Promoting the Science of Ecology

AN ENERGETIC MODEL OF MICROHABITAT USE FOR RAINBOW TROUT AND ROSYSIDE DACE[1]

JENNIFER HILL[2] AND GARY D. GROSSMAN

School of Forest Resources, University of Georgia, Athens, Georgia 30602 USA

Abstract. We constructed an energetic model to determine the optimal focal point current velocity (i.e., microhabitat) for rainbow trout (*Oncorhynchus mykiss*) and rosyside dace (*Clinostomus funduloides*) in Coweeta Creek, a fifth-order stream in North Carolina, USA. Energetic costs were evaluated by quantifying the metabolic expenditure associated with swimming at a given velocity. We estimated benefits by measuring potential energetic gains of feeding at a given velocity. This included estimates of the ability of the fish to capture prey at different current velocities as well as estimates of the frequency and the energy content of drifting prey at various velocities. We derived separate models for small (53–70 mm SL [standard length]) and medium (71–125 mm SL) trout, and medium (47–52 mm SL) and large (53–70 mm SL) dace for all seasons, deriving net energy gain as a function of current velocity.

We predicted fishes would occupy velocities at which net energy gain was maximized. Predicted velocities were compared with those utilized by fishes inhabiting Coweeta Creek. Optimal velocities predicted by energetic models ranged from 7.7 to 22.1 cm/s, and closely matched actual velocity use (average deviation = 2.6 cm/s). Prey capture success appeared to be the most important component in the models. Consequently, we constructed models based solely upon aspects of capture success; the average deviation from velocity use with these models was only 1.8 cm/s. Thus, the ability of dace and trout to capture prey at varying velocities appears to be the dominant factor affecting microhabitat selection in these species.

Key words: fish ecology; habitat selection; microhabitat use; optimization models; stream ecology; stream fishes.

INTRODUCTION

Fishes that live in temperate streams occupy environments that are heterogeneous in both time and space. This variability may manifest itself in the habitat use patterns of stream fishes, which frequently exhibit broad overlap in the use of spatial resources (Baker and Ross 1981, Baltz and Moyle 1984, Angermier 1987, Grossman and Freeman 1987, Grossman et al. 1987*a, b*). In fact, microhabitat specialization (i.e., the occupation of physicochemically or spatially discrete microhabitats) is not common in many stream fish assemblages. This lack of microhabitat specialization represents a paradox for researchers interested in questions of habitat selection. Are many microhabitats of equal selective value to stream fishes, or is the importance of one or two critical physical parameters being masked by the high variability/heterogeneity of stream systems? These possibilities suggest that descriptive approaches to habitat selection, with their reliance on correlational statistical analyses, may be of limited use in determining the causal mechanisms influencing microhabitat selection in stream fishes. They also imply that experimental, mechanistically based, studies may be necessary to elucidate the mechanisms governing microhabitat use in these organisms.

A mechanistic approach that has been productive for studies of habitat use in other environments (see Rudstam and Magnuson 1985, Stephens and Krebs 1986, Dill 1987, Godin and Rangeley 1989, Pulliam 1989, Hughes and Dill 1990) is based on the tenet that natural selection will favor individuals that choose habitats that maximize their fitness. Net energy intake is often used as the link between habitat use and fitness, based on the assumption that measures of net energy intake ultimately translate into measures of fitness (e.g., an increase or decrease in growth or reproductive output). Fishes that feed and occupy water-column microhabitats in streams, represent model organisms for tests of the energy intake–fitness maxim (Jenkins 1969*b*, Fausch 1984, Hughes and Dill 1990). Current velocity appears to be an important component of microhabitat use for many water-column species (Grossman and Freeman 1987), and these species incur a direct and readily measurable cost (i.e., the metabolic cost of holding position) by occurring at a given velocity (i.e., microhabitat) in the water column. Because most water-column fishes consume drifting prey, the benefits of occupying a given velocity also can be quantified by measuring prey utilization and availability. Estimates of both the cost and benefit of occupying a range of
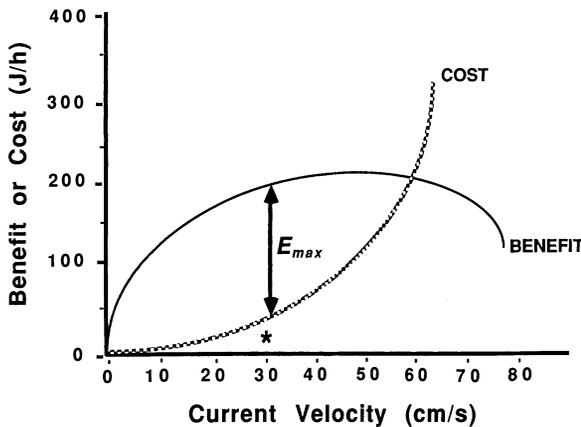
FIG. 1. A graphical example of an energy-based cost benefit model for microhabitat (i.e., focal point current velocity) use. E_{max} is the maximum difference between the cost and benefit curves and represents the current velocity at which net energy intake will be maximized. The asterisk represents the velocity at E_{max}.

velocities can then be used to derive cost and benefit curves for fishes occupying a given stream reach. One can then construct an energy maximization model by determining the maximum difference between cost and benefit curves (Fig. 1). This model will yield a predicted velocity at which net energy intake will be maximized for individuals of a given species inhabiting the reach examined.

