to values that reflect calibration of the model to similar small streams in northwestern California; these values are supported by empirical measurements of predator encounter rates (Harvey and Nakamoto 2013).

To contrast scenarios in which fish fed only on drift and those in which both drift and search food were available, we performed separate calibrations for each experimental unit of model versions with and without search feeding, using the food parameters for calibration. Ranges used in calibration of drift concentration and search food availability (in the version that included it) covered 25 – 300 % of values commonly obtained in calibration of the model to similar systems. The calibrated drift and search food parameters were identified as those producing the lowest root mean squared difference between simulated and observed absolute growth for all the surviving trout in an experimental unit. To test the model's ability to predict the contrast between treatments in the experiment (the observed effect of reduced streamflow on trout growth), we also applied the among-unit mean calibration values from the control units to the reduced-flow units for both the drift-only and drift + search scenarios. We contrasted calibration results under drift-only versus drift + search scenarios by conducting paired *t*-tests using the average root mean squared differences between simulated and observed individual growth for the two scenarios in each experimental unit.

Results

The field experiment yielded broad ranges of individual growth within experimental units and substantial variation in patterns of individual growth among experimental units and between treatments (Fig. 2). Competition appears to have influenced growth. Absolute growth increased with fish size. Similar, large gains in mass by multiple fish within an experimental unit occurred only in units where either the largest fish or the two largest fish were not recovered at the end (e.g. Units 5 and 7).

Calibration results from simulations of fish in control units of the field experiment yielded consistently better fit to the observed data when fish were allowed to feed on both drift and search food, compared to calibration of drift concentration with search food set to zero (paired *t*-test, 3 df, P=0.022). The drift-only calibration that minimized the root mean square difference between observed and simulated absolute growth tended to underestimate the growth of both the smallest and the largest individuals in the experimental units (Fig. 3). In providing closer overall fits to field observations, the drift + search calibration closely matched observed results for one experimental unit (Unit 3), and otherwise tended to overestimate growth by smaller individuals and underestimate growth by larger individuals. Results of calibration of the control units in the drift + search scenario also closely matched observations with mass change quantified as relative growth rate. Observed among-unit mean relative growth rate was 0.42 %/d while the drift + search calibration result was 0.46 %/d. Drift-only calibration yielded an among-unit mean relative growth rate of 0.07 %/d. Drift concentrations that would bring mean relative growth rates for the drift-only scenario closer to observed values would have dramatically over-predicted the absolute growth rates for larger individuals.

Calibration to growth of individuals in experimental units with streamflow reduced by 80 % yielded the same pattern in the relative fits to observed results of drift + search versus drift-only simulations: drift + search was superior (paired *t*-test, 3 df, P=0.033; Fig. 4). A tendency to underestimate absolute growth rate for both the smallest and largest individuals in drift-only calibrations paralleled the results for control units. Also parallel to the results for control units, drift + search calibration tended to slightly overestimate the growth of small individuals and underestimate the growth of large individuals.

