

# A new optimal foraging model predicts habitat use by drift-feeding stream minnows

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**Abstract** – There is substantial need for models that accurately predict habitat selection by fishes for purposes ranging from the elaboration of ecological theory to the preservation of biodiversity. We have developed a new and highly tractable optimal foraging model for drift-feeding fishes that is based on the profitability of occupying varying focal-point velocities in a stream. The basic model can be written as:  $I_x = (E_x * P_x) = \{(D * A * V) * [1/(1 + e^{(b + cV)})]\} - S_x$ , where: (1)  $I_x$  is the net energy intake at velocity  $x$ ; (2)  $E$  is prey encounter rate; (3)  $P$  is prey capture success rate which can be modelled as  $1/(1 + e^{(b + cV)})$  where  $b$  and  $c$  are fitting constants from the prey capture success curve; (4)  $D$  is the energy content of prey ( $J/m^3$ ) in the drift; (5)  $A$  is the visual reactive area of the fish; (6)  $V$  is velocity (cm/s); and (7)  $S$  is the cost of maintaining position ( $J/s$ ).

Given that  $D$ ,  $A$  and  $S$  can be considered constant over the range of velocities occupied by these fishes, the model reduces to  $e^{(b + cV)} = 1/(cV - 1)$  which we solved iteratively to yield an optimal focal-point velocity for species in each sample. We tested the model by comparing its predictions to the mean focal-point velocities (i.e. microhabitats) occupied by four species of drift-feeding minnows in two sites in a stream in North Carolina, USA. The model successfully predicted focal-point velocities occupied by these species (11 out of 14 cases) in three seasonal samples collected over 2 years at two sites. The unsuccessful predictions still were within 2 cm/s of the 95% confidence intervals of mean velocities occupied by fishes, whereas the overall mean deviation between optimal velocities and mean fish velocities was small (range = 0.9 and 3.3 cm/s for the warpaint shiner and the Tennessee shiner, respectively). Available focal-point velocities ranged from 0–76 to 0–128 cm/s depending on site and season. Our findings represent one of the more rigorous field tests of an optimal foraging/habitat selection model for aquatic organisms because they encompass multiple species and years, and for one species, multiple sites. Because of the ease of parameterization of our model, it should be readily testable in a range of lotic habitats. If validated in other systems, the model should provide critical habitat information that will aid in the management of riverine systems and improve the performance of a variety of currently used management models (e.g. instream flow incremental methodology (IFIM) and total maximum daily load calculations (TMDL)).

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**Key words:** cost-benefit; focal-point velocity; foraging success; IFIM; interspecific competition; microhabitat; optimization; stream fishes; TMDL

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Un resumen en español se incluye detrás del texto principal de este artículo.

## Introduction

The question of why animals prefer certain habitats and avoid others has intrigued ecologists and natural historians for millennia. In fact, over the

past 50 years, the construction and testing of synthetic models of habitat selection have been crucial to theoretical advancement in ecology, ethology, and fisheries science (Stephens & Krebs 1986; Pulliam 1989; Wootton 1999). Although the study of

habitat selection has its roots in basic ecology and ethology, there also are strong societal needs for models that elucidate the mechanisms determining habitat selection in aquatic organisms. For example, such models are essential for the preservation of aquatic biodiversity, which has been strongly affected by the continued alteration and degradation of aquatic habitats (Moyle & Cech 2000). Such degradation will probably increase as anthropogenic disturbances such as (1) impoundments (Hill 1996), (2) non-point source pollution [e.g. total maximum daily load (TMDL); <http://www.epa.gov/owow/tmdl/proprule.html>] and (3) global climate change (Meyer et al. 1999) continue to increase.

Despite these compelling scientific and societal needs, the majority of models currently used to assess habitat requirements for fishes are based on correlative analyses of fish abundance data and physical habitat variables, rather than on identification of the specific mechanisms underlying habitat selection by fishes (Grossman et al. 1995; Baker & Coon 1997). For example, many stream fishes preferentially occupy high-velocity microhabitats and reaches (Grossman & Ratajczak 1998; Matthews 1998; Thompson et al. 2001), but few correlational studies enable us to deduce the reason behind this pattern (e.g. Do these reaches have higher prey availability? Do they offer greater protection from predators? Do they provide essential spawning habitat?). This shortcoming limits both our basic understanding of the process of habitat selection in fishes as well as our ability to scientifically manage these species.

In contrast to correlational techniques, optimal foraging theory is a mechanistic approach that can be used to predict habitat selection by animals via the assumption that natural selection will produce individuals that behave in a manner that maximizes individual fitness (Stephens & Krebs 1986; Rosenzweig & Abramsky 1997). Although fitness is the currency of optimal foraging theory, it generally is not measured directly because of the logistical difficulties inherent in measuring reproductive success (number of offspring surviving) especially for fishes. Consequently, many investigators test habitat selection predictions of optimal foraging theory using parameters that are generally considered to be strongly correlated with fitness; for example, net energy intake (Werner & Hall 1979; Hill & Grossman 1993; Wootton 1999). A researcher can then determine whether specimens are behaving in concordance with the predictions of optimal foraging theory by examining whether they occupy microhabitats that maximize their net rate of energy intake, although constraints such as predator avoidance and nutrient limitation may

need to be included in analyses (Stephens & Krebs 1986; Gilliam & Fraser 1987; Pulliam 1989). Such approaches have been successfully used to predict microhabitat selection for several fish species (Fausch 1984; Dill 1987; Hughes & Dill 1990; Hill & Grossman 1993; Hughes 1998). These studies, which have focused on drift-feeding stream salmonids, all have shown that focal-point velocity (i.e. velocity at the position of the fish; see Grossman & Freeman 1987) is a crucial component of optimal habitat selection.