We employed this mechanistic approach to develop and test an energy maximization model of microhabitat (= current velocity) use for two lotic, water-column fishes: rainbow trout (Oncorhynchus mykiss) and rosyside dace (Clinostomus funduloides). Rainbow trout and rosyside dace are dominant members of the fish assemblage in Coweeta Creek, North Carolina, USA (Freeman et al. 1988). In addition, current velocity is known to be an important component of microhabitat use for both species in Coweeta Creek (Grossman and Freeman 1987, Facey and Grossman 1990, 1992). Consequently, we based our microhabitat model on the costs and benefits of occupying a given current velocity. We constructed the model by: (1) calculating a time budget for trout and dace, (2) estimating the metabolic cost of occupying a given velocity through the use of swimming respirometry data for trout and dace, and (3) estimating the potential energetic benefit of a microhabitat by measuring food abundance and prey capture success of these species at a given velocity. We tested our model by comparing velocities occupied by two size classes of trout and dace in Coweeta Creek with those predicted by the model.

METHODS

Study site

Our study site was Coweeta Creek, a fifth-order stream located in the southern Blue Ridge Mountains

in North Carolina. A description of the site is presented in Grossman and Freeman (1987). Streamside vegetation was dominated by Rhododendron and mountain laurel (Kalmia latifolia), and there was considerable overstory. Elevation was ≈700 m. Stream width ranged from ≈2 to 11 m, and our study reaches encompassed pool, run, and riffle habitats. Current velocities generally ranged from ≈0 to 100 cm/s (J. Hill and G. Grossman, personal observations).

The fish assemblage of our study site included both water-column and benthic habitat guild members (Grossman and Freeman 1987). Trout and dace were the only two abundant water-column species, although other cyprinids (warpaint shiner, Notropis coccogenis Tennessee shiner, Notropis leuciodus, and creek chub, Semotilus atromaculatus) and a catostomid (northern hogsucker, Hypentelium nigricans) were occasionally present in low abundance. The benthic guild consisted of mottled sculpin, Cottus bairdi, longnose dace, Rhinichthys cataractae, and greenside darter, Etheostoma blennioides. Several benthic species occurred seasonally, including rockbass Ambloplites rupestris, and largescale stoneroller, Campostoma oligolepis. A more detailed description of similar assemblages located at nearby sites in Coweeta Creek is presented in Freeman et al. (1988).

The model

We constructed the model by determining the net energy (E_x) gained from holding position at current velocity x (i.e., focal point velocity), by subtracting the cost (C_x) of occupying that velocity from the benefits (B_x) obtained at that velocity. Thus:

$$E_x = B_x - C_x. \qquad (1)$$

Model formulation involved two phases. In the first phase, we obtained time budgets for both trout and dace. Because both costs and benefits can vary with the type of activity being undertaken, these data were essential to our model. The second phase consisted of parameterization of the complete model and included estimates of (1) standard and active metabolic rate, (2) food utilization efficiency, (3) prey capture success, and (4) prey abundance, over a range of velocities. Individual models were derived for each season and for two size classes of each species. Hence, there were 16 models (4 seasons × 2 species × 2 size classes).

Time budgets

We calculated time budgets by snorkeling and recording the time (in seconds) of all activities of an arbitrarily selected fish (total $n = 427$) during 3-min observation periods. Activity categories were as follows: (1) feeding, (2) chasing, (3) being chased, and (4) resting. We considered a fish to be feeding if it oriented to or struck at drifting objects (i.e., apparent prey). We defined "chasing" as orientation and accelerated

movement directed towards another fish. Conversely, "being chased" was defined as orientation and accelerated movement away from another fish. We considered a fish to be resting if it maintained position and did not orient to or attempt strikes at apparent prey.

We obtained time budgets for both species in all seasons, and recorded water temperatures to determine whether temperature affected activity level. Fishes were observed during an average of eight sampling periods per season. Observations were made during night, dawn, day, and dusk in all seasons except winter, when only daytime observations were made. Because it appeared that fishes could detect artificial lighting (including ultra-violet and red-filtered), we made night observations by snorkeling with a covered light and then flashing the light in each area of the stream. Although this technique did not allow for prolonged observations on each fish, it did permit observation of the location and orientation of undisturbed fish in the stream.

Energetic costs

Respiration rates at varying temperatures and current velocities have been determined for rainbow trout (Rao 1968, Feldmeth and Jenkins 1973, Facey and Grossman 1990) and rosyside dace (Facey and Grossman 1990). We used the data of Facey and Grossman (1990) because they were obtained from fishes collected in the Coweeta Creek drainage. Different estimates of metabolic expenditure were used for each season because metabolic rates varied with time of year as well as temperature (Facey and Grossman 1990).