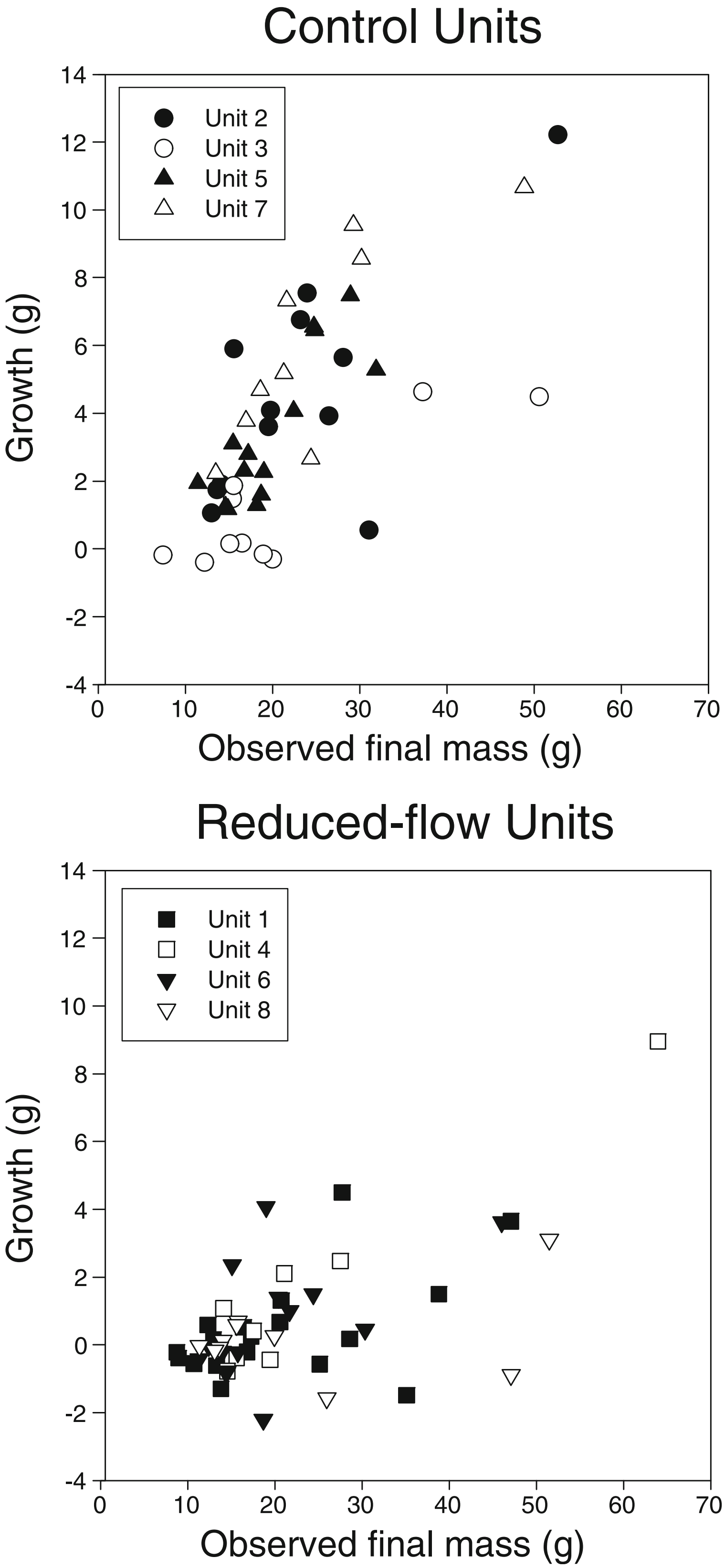

Fig. 2 Individual growth results for rainbow trout from a field experiment in northwestern California in which streamflow was reduced by about 80 % in 4 of 8 experimental units in a small stream