In this report, we present a new and highly tractable optimal foraging model that successfully predicts the microhabitats (i.e. focal-point velocities) occupied by four species of drift-feeding minnows (family cyprinidae) in a stream in North Carolina, USA. Our study species were rosyside dace, *Clinostomus funduloides* Girard; warpaint shiner, *Luxilus coccogenis* (Cope); Tennessee shiner, *Notropis leuciodus* (Cope); and yellowfin shiner, *Notropis lutipinnis* (Jordan & Brayton). One of these species, rosyside dace, is a species of special concern (NCWRC Year?). Minnows are the most abundant freshwater fish taxon world-wide, with the exception of South America and Australia (Moyle & Cech 2000), and drift-feeding minnows are frequently the most diverse and abundant fish taxon in lotic systems (Matthews 1998). Consequently, our model may be applicable to a large number of species found over a broad geographical range. In addition, our findings represent a relatively rigorous field test of an optimal foraging/habitat selection model because they encompass multiple species and years, and for one species, multiple sites within a stream.

## Materials and methods

### Model

As discussed previously, a habitat selection model based on optimal foraging theory should predict that drift-feeding fishes will occupy focal-point velocities (all further references to fish velocities refer to focal-point velocity) that maximize the fish's net rate of energy intake (Fausch 1984; Hughes & Dill 1990; Hill & Grossman 1993; Hughes 1998). For drift-feeding fishes, the rate of energy intake is a function of: (1)  $V$ , velocity (cm/s); (2)  $A$ , the visual reactive area of the fish (as per Hughes & Dill 1990; Hughes 1998), where  $A$  is the area of a transverse section (cm<sup>2</sup>) through the reactive volume of the fish (ideally, a sphere whose radius is the maximum distance at which the fish can visually detect prey) taken at its head; and (3)  $D$ , the energy content of prey (J/m<sup>3</sup>) in the drift. Given that  $D$  is not dependent on  $V$  within a given pool or riffle (Allan & Russek 1985; Matthaei et al. 1998), then  $E$ ,

the prey encounter rate [i.e. the rate at which  $D$  crosses  $A$  (J/s)] is linearly related to  $V$  as  $E = D * A * V$  (Hughes 1998). Energy intake is also a function of the prey capture success of the fish ( $P$ , the proportion of prey crossing  $A$  that are captured) and the cost of maintaining position [ $S$  (J/s)] at a given velocity. The relationship between  $P$  and velocity (see Hill & Grossman 1993) can best be described by:

$$P = 1/(1 + e^{(b+cV)}) \quad (1)$$

where  $b$  and  $c$  are fitting constants. We have previously shown that swimming costs are small and relatively constant within the range of velocities for which  $P > 0$  (Facey & Grossman 1990); consequently, net energy intake ( $I$ ) at velocity  $x$  can be expressed as:

$$I_x = (E_x * P_x) \\ = \{(D * A * V) * [1/(1 + e^{(b+cV)})]\} - S_x \quad (2)$$

and fishes should occupy the velocity that maximizes  $I$ . We derived a value for this velocity by solving  $dI/dV = 0$  for  $V$ . Given that  $D$ ,  $A$  and  $S$  can be considered constant over the range of velocities occupied by these fishes (Facey & Grossman 1990; Hughes & Dill 1990; <sup>4</sup>Hill & Grossman 1993), we obtain:

$$e^{(b+cV)} = 1/(cV - 1) \quad (3)$$

which we solved iteratively to yield an optimal fish velocity. The significance of this finding is that determination of optimal velocity depends only upon the readily obtained parameters  $b$  and  $c$  of the prey capture success curve (i.e.  $P$  versus  $V$ ), rather than on  $A$  or  $S$ , which are quite difficult to measure (Hill & Grossman 1993).

#### Experimental procedures

We constructed prey capture success curves (i.e. obtained values for parameters  $b$  and  $c$  for our model) using field and experimental methods similar to those of Hill & Grossman (1993). In brief, we captured fishes during 1998 in Coweeta Creek, Macon County, NC, USA, (general site description in Hill & Grossman 1993) at water temperatures of 18–20°C. Fishes were returned to the laboratory and held in tanks at 18°C and water velocities of approximately 5 cm/s for 2–3 days before being used in prey capture success trials (conducted at 18°C). Prior to experiments, we fed the fishes trout chow pellets (~1.5 mm in diameter) and live *Hyaella azteca* (Amphipoda, 4–7 mm in length) at levels which approximated a maintenance ration (Hill & Grossman 1993).