Facey and Grossman (1990) presented regressions of metabolic cost (O_2 consumption rate per unit body mass, in milligrams per gram per hour) vs. current velocity (body lengths/s). We transformed these regressions to convert metabolic costs to units consistent with the dependent amd independent variables for the remainder of the model (i.e., J/h and cm/s, respectively). Regressions were transformed based on mean fish mass, mean fish length, and a conversion factor, 13.556 J/mg O_2 (Elliott and Davison 1975). We estimated masses of trout and dace collected from Coweeta Creek using the following length–mass regressions:

rainbow trout

$$\ln(M) = -11.07 + 3.01 \ln(L) \quad (n = 234, r = .99)$$

rosyside dace

$$\ln(M) = -11.07 + 3.02 \ln(L) \quad (n = 373, r = .95).$$

The sizes (mean ± 1 SD) of rosyside dace and rainbow trout used in laboratory experiments (see *Benefit assessment* below) were: small trout—65.7 ± 1.5 mm, 4.52 g; medium trout—89.9 ± 8.1 mm, 11.55 g; medium dace—48.3 ± 0.7 mm, 1.87 g; large dace—60.9 ± 0.7 mm, 3.77 g). Using the mean size of each group of fish, we converted equations of metabolic cost to energetic expenditure to estimate C_x (J/h).

Benefit assessment

We assessed prey abundance and determined the utilizable portion of the available prey, based on: prey availability, prey selection, prey capture success, and utilization efficiency (incorporating specific dynamic action). Thus, B_x in Eq. 1 is a function of these variables.

Prey availability.—We quantified prey availability by drift sampling, because dietary information indicates that rainbow trout and rosyside dace feed on drift in both the Coweeta Creek drainage (trout: Tebo and Hassler 1963, trout and dace: Stouder 1990) and in other regions (trout: Flemer and Wolcott 1966, Elliott 1973, Bisson 1978, but see Tippets and Moyle 1978; dace: Breder and Crawford 1922, Gatz 1981). In addition, behavioral observations in Coweeta Creek indicated that trout and dace fed predominantly in the water column, and struck at the bottom and surface only rarely (Hill 1989). Hence, the energetic value of the drift probably is a reasonable estimate of prey availability for these fishes.

We sampled drift seasonally using a modified plankton sampler with a 12 cm diameter opening and a net mesh of 212 μm. The sampler broadened behind the opening to reduce turbulence. Prior to sampling we verified that velocities measured at various positions in the mouth of the sampler did not differ statistically (ANOVA, $P > .05$). During each 1-h sample, we made five velocity measurements at the head of each drift sampler, with an electronic velocity meter. These readings were averaged to obtain the mean velocity per sample. Samplers were placed at random locations within the sites, and were centered at ≈10 cm above the substrate. We selected this distance because it was almost identical to the mean distance from the substrate occupied by trout (9.8 cm) and dace (10.9 cm) in field measurements made in Coweeta Creek (G. D. Grossman et al., *unpublished data*).

We collected seasonal drift samples in: (1) winter 1986 and 1987 (December–February), (2) spring 1986 and 1987 (March–May), (3) summer 1986 (June–August), and (4) fall 1986 (September–November). Samples taken in the same season in different years were pooled. Eight (4 morning and 4 afternoon) 1-h samples were collected over a 2-d period in each site, for a total of 32 samples per season.

We preserved drift samples in a rose bengal–10% formalin mixture, because formalin fixation does not cause significant changes in biomass (Leuven et al. 1985). Organisms were then identified to order and separated into size classes (nearest 0.5 mm) using a dissecting microscope. To determine the energy available at each velocity, we used length-mass regressions and size-specific energetic values (by order) from several sources (Andrassy 1956, Cummins and Wuycheck 1971, Yeates 1972, 1979, Rogers et al. 1977, Smock 1980; A. Huyrn, University of Alabama, *unpublished data*).

Prey utilization.—Rainbow trout are opportunistic (Tebo and Hassler 1963, Antonelli et al. 1972, Stouder 1990), size-selective predators (Bisson 1978, Tippets and Moyle 1978). Rainbow trout (3–45 g) have a minimum prey size of 2 mm (Bisson 1978). An analysis of stomach contents of rosyside dace from Coweeta Creek (D. Stouder, University of Georgia, *unpublished data*) showed that at least 95% of prey consumed were ≥2 mm in length, even though the majority of prey in the drift were smaller than this length. Dr. A. J. Gatz (Ohio Wesleyan University, *personal communication*) confirmed these findings regarding minimum prey sizes for dace, based on his studies of a different dace population in North Carolina. Consequently, we based estimates of the energy available to trout and dace at a given velocity on the abundance of prey that were ≥2 mm in length.