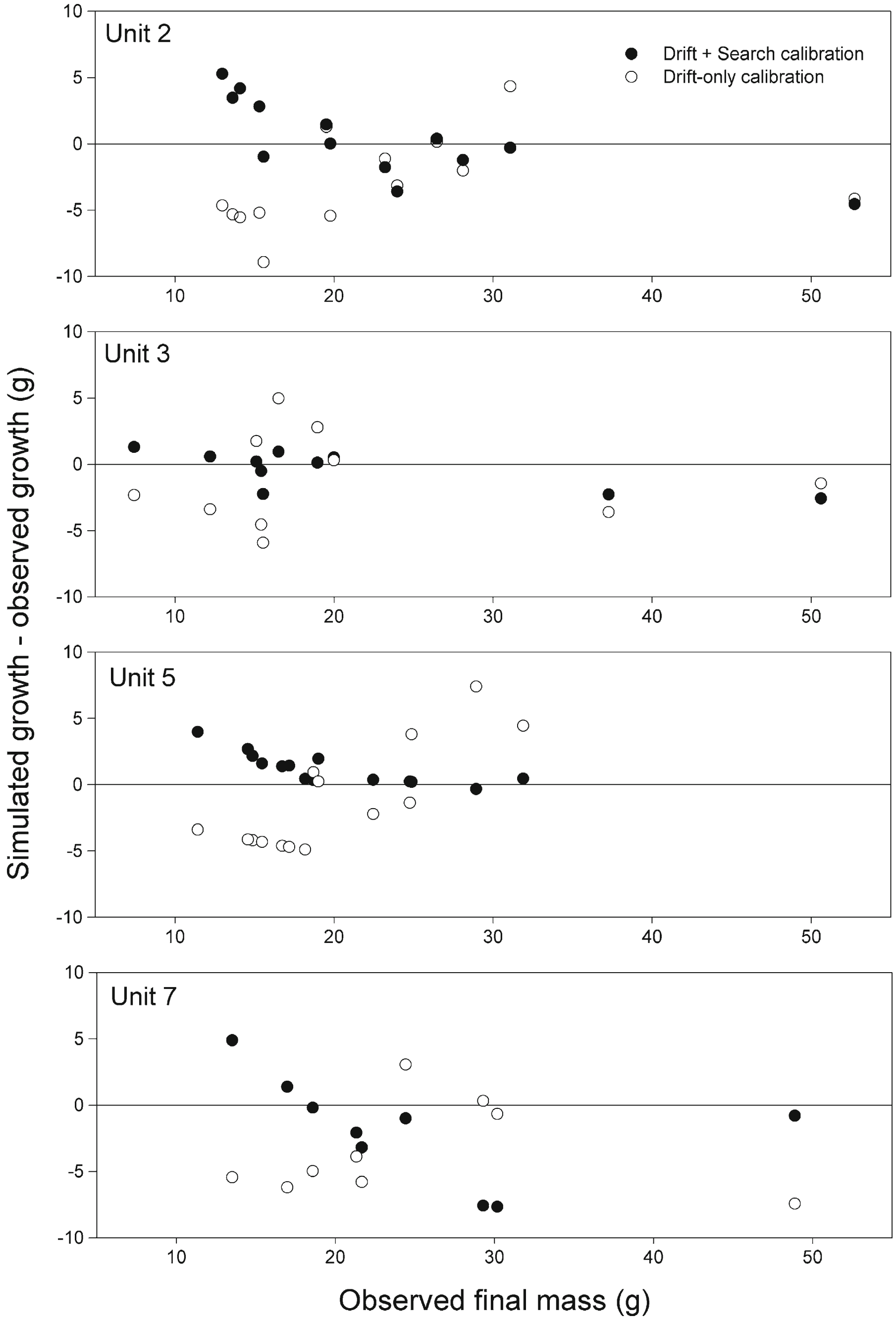

Fig. 3 IBM simulation results for individual masses of fish at the end of the field experiment in the four experimental units with unaltered streamflow. Simulation results are expressed as differences from the observed masses of individual fish. Values for Drift + Search and Drift-only scenarios reflect the results of unit-specific calibrations that minimized the root mean square differences between observed and simulated individual masses

The most striking result of the simulations was inSTREAM's ability, when drift and search food availability were calibrated to the control units, to predict individual masses in the reduced-flow units (Table 1; Fig. 4). The model version including both drift and search feeding predicted growth in reduced-flow units more accurately than did the drift-only version (paired *t*-test, 3 df, *P*=0.007; Table 1; Fig. 4).