We conducted prey capture success trials in a fibreglass artificial stream equipped with a Plexiglas

as viewing window. The stream was 183 cm long by 91.5 cm wide by 35.5 cm deep, and was partitioned with mesh screen and Plexiglas into a test chamber 90 cm long by 35 cm wide by 35.5 cm deep. We marked both the sides and bottom of the test chamber with grids to facilitate identification of the exact position of a specimen during trials. To reduce disturbance, we made observations from behind a black plastic blind. We maintained water flow in the test chamber with a continuously variable speed 12-V motor (thrust = 16.8 kg) which drove a propeller positioned at the front of the stream. A honeycomb collimator placed between the motor and the test chamber produced laminar flow (i.e.  $R_e = 400$ ) throughout the chamber. Although drift-feeding fishes live in environments that contain turbulence, the introduction of small-scale turbulence into prey capture experiments would have made accurate velocity measurements intractable.

We began a trial by presenting live *H. azteca* (4–7 mm long) to test specimens via a piece of flexible plastic tubing (3 mm inside diameter) attached to a screen bounding the upstream portion of the test chamber (delivery depth 5 cm from the water's surface). Individual prey were placed in the water-filled tube and delivered by opening a clamp, which released the amphipod into the current. A series of pilot experiments enabled us to track the typical trajectory of prey in the test chamber and we adjusted the motor to produce treatment velocities (at the fishes focal position) ranging from 5 to 40 cm/s (5-cm/s intervals). We used live *H. azteca* in prey capture success trials because: (1) fishes fed on *H. azteca* using foraging behaviours similar to those displayed when foraging on native prey (Freeman & Grossman 1992; G. Grossman, personal observation); (2) at all test velocities, *H. azteca* remained in the water column throughout the length of the test chamber; and (3) in contrast to prey found in Coweeta Creek, *H. azteca* were readily cultured. This species is not found in drift samples from Coweeta Creek; however, amphipods are important components of drift in many streams (Brittain & Eikeland 1988).

We ascertained that a test subject would feed by first placing it in the test chamber and giving it 10 min to acclimate at 10 cm/s, and then delivering prey until it made one capture. (The few specimens that refused to feed were not used in trials.) The apparatus was then gradually adjusted until treatment velocity was reached (treatment velocities were calculated at the position of the fishes to permit tests using field fish velocity measurements). We then began releasing individual prey at approximately 20-s intervals until 10 prey were delivered while an observer tabulated the total num-

ber of prey captured. During trials, we recorded both the focal position occupied by a fish prior to a strike as well as the location of each prey strike. After completion of a trial, we measured velocities ( $\pm 0.1$  cm/s) at these locations using an electromagnetic flow meter (Hill & Grossman 1993). We conducted trials using solitary fish between 0900 and 1930h and each subject was tested at two or three velocities in a given day in an order that minimized the effects of satiation and fatigue. Trials were conducted during daylight hours because these species forage throughout the day and generally become quiescent at night (Freeman & Grossman 1992; Hill & Grossman 1993; G. Grossman et al., personal observation).

We derived species-specific prey capture success curves from: (1) 28 rosyside dace (35–68 mm, all lengths represent standard length), 29 warpaint shiners (31–100 mm), 26 Tennessee shiners (33–58 mm) and 23 yellowfin shiners (44–69 mm). Because fish size affects both the prey capture success (Hill & Grossman 1993) and velocity use of fishes in streams (Grossman & Ratajczak 1998), we developed separate prey capture success curves for up to three size classes for each species. We fit curves using equation 1 and the Statistica non-linear least squares regression computer program (StatSoft, Inc., Tulsa, OK, USA).

#### Field test

We tested predictions of our model through comparison with mean fish velocities utilized by the four species in Coweeta Creek (site 4) during July 1996, and June and August 1997. In addition, we tested model predictions for rosyside dace at a second site (same months, site 1) where it was the only drift-feeding cyprinid present. These sites were typical of fifth-order streams within the region and had mixed substrata dominated by boulder, cobble and gravel (site 4 = 71%; site 1 = 86%). Nonetheless, depositional substrata (e.g. sand, silt and debris) also were present within both sites. The mean depths of the sites were 22 cm (site 1) and 25 cm (site 4), and the mean velocities for the sampling periods are presented in the 'Results' below. Geographically, site 1 was slightly upstream from the study reach of Grossman et al. (1998) and the site 4 was approximately 1.2 km downstream.

We tested our model using each species by sample by site combination ( $n = 14$ ). We measured both fish velocities and mean water column velocities (100 random measurements) available in each site during each sample period using standard methods Grossman & Freeman 1987; Grossman & Ratajczak 1998; Grossman et al. 1998). We obtained predicted optimal velocities from our model

using equation 3 and the prey capture success curve parameters (i.e.  $b$  and  $c$ ) for each fish size class. We solved equation 3 for each size class iteratively using the Solver (quasi-Newton) algorithm of the Excel 97 computer program (Microsoft Inc., Redmond, WA, USA). Then we sorted field fish velocity measurements into size classes and weighted predicted optimal velocities by size-specific model values (i.e. if a field sample contained 10 velocity observations for fish between 50 and 60 mm, and eight observations for fish  $> 60$  mm, we calculated an optimal velocity by multiplying the prediction for 50–60 mm fish by 10 and the prediction for  $> 60$  mm fish by eight, summed the total, and then divided by 18). Field observations of fish velocities included individuals in the following size classes: (1) rosyside dace (50–70 mm); (2) warpaint shiner ( $\geq 80$  mm); (3) yellowfin shiner (50–60 mm); and (4) Tennessee shiner (50–60 mm). Because we could not obtain exact size duplicates for both fish velocity measurements and prey capture success curves, we excluded some specimens/curves from analyses. Our model produced a single value for optimal velocity, and consequently, we evaluated each prediction statistically by determining whether or not it fell within the 95% confidence interval (CI) for a particular field fish velocity sample mean (Johnson 1999). If a prediction fell within the 95% CI, then the model successfully fit the data, whereas predictions that fell outside the 95% CI were considered unsuccessful (Johnson 1999).