Prey capture success.—A major factor influencing the potential benefit of maintaining position at a given velocity is the ability of the predator to capture prey. We examined the effects of velocity on prey capture success of trout and dace, by conducting experiments in a temperature-controlled, flow-through, artificial stream. This stream was oval in shape with the following channel dimensions: length—10 m, height—1 m, and width—1 m. Water quality parameters for the stream are presented in Hill (1989). All parameters were within acceptable limits for growth of trout and dace (Grossman and Boulé 1991).

We collected fishes for experimental trials from the Coweeta Creek drainage by electrofishing. Barrett and Grossman (1988) found that Coweeta fishes did not exhibit mortality after exposure to similar electrofishing techniques. Fishes were transported to the laboratory and held for at least 2 wk prior to testing. We maintained specimens on a mixed diet of thawed chironomid midges, Euphausiidae, and *Tenebrio* sp.

Chironomid midges were selected as the test prey because: (1) they are common natural prey of both rainbow trout and rosyside dace in Coweeta Creek (Stouder 1990), (2) they can be released and captured in the water column (the foraging habitat of trout and dace), and (3) they are large enough for visual detection by the observer, yet small enough for all tested fish to ingest at least 30 individuals before becoming satiated (J. Hill and G. D. Grossman, *personal observation*). In addition, there were more dipterans (primarily chironomids) of potential prey size (>2 mm length) in the drift than all other types of potential prey combined (i.e., dipterans represented 72% of the potential prey in winter, 62% in spring, 52% in summer, and 65% in fall). The use of a single prey type also enabled us to assess the effects of current velocity on prey capture success, independent of prey type. However, using a single prey type introduced a bias in our experiments, because capture success may vary with prey type. Given that trout and dace consume chironomid larvae and

similar invertebrates in Coweeta Creek (Stouder 1990), we do not believe that this bias was substantial.

Season and fish size also may affect capture success. To account for the effect of season, we tested naturally acclimatized fish at winter and summer mean temperatures of 5°C and 15°C, using the normal photoperiod for each season. These data were averaged to obtain capture success estimates for spring (10°C) and fall (10°C). We acknowledge that estimating spring and fall values for capture success as intermediate between winter (5°C) and summer (15°C) values, incorporates a potential source of error in the model. Nonetheless, because capture success ultimately is limited by the rate of muscle contraction, it is probably directly correlated with temperature. To determine the effect of fish size on prey capture success, we conducted experiments on two size classes of each species. These size groups were as follows: small and medium trout ranged from 53 to 70 mm SL (standard length), and 71 to 125 mm SL, respectively, and medium and large rosyside dace ranged from 47 to 52 mm SL and 53 to 70 mm SL, respectively.

We tested capture success responses of both species at velocities ranging from 0 to 40 cm/s, at 5-cm/s intervals. This range encompassed at least 75% of all velocities available in the study reaches. In addition, it completely encompassed the range of focal point velocities occupied by trout and dace in Coweeta Creek. We conducted trials at one randomly chosen velocity each day. After testing, fishes were fed to satiation. By holding two groups of fish separately, we could deprive each group of food for 1 d between trials.

Rainbow trout were tested individually in prey capture success trials. Because solitary rosyside dace would not feed in the artificial stream, we conducted dace trials using groups. When tested in groups of four, all dace exhibited natural feeding behavior. With group sizes <4, however, not all fishes fed regularly, hence, our decision to use a group size of four. During a trial, we recorded the percentage of successful strikes by a focal individual, for each prey released into the stream. Dace were uniquely marked (Hill and Grossman 1987a) to ensure that each fish was tested at all velocities. Sample sizes for capture success experiments varied depending upon field availability of fishes. Sample sizes for trout and dace were as follows: trout: summer, small—$n = 4$, medium—$n = 5$; winter, small—$n = 3$, medium—$n = 12$; dace: summer, medium—1 group of 4, large—5 groups of 4; winter, medium—1 group of 4, large—4 groups of 4.

We evaluated capture success for prey that passed within the fish's strike range. Fausch (1984) estimated the strike range of rainbow trout to be about two body lengths (fork length); we assumed that the strike range of dace was similar. To verify these assumptions we conducted a pilot study, in which we released prey at: (1) the focal point (i.e., the anteriormost position oc-

cupied by the specimen prior to disturbance), (2) one standard length, and (3) two standard lengths away from the fish, while recording capture success. This study indicated that there was a positive correlation between the number of missed strikes and distance of the prey from the predator. Consequently, we recorded data separately for different prey distances. We did not include data for prey that passed beyond 2.5 standard lengths from a predator, because this appeared to be outside of the typical strike range of both trout and dace (Hill 1989).