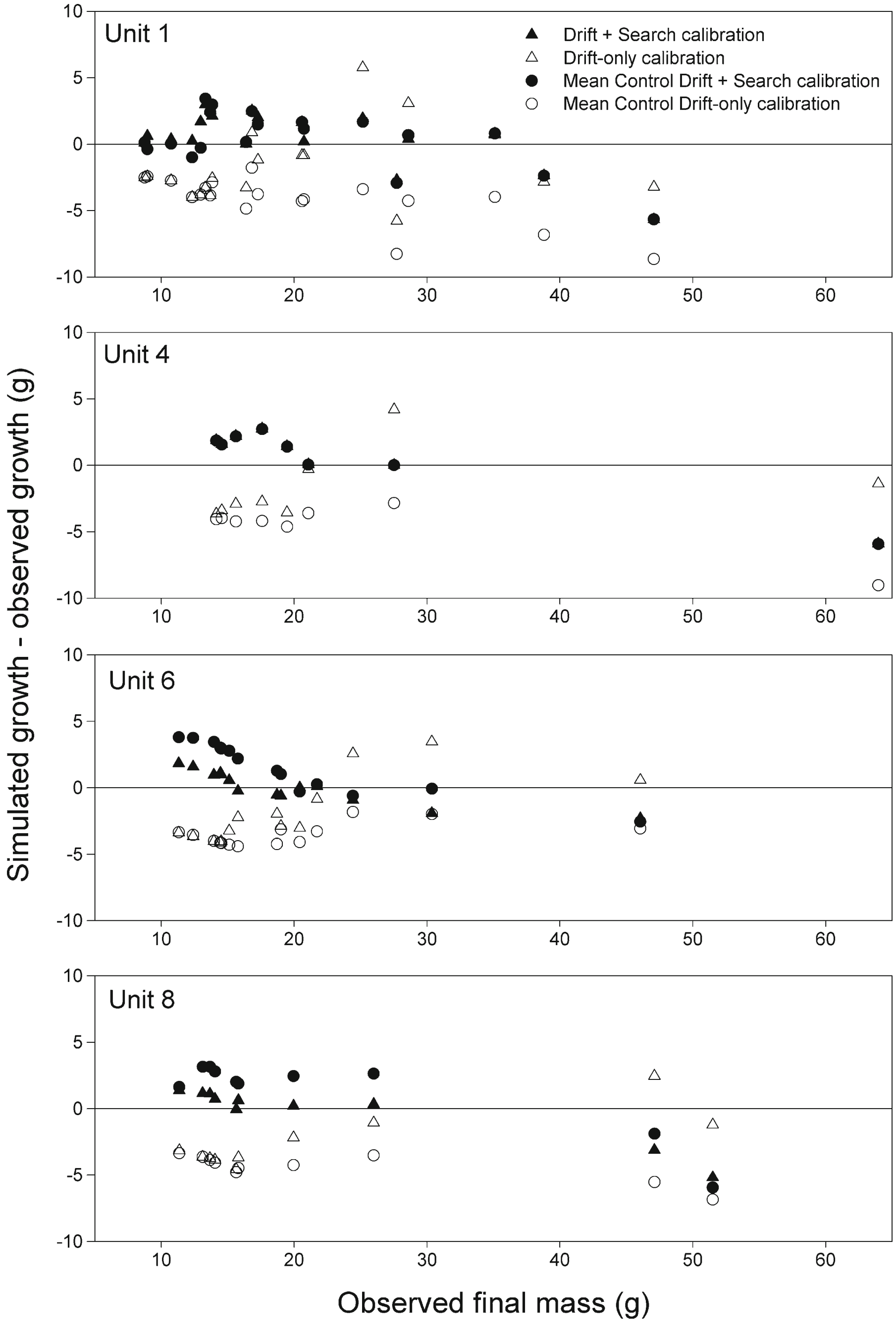

Fig. 4 IBM simulation results for individual masses of fish at the end of the field experiment in the four experimental units with streamflow reduced by 80 %. Simulation results are expressed as differences from the observed masses of individual fish. "Drift + Search Calibration" and "Drift-only Calibration" reflect the results from unit-specific calibrations that minimized the root mean square differences between observed and simulated individual masses. The other two sets of results reflect simulation of reduced-flow units using mean food availability parameters from calibration of the four control units

Drift concentrations obtained by model calibration approximated those measured in the field, with the exception of drift-only calibration values from reduced-flow units. Mean drift concentrations measured in the control units declined from 2.2×10^{-9} to 1.0×10^{-9} g/cm^3 during the experiment (Harvey et al. 2006), while

Table 1 Results from individual-based-model simulation of fish in a field experiment on the effects of streamflow on fish growth and survival. Results are for four experimental units subject to a streamflow reduction of about 80 %. Values indicate root mean squared differences (g) between simulated and observed masses of individuals collected from each unit at the end of the experiment, under scenarios in which both drift and search food were available and scenarios in which only drift was available. The two columns on the right show results using the mean calibrated food availabilities from four experimental units with unaltered streamflow

	Scenario			
Unit	Drift + search, unit-specific calibrations	Drift-only, unit-specific calibrations	Drift + Search, mean of control calibrations	Drift-only, mean of control calibrations
1	2.1	3.2	2.2	4.6
4	2.6	3.0	2.6	4.9
6	1.2	3.1	2.4	3.6
8	2.0	3.2	3.0	4.6

calibration values in the drift + search scenario ranged 1.5×10^{-9} g/cm^3 to 2.2×10^{-9} g/cm^3 and calibration values in the drift-only scenario ranged 1.1×10^{-9} g/cm^3 to 2.5×10^{-9} g/cm^3. Drift + search calibration of the reduced-flow units produced calibrated drift concentrations of 1.5×10^{-9} g/cm^3 to 2.2×10^{-9} g/cm^3. In contrast, under the drift-only scenario calibrated values of drift concentration in the reduced-flow units ranged 3×10^{-9} g/cm^3 to 4.4×10^{-9} g/cm^3. Note that even these high values commonly produced underestimates of individual growth in the drift-only scenarios.