We have previously shown that the velocity at which the third derivative of the prey capture success curve reached zero (i.e. the point of maximum deceleration of the curve; see Hill & Grossman 1993) was a good predictor of velocities occupied by rainbow trout, *Oncorhynchus mykiss* (Walbaum), and rosyside dace in Coweeta Creek.

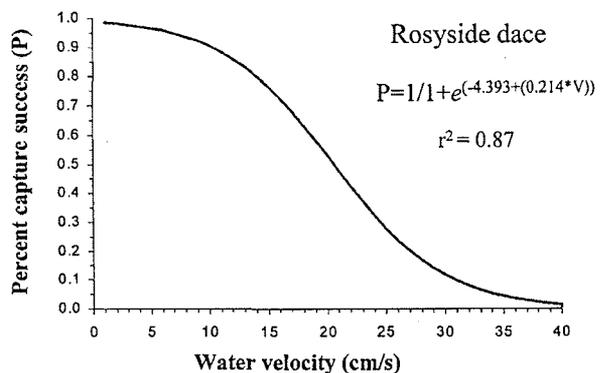


Fig. 1. A prey capture success curve for rosyside dace (56–68 mm SL,  $n = 13$ ) which is representative of the curves described in Table I. All curves had very high  $R^2$  values (mean = 90%, range = 81–96%); hence, we did not plot the individual points.

Consequently, we also compared predictions based on the third derivative of prey capture success curves to field fish velocities. We then compared the number of successful predictions of the third derivative to those of our new model to ascertain which model yielded the greatest number of successful predictions for field data.

**Results**

The prey capture success curves were non-linear for all species (Fig. 1) and best fit by equation 3 (Hill & Grossman 1993). These curves explained a very high amount of variance in the data, with a mean  $R^2$  value of 0.90 (range = 0.81–0.96, ‘all size-class’ regressions omitted, see Table I). The range of velocities present in the Coweeta Creek sites during field tests was substantial and varied from 0–76 cm/s to 0–128 cm/s (Figs 2–5). None of the sample means for velocity availability data fell within the 95% CI of mean fish velocities, demonstrating that fishes did not occupy velocities at random (Figs 2–5). Despite the wide range of velo-

Table 1. Model parameters for prey capture success curves. Curves were fit with the following equation:  $P = 1/(1 + e^{(b - cV)})$ , where  $P$  is prey capture success,  $V$  is velocity, and  $b$  and  $c$  are fitting constants. All regressions were significant at  $P \leq 0.01$ .

Species	Size class (SL, mm)	$n$	$b$	$c$	$R^2$
Rosyside dace	All	28	-3.956	0.215	0.83
	35-41	5	-3.302	0.249	0.81
	44-52	10	-4.299	0.237	0.93
	56-68	13	-4.393	0.214	0.87
Warpaint shiner	All	29	-4.027	0.258	0.86
	31-42	7	-4.112	0.366	0.93
	49-65	13	-4.576	0.288	0.91
Tennessee shiner	All	26	-3.730	0.282	0.82
	33-47	15	-4.548	0.407	0.87
	50-58	11	-4.154	0.257	0.87
Yellowfin shiner	All	23	-4.091	0.234	0.92
	44-52	7	-4.006	0.224	0.90
	55-69	16	-4.137	0.239	0.93

cities available, our model successfully predicted fish velocities in Coweeta Creek in 11 out of 14 cases (79%; Figs 2–5). In addition, even the three