Trials were conducted by releasing a total of 30 prey (10 per distance) at each of three distances from test specimens (focal point—from 0 to 0.5 SL, 1 SL away— from 0.5 to 1.5 SL, and 2 SLs away—from 1.5 to 2.5 SL). We then obtained a weighted average (weighted by the area at each distance from the fish) of the percent of prey captured (i.e., prey capture success) by a test specimen at each velocity. Using nonlinear least squares regression, we then obtained regressions of capture success vs. current velocity for each season, species, and size class. These data were then included in the calculation of I_x, where:

$$I_x = (A_x \cdot S_x) \qquad (2)$$

and I_x = total energy intake at velocity x, A_x = energetic value of prey available at velocity x, S_x = capture success for velocity x. The benefit component of the model B_x, was calculated by multiplying I_x times the utilization efficiency for prey. Because we did not perform experiments at fall and spring temperatures, we derived equations for these seasons by averaging capture success data from winter (5°C) and summer (15°C) experiments. Recall that mean temperatures for both fall and spring were 10°C.

Utilization efficiency.—Although the energetic values of potential prey for dace and trout are known, to derive a more accurate estimate of the energy available from these prey, one should calculate the organic components of prey and then substract away the energy associated with the insoluble and indigestible portions (McClintock 1986). Net energy gain for microhabitat x can then be summarized as:

$$E_x = [I_x - (R_{SDA} + F + U)] - C_x, \qquad (3)$$

where R_{SDA} = specific dynamic action, F = egestion rate, U = excretion rate (Rice et al. 1983), C_x = cost of occupying current velocity x, and energetic benefit at velocity x, $B_x = [I_x - (R_{SDA} + F + U)]$. A description of how I_x and C_x were determined has been presented previously. Specific dynamic action includes the costs associated with ingestion, assimilation, transport, biochemical treatment, and incorporation of prey consumed (Webb 1978). To our knowledge, estimates of R_{SDA}, F, and U, for either rainbow trout or rosyside dace are not currently available. However, the data of Beamish (1972, 1974) and Niimi and Beamish (1974)

indicate that a total of 32% of total energy intake for largemouth bass (*Micropterus salmoides*) was lost by R_{SDA} (14%), F (10%), and U (8%). These estimates were identical for fish kept at either maintenance or maximum rations. Because largemouth bass are active, freshwater carnivores, we assumed that these estimates could be used as approximations of R_{SDA}, F, and U, for trout and dace. Consequently, we multiplied the energy content of potential prey by a constant (0.68 = 1 − 0.32) to determine the utilizable fraction of the prey available. Then net energy gain may be expressed as:

$$E_x = (I_x \cdot 0.68) - C_x. \qquad (4)$$

Model evaluation

We tested our model by comparing the water velocities (i.e., microhabitats) occupied by trout and dace in Coweeta, with those predicted by the model. To obtain these data, we snorkeled upstream through two 25-m sections of Coweeta Creek while recording data on undisturbed fishes (Grossman and Freeman 1987). These sections appear to encompass the home ranges of rainbow trout (Stefanich 1952, Edmundson et al. 1968, Whitworth and Strange 1983), and dace (Hill and Grossman 1987b). For each individual, we recorded focal point velocity, distance from the substrate, and water-column depth.

In each study site, we established a series of bank-to-bank transects, 1 m apart. We then measured average velocity (Bovee and Milhous 1978) at 1-m intervals along each transect during six seasons. These data were collected over 2 d during each season and consisted of ≈150 measurements of average velocity per season. At least 10 d recovery time was allowed in each site prior to the resumption of fish microhabitat observations. We then compared these data to the mean velocities occupied by trout and dace using a chi square test (P = .05), to determine whether fishes exhibited nonrandom velocity use during the study.

Several investigators have observed that rainbow trout may not feed at their exact focal positions (Jenkins 1969a, Alley 1974, Smith and Li 1983, Fausch 1984). Typically, trout have been observed to move forward and upward to strike at drifting items. Rosyside dace exhibit a similar behavior. Because the test of our model involved comparison of predicted and observed focal point velocities based upon the benefits of feeding positions, it was necessary to examine this possibility. Consequently, we snorkeled in the test sections and observed a fish until it struck at a drifting item. Velocities were then recorded for the focal position and the position at which the item was struck (i.e., strike position). We compared the velocities at these two positions statistically using a paired t test (P = .05).

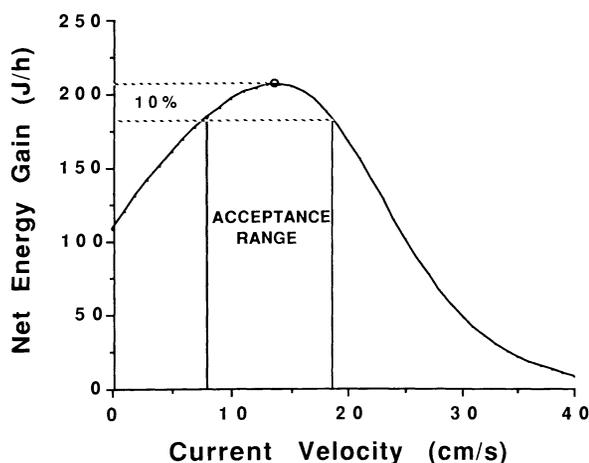We tested the model by comparing velocities at which

FIG. 2. A graphical representation of how the acceptance range for the model was determined.