The previous paragraph reveals greater among-unit similarity in the calibrated values for drift concentration in the drift + search versus the drift-only scenario. Calibration values for search food availability also exhibited consistency among units in the drift + search scenario. These values ranged 1.2×10^{-6} to 1.8×10^{-6} g/cm^2/h over all 8 experimental units, with the same mean of 1.4×10^{-6} g/cm^2/h in both control units and reduced-flow units.

Finally, one contrast in the field data also suggests the significance of search feeding during the experiment and thus supports the superior performance of simulations that included search feeding. While Trichoptera larvae were not captured in any of the drift samples, they accounted for 27 % of the biomass in the diet samples taken at the end of the field experiment and had an 85 % frequency of occurrence in those samples.

Discussion

We had success in simulating with an individual-based model the individual growth of trout in a small stream. Inclusion of both drift- and search-feeding significantly influenced that success, providing better estimates of individual fish mass than scenarios in which fish fed only on drift. This result notwithstanding, whether it is appropriate to complicate salmonid population models with multiple foraging modes depends on the system of interest. Hayes et al. (2000) showed that for models representing growth of fish where drift clearly dominates feeding, inclusion of search feeding can be unnecessary. However, researchers have identified situations where search feeding likely influences population-level outcomes in lotic systems, including: 1) multiple-species systems with interspecific differences in the propensity for search feeding (Nakano et al. 1999); 2) high turbidity (e.g. Tippets and Moyle 1978; Harvey and Railsback 2009); 3) where low-velocity habitat such as beaver ponds are important (Rosenfeld and Raeburn 2009); and 4) when drift food availability is otherwise reduced (Fausch et al. 1997). Inclusion of search feeding may be critical to model performance in such settings. Considering streamflow's influence on water velocity and thus its likely consequences for the relative importance of drift and search feeding, inclusion of search feeding may be generally important for models designed to address the effects of streamflow on fish populations, especially in modest-sized or low-gradient streams.

While the inclusion of both drift- and search-feeding modes increases its complexity, inSTREAM represents both modes in relatively simple ways. In some cases, simplifying assumptions can be incorporated in the calibration process. For example, drift concentration is treated as a calibration parameter that can capture the effects of a variety of processes not in the model, such as variation in drift size and diel variation in when fish feed. Nevertheless we found some reassurance in the correspondence between calibrated drift concentrations and those measured in the field in this application. Some simplifying assumptions may not introduce biologically meaningful bias. For example, the assumption of homogenous drift concentrations among habitat cells may reasonably approximate reality in some settings (Leung et al. 2009). Many simplifying assumptions are justified by the costs, in model complexity and uncertainty, of the alternatives. For example, Petty and Grossman (2010) demonstrated the occurrence and significance for stream fish of spatial variation in benthic food availability, but including such variation in models like inSTREAM would make the models substantially more complex and require extensive empirical measurements for meaningful calibration. However, the assumption of uniform search food availability could explain the general pattern of over-prediction of growth by small fish and under-prediction of growth by large fish in scenarios with both drift and search feeding: Control by larger fish of habitat with elevated search food availability, parallel to observations of mottled sculpin (*Cottus bairdi*) by Petty and Grossman (2010), could explain the main difference between observations and model predictions in this study.

The individual-based model applied here, while relatively successful in predicting streamflow effects on fish growth in a brief, small-scale experiment, is designed to address the effects of environmental factors on fish populations over longer timespans and on larger spatial scales. One potential challenge for such larger scale applications is the sensitivity of model results to food availability (e.g. Railsback and Harvey 2011), and the paucity of information on the effect of streamflow regime, and other important environmental factors, on food availability for fish. This study suggests the feeding mode flexibility of trout heightens the challenge of obtaining such information, in that drift sampling alone may not be sufficient to quantify food availability. The challenge of understanding food availability for stream salmonids seems likely to be met only by the classic combination of experimentation, spatio-temporally extensive datasets, and modeling. This study demonstrates one way modeling can contribute, by using fish survival and growth to "back out" information on food resources.

Acknowledgments Colin Sheppard made key contributions to the development of the version of inSTREAM used in this paper. Travis Ayres, Rodney Nakamoto and Jason White had critical roles in completing the field experiment. The City of Arcata allowed access to the study stream.

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