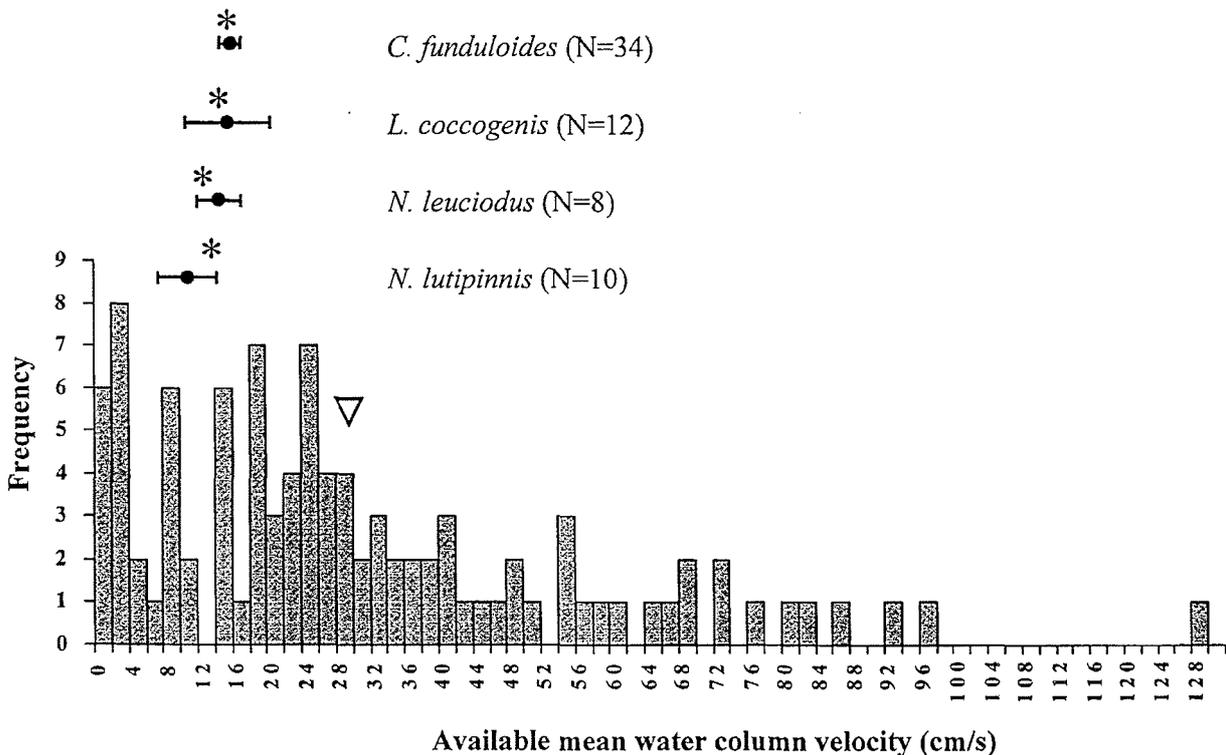


Fig. 2. Optimal velocities (\*) predicted by the model, mean observed fish velocities (●) and 95% confidence interval (CI), and mean water column velocities available within site 4 during July 1996. The mean of mean water column velocity measurements is shown by ▽. All model predictions were successful (i.e. they fell within the 95% CI of mean fish velocities). We made fish measurements on 3, 6 and 8 July, and habitat availability measurements within two weeks of fish measurements. Predictions for the alternative model of Hill & Grossman (1993), i.e. the third derivative of the prey capture success curve, were as follows: rosyside dace, 13.9 cm/s; warpaint shiner, 13.4 cm/s; yellowfin shiner, 11.8 cm/s; and Tennessee shiner, 11.0 cm/s. Predictions of the alternative model failed for both rosyside dace and Tennessee shiner.

unsuccessful predictions lay within 2cm/s of the 95% CI (Figs 2–5). Finally, our new model was a better predictor of fish velocities in Coweeta Creek than the third derivative (11 out of 14 successful predictions versus nine out of 14; Figs 2–5).

**Discussion**

Our results indicate that an optimal foraging model can be used to predict the focal-point velocities occupied by several species of stream minnow, and it is likely that optimization theory will continue to be an efficacious tool for understanding habitat selection in fishes (Werner & Hall 1979; Persson 1990; Grand & Grant 1994; Tyler & Gilliam 1995; Grand 1997). In addition, this model has several advantages over previous models including: (1) its mechanistic basis (i.e. it is likely that measuring prey capture success at different focal-point velocities actually quantifies a factor crucial to microhabitat selection); (2) it is based on a currency (i.e. maximization of energy intake) which is probably strongly correlated with individual fitness; and (3) it is highly tractable and easily parameterized (i.e. there is no need to estimate *D*, *S* and *A*). The tractability and ease with which model

parameters can be obtained through relatively simple experiments provide a stark contrast to the extensive laboratory work required for the construction of energy-based cost–benefit models (Facey & Grossman 1990; Hill & Grossman 1993).

Although the model success rate was not 100% (i.e. 79%), sample sizes for some analyses were low (i.e. <15 individuals), and experimental temperatures were higher (18°C) than many field fish velocity measurements (i.e. made between 15.9 and 18.3 °C). However, the agreement between most model predictions and 95% CIs of velocities occupied by fishes in Coweeta Creek is particularly noteworthy because the 95% CIs were relatively small (mean = 5.9 cm/s), especially when compared to the range of velocities available in the creek (i.e. between 78 and 128 cm/s, depending on season). In addition, deviations between the optimal velocity predicted by the model and mean velocities occupied by fishes in Coweeta Creek were also small, ranging from 0.9 cm/s (warpaint shiner) to 3.3 cm/s (Tennessee shiner). In fact, even unsuccessful predictions were very close to the boundaries of successful predictions (i.e. within 2 cm/s of 95% CIs). These results suggest that our model was a robust predictor of fish microhabitat selection in Coweeta Creek.