net energy gain was maximized (E_{max}) with focal point velocities utilized by trout and dace in Coweeta Creek. As a test criterion, we considered an observed, mean focal point velocity to be in agreement with the model, if it fell within the range of velocities that produced a net energy gain within 10% of E_{max} (Fig. 2). This criterion was based on the following logic. Consider two curves of net energy gain as a function of velocity. The first has a steeply rising and falling peak. In this case, there would be strong selection for individuals to occupy a velocity very close to E_{max}. The second curve, however, has a broad flat peak. As a consequence, there would be reduced selective pressure to utilize a velocity close to E_{max}, because a deviation from the peak would only slightly decrease net energy benefits. Because the steepness of the peaks of our model curves varied among the models (Hill 1989), it seemed reasonable to use a criterion that was a function of the maximum to delineate areas within which to accept or reject the model.

Hence, we arbitrarily chose 10% of the maximum as the acceptance range.

Our use of this criterion, however, meant that acceptable focal point velocities ranged from 15 to 27% of the total velocities used in the model (i.e., 0–40 cm/s). This range varied, depending on species, season, and size class. To determine whether habitat use was in greater agreement with the model than would be expected at random, we compared the percentage of focal point velocity observations within the 10% acceptance range to the percentage of habitat availability observation in same range. A Wilcoxon signed-ranks test was used to test this hypothesis. Because the mean distance from the substrate for both trout and dace was ≈10 cm, velocity availability was recorded at this position in the water column.

RESULTS

Time budgets

We recorded activity patterns of fishes by observing 344 dace and 83 trout during daylight, dawn, and dusk. At water temperatures above 2°C, both species spent at least 98% of their time feeding. When temperatures fell to 2°C or lower, trout and dace occupied cavities in the substrate (e.g., underneath cobbles), and only occasionally arose out of the substrate. When trout and dace left these cavities, they spent 100 and 92% of their time foraging before returning to shelter.

During the night, both species occupied different habitats than during the day (including clear nights with a full moon). Trout and dace appeared to leave deeper portions of the water column at dusk and return at dawn. At night, we only observed dace in shallow-water areas without noticeable current at night. Because we observed trout and dace to be inactive at night, it was not necessary to include nighttime observations in the model. In addition, because fishes spent

TABLE 1. Metabolic cost (J/h) as a function of current velocity, CV (cm/s). Regression coefficients are for transformed equations, with data derived from Facey (1987).

| Species	Size	Season	Cost estimate model	Regression coefficient
Trout	Small	Winter	$= 61.253 \times 10^{-1.06 + 0.0122CV}$	0.59
		Spring	$= 61.253 \times 10^{-0.57 + 0.0076CV}$	0.51
		Summer	$= 61.253 \times 10^{-0.67 + 0.0107CV}$	0.62
		Fall	$= 61.253 \times 10^{-0.67 + 0.0122CV}$	0.77
Trout	Medium	Winter	$= 156.565 \times 10^{-1.06 + 0.0089CV}$	0.59
		Spring	$= 156.565 \times 10^{-0.57 + 0.0056CV}$	0.51
		Summer	$= 156.565 \times 10^{-0.67 + 0.0078CV}$	0.62
		Fall	$= 156.565 \times 10^{-0.67 + 0.0089CV}$	0.77
Dace	Medium	Winter	$= 4.058 - 0.013CV$	0.14
		Spring	$= 8.368 + 0.033CV$	0.26
		Summer	$= 25.355 \times 10^{-0.85 + 0.0187CV}$	0.66
		Fall	$= 17.493 + 0.113CV$	0.33
Dace	Large	Winter	$= 8.175 - 0.020CV$	0.14
		Spring	$= 16.861 + 0.052CV$	0.26
		Summer	$= 51.087 \times 10^{-0.85 + 0.0148CV}$	0.66
		Fall	$= 35.250 + 0.181CV$	0.33
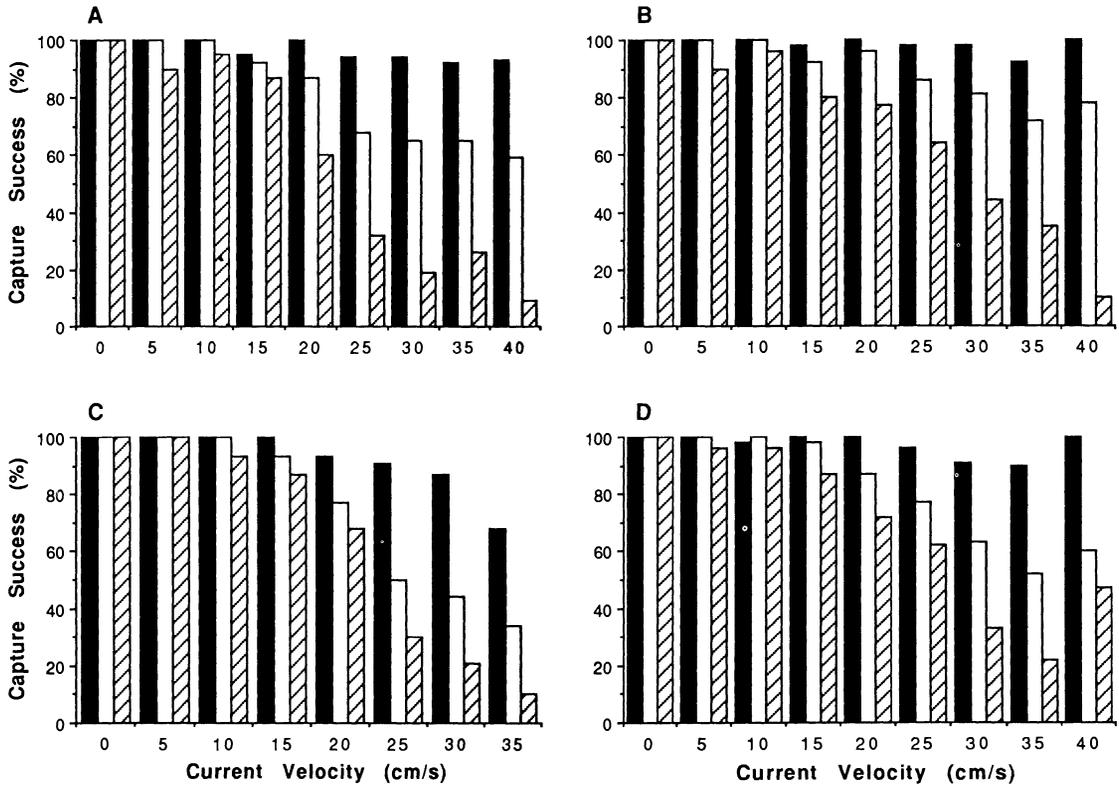
FIG. 3. Prey capture success of trout as a function of velocity and distance from the predator. Data are separated on the basis of the distance between the prey and the fish at: 0–0.5 standard lengths (SL) away (■), 0.5–1.5 SLs away (□), and 1.5–2.5 SLs away (▨). Data are presented for small (A) and medium (B) trout held at 15°C and small (C) and medium (D) trout held at 5°C.