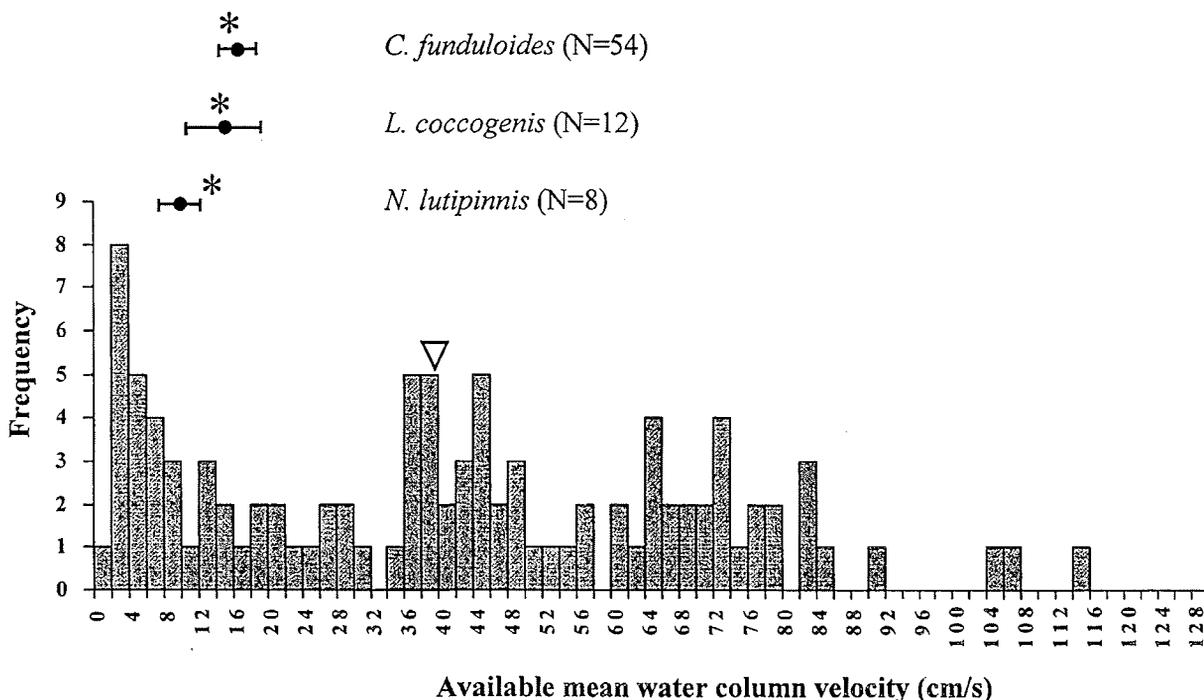


Fig. 3. Optimal velocities (\*) predicted by the model, mean observed fish velocities (●) and 95% confidence interval (CI), and mean water column velocities available within site 4 during June 1997. The mean of mean water column velocity measurements is depicted by ▽. Only the model prediction for yellowfin shiner fell outside of the 95% CI of mean fish velocities (i.e. model failure). We made fish measurements on 25 and 26 June, and habitat availability measurements on 31 May. Predictions for the alternative model of Hill & Grossman (1993) were as follows: rosyside dace, 13.9 cm/s; warpaint shiner, 13.4 cm/s; and yellowfin shiner, 11.8 cm/s. The prediction of the alternative model fell outside the 95% CI of mean fish velocities for rosyside dace (i.e. the alternative model failed).

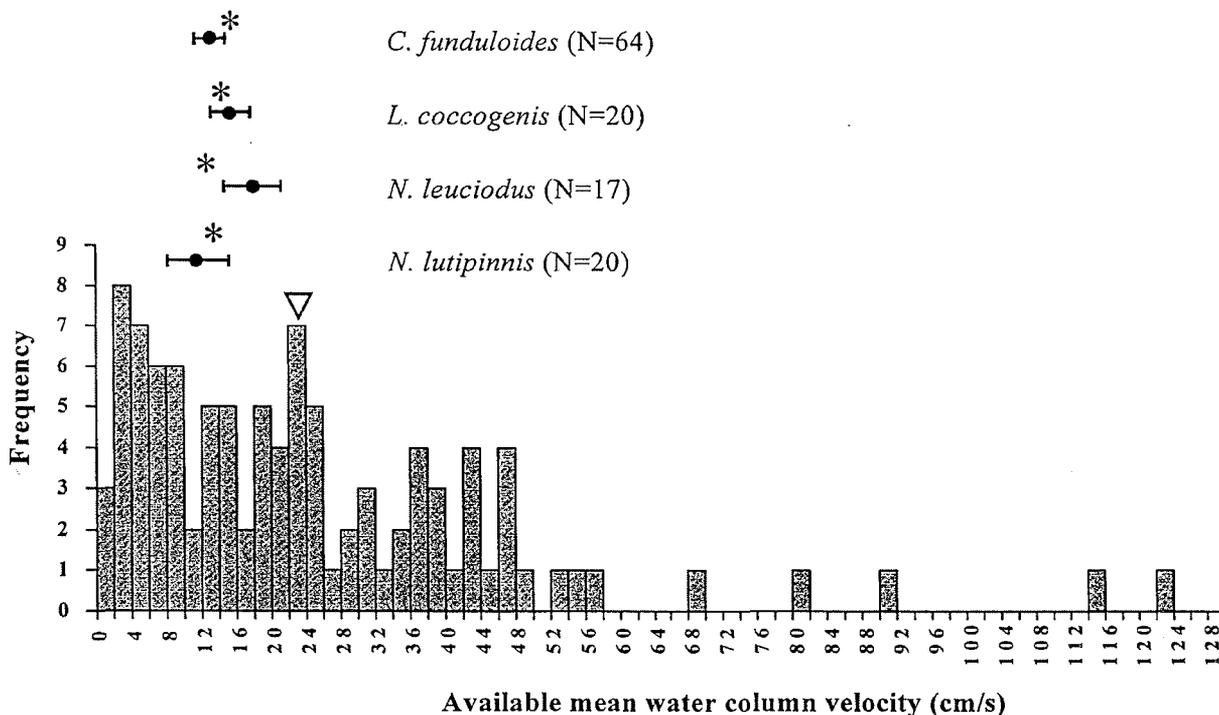


Fig. 4. Optimal velocities (\*) predicted by the model, mean observed fish velocities (•) and 95% confidence interval (CI), and mean water column velocities available within site 4 during August 1997. The mean of mean water column velocity measurements is depicted by  $\nabla$ . Model predictions for rosyside dace and Tennessee shiner fell outside of the 95% CI of mean fish velocities (i.e. model failure). We made fish measurements on 12 and 16 August, and habitat availability measurements within two weeks of these dates. Predictions for the alternative model of Hill & Grossman (1993) were as follows: rosyside dace, 13.9 cm/s; warpaint shiner, 13.4 cm/s; yellowfin shiner, 11.8 cm/s; and Tennessee shiner, 11.0 cm/s. Predictions of the alternative model fell outside of the 95% CI of mean fish velocities for both warpaint shiner and Tennessee shiner (i.e. the alternative model failed).

The finding that Coweeta Creek fishes typically occupied 'optimal velocities' also supports previous conclusions that habitat selection by fishes in this system is not strongly affected by either interspecific competition or predation (Grossman et al. 1998). Such results may not pertain to other lotic systems (Power et al. 1985; Gilliam & Fraser 1987; Schlosser 1987), although it is clear that fish assemblages with characteristics similar to those of Coweeta Creek are not uncommon (Harvey & Stewart 1991; Matthews 1998). If our model is validated on a broader scale it is possible that it will be useful as a heuristic tool (via unsuccessful predictions) to identify systems in which habitat selection is dominated by processes other than energy maximization (e.g. predation or interspecific competition).

The simplicity and tractability of our model will probably facilitate its use for a variety of purposes. For example, it may prove useful in identifying essential habitat characteristics (i.e. focal-point velocity) for threatened/endangered species or for tropical species for which ecological information generally is lacking. Data from our model also can be directly inserted into hydrologically based manage-

ment models (e.g. PHABSIM; Bovee 1982) that are currently utilized to estimate the potential biological and physical impacts of impoundments and water diversions on lotic systems.

In conclusion, our model proved highly successful in predicting habitat selection over multiple years by four species of stream cyprinids: members of perhaps the most widespread and speciose family of freshwater fishes. Nonetheless, the generality and robustness of the model now need to be assessed in a diversity of habitats. For example, it may be necessary to modify several simplifying assumptions (e.g. the independence of  $D$  and  $V$ , and the independence of  $D$  and habitat type) to achieve successful predictions for non-cyprinid drift feeders or for species in other systems. In addition, although our model predictions were empirically derived, they happened to fall within a relatively small range of velocities (see Figs 2–5), which limited the strength of our conclusions. Nevertheless, if the model is validated in other systems, it should become a highly efficacious tool for both the study of habitat selection and the management of aquatic organisms across a range of habitats.