almost all their active hours foraging, we were able to base the model exclusively on the velocities of feeding positions occupied by trout and dace.

Energetic costs

An exponential model yielded the best fit for oxygen consumption–velocity regressions for trout, whereas results for dace were more variable. The regression model that produced the best fit for dace in summer was exponential, whereas a linear model had the best fit for the three remaining seasons (Table 1). Metabolic cost was positively correlated with velocity in all cases except for dace in winter and spring, when regression slopes were not significantly different from zero (Facey and Grossman 1990). In all models the energetic cost associated with maintaining position at a given current velocity (C_x) was low in comparison to the energy available (B_x) at that velocity (for the range of velocities utilized by these fishes).

Benefit assessment

Food availability. — The total energy content of drifting prey (>2 mm in length) was positively correlated with velocity in all seasons (Hill 1989). In spring, summer, and fall, the relationship between velocity and energy content of the drift was linear; however, in win-

ter an exponential relationship provided the best fit. Correlation coefficients for those equations ranged from 0.49 to 0.67. The majority of drifting organisms were smaller than the minimum size of prey typically consumed by trout and dace (i.e., <2 mm). Of 37 344 invertebrates measured in drift samples, 80% were between 0.25 and 2.00 mm in length. The percentage of organisms >2 mm in length (i.e., potential prey) increased as velocity increased. However, the mean size of potential prey did not vary significantly with velocity (ANOVA by site and season, all $Ps > .05$).

Food utilization. — Capture success of medium dace dropped below 90% at an average of 8 cm/s, whereas that of large-sized dace and trout dropped below 90% at an average of 11 cm/s (Figs. 3 and 4). Medium trout had high capture success (>90%) up to velocities of 16 cm/s. At higher velocities, capture success decreased dramatically. Capture success generally dropped off at lower velocities for smaller fish foraging at lower temperatures. Similar-sized trout and dace had similar responses of capture success to current velocity. Capture success was size, rather than species, dependent for these fishes.