## Optimal foraging in stream fishes

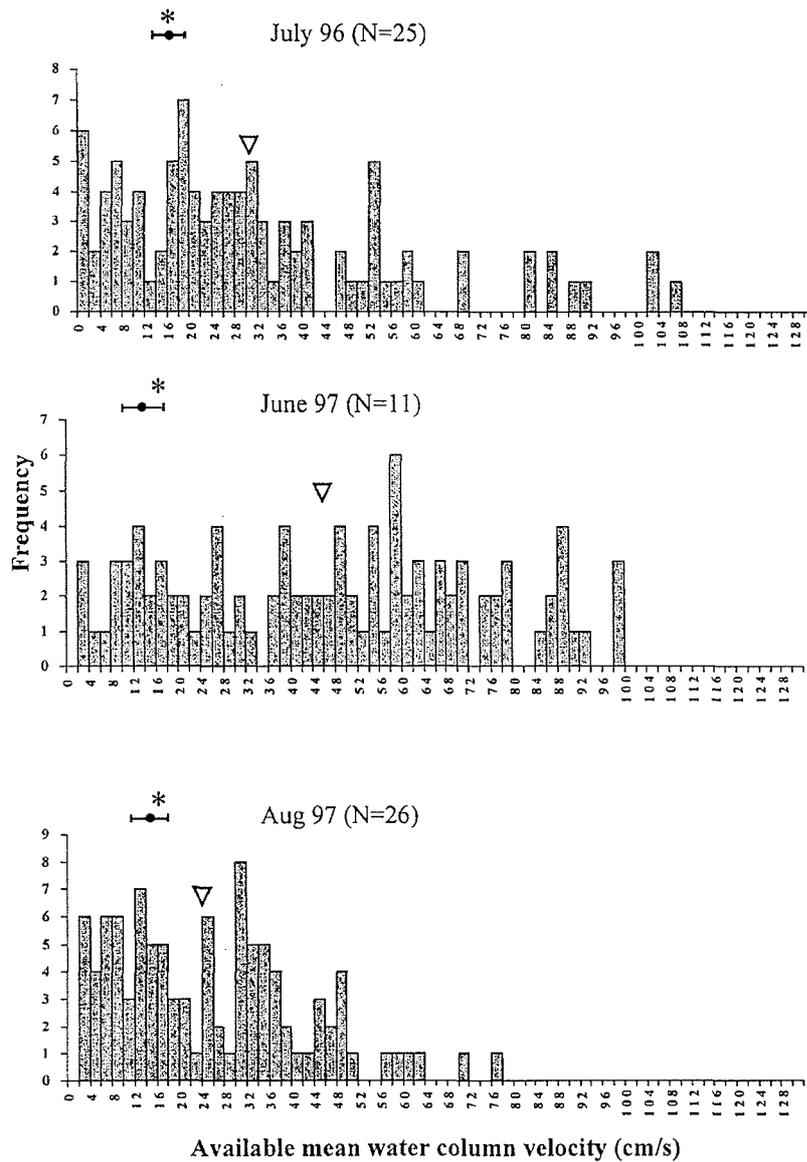


Fig. 5. Optimal velocities (\*) predicted by the model, mean observed fish velocities (●) and 95% confidence interval (CI) for rosyside dace, and mean water column velocities available within site 1 during July 1996, June 1997 and August 1997. The mean of mean water column velocity measurements is depicted by ▽. All model predictions fell within the 95% CI of mean fish velocities. We made fish measurements on 2 and 4 July 1996, 23 June 1997, and 13 and 15 August 1997, and habitat availability measurements in July 1996, June 1997 and August 1997 (See Figs 2–4). The prediction of the alternative model of Hill & Grossman (1993), i.e. the third derivative of the prey capture success curve, was 14.4 cm/s for all three samples and all fell within the 95% CI of mean fish velocities.

## Resumen

1. Existe una grave necesidad de modelos que predigan con precisión la selección de hábitat por parte de los peces con fines que van del desarrollo de la teoría ecológica a la conservación de la biodiversidad. Nosotros hemos desarrollado un modelo nuevo y de fácil manejo de alimentación óptima para peces que se alimentan de la deriva que se fundamenta en los diferentes beneficios energéticos derivados de ocupar velocidades focales distintas en un río.

2. El modelo básico puede formularse como:  $I_x = (E_x * P_x) = \{(D * A * V) * [1/(1 + e^{(b + cV)})]\} - S_x$ , donde: (1)  $I_x$  es la energía neta obtenida a la velocidad,  $x$ ; (2)  $V$  es la velocidad (cm/s); (3)  $A$  es el área visual de reacción del pez; (4)  $D$  es la energía contenida en las presas ( $J/m^3$ ) en la deriva; (5)  $E$  es la tasa de encuentro de presas; (6)  $P$  es la probabilidad de captura de la presa, que puede representarse como  $1/(1 + e^{(b + cV)})$  donde  $b$  y  $c$  son constantes; y (7)  $S$  es el coste de nadar para mantener la posi-

ción en la corriente ( $J/s$ ). Puesto que  $D$ ,  $A$  y  $S$  pueden considerarse constantes en el rango de velocidades que ocupan estos peces, el modelo se reduce a  $e^{(b + cV)} = 1/(cV - 1)$  que resolvimos iterativamente para obtener una velocidad focal óptima para cada especie en cada muestreo.

3. Probamos el modelo comparando sus predicciones con las velocidades focales medias (i.e. microhabitats) ocupadas por cuatro especies de ciprínidos que se alimentan de la deriva en un río de Carolina del Norte. El modelo predijo con éxito las velocidades focales ocupadas por estas especies (11/14 casos) en tres muestreos estacionales llevados a cabo a lo largo de dos años en dos estaciones. Incluso las predicciones fallidas se diferenciaron en menos de 2 cm/s del límite de confianza al 95% CIs de las velocidades medias ocupadas, y la diferencia media entre predicciones y observaciones fue pequeña (rango = 0.9 cm/s warpaint shiner, a 3.3 cm/s Tennessee shiner). El rango de las velocidades focales medias disponibles fue de 0–76 cm/s a 0–128 cm/s dependiendo de la localidad y estación del año.

4. Nuestros resultados son una de las pruebas de campo más

rigurosas de un modelo de alimentación óptima/selección de hábitat para organismos acuáticos puesto que incluyen diversas especies, años y, para una de las especies, localidades. La facilidad de la estima de los parámetros del modelo hace que sea fácil probarlo en diversos hábitats lóticos. Si es validado en ellos, el modelo debería proporcionar información valiosa que ayudará a la gestión de los sistemas fluviales y mejorará los resultados obtenidos a través de varios modelos usados actualmente para la gestión (p.e. IFIM y cálculos TMDL).

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