Focal point and strike velocities. — A comparison of focal point and strike velocities indicated that both species maintained position at significantly lower ve-
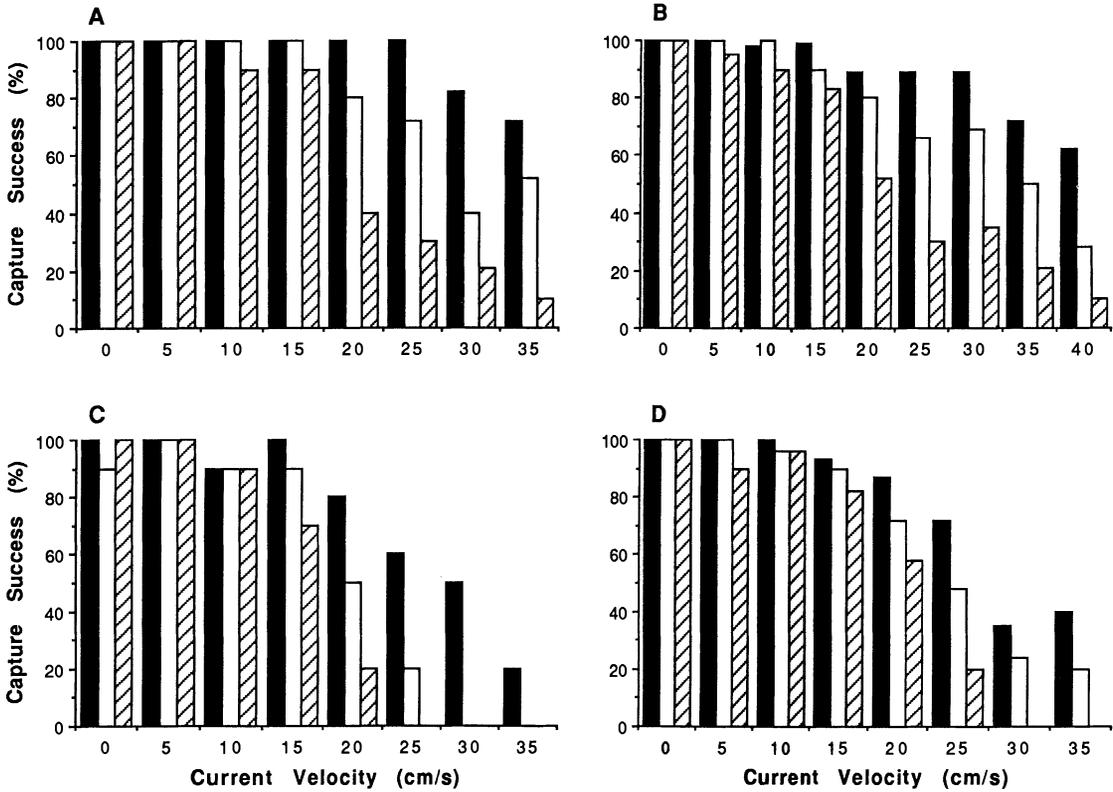
FIG. 4. Prey capture success of dace as a function of velocity and distance from the predator. Data are presented as in Fig. 3. Component graphs are for medium (A) and large (B) dace held at 15°C and medium (C) and large (D) dace held at 5°C.

locities than the velocity at which food was captured (trout: $t = 6.27$, df = 58, $P < .0001$, dace: $t = 10.80$, df = 207, $P < .0001$). Velocities (mean and 95% CI) of strike positions for dace and trout were 4.6 ± 0.8 cm/s and 5.6 ± 1.8 cm/s higher than their respective focal point velocities, and were similar for all seasons. Because this indicated that fishes were not being subjected to the costs and benefits of a single velocity, we

TABLE 2. Comparison of the predicted current velocity at maximum (and acceptance range of) net energy gain from the model with mean focal point velocities (i.e., microhabitats) utilized by dace and trout in Coweeta Creek. Also presented are the maximum energy gain (E_{max}) possible and the energy gain obtained at velocities occupied by trout and dace.

Species	Size	Season	E_{max} (J/h)	Predicted velocity (cm/s)		No. observations	Utilized velocity (cm/s, 95% CI)	E_{max} at utilized velocity (J/h)
				Mean	Range			
Trout	Small	Winter	724.3	13.4	7.8–17.8	21	15.0 ± 3.2	715.9
		Spring	324.7	13.6	8.2–18.1	11	17.7 ± 3.6	296.6
		Summer	189.9	17.1	12.4–21.5	8	13.4 ± 7.9	177.8
		Fall	124.3	15.5	11.3–19.3	45	12.8 ± 3.0	118.8
Trout	Medium	Winter	1458.5	16.1	9.9–20.9	25	18.0 ± 3.5	1437.6
		Spring	692.9	17.2	11.2–22.2	31	20.6 ± 3.2	662.7
		Summer	509.6	22.1	17.1–26.4	37	21.1 ± 3.8	507.5
		Fall	285.8	19.3	14.5–23.6	40	17.5 ± 2.7	281.2
Dace	Medium	Winter	297.1	7.7	3.2–11.4	33	13.9 ± 2.7	211.7*
		Spring	146.0	10.2	5.9–14.3	54	12.8 ± 1.6	140.2
		Summer	104.2	16.5	12.4–20.2	236	14.5 ± 0.8	101.3
		Fall	35.1	11.9	8.8–14.9	118	11.4 ± 1.0	35.1
Dace	Large	Winter	571.1	11.8	6.8–15.6	73	12.7 ± 1.4	568.2
		Spring	266.5	13.0	8.3–17.1	62	15.2 ± 1.6	259.4
		Summer	175.3	18.1	13.6–22.3	29	14.4 ± 3.2	163.2
		Fall	68.6	14.6	11.3–17.5	155	10.4 ± 0.8	57.7*

* Net energy gain at velocity utilized > 10% below E_{max}.

then increased benefit estimates by the energy available at velocities 5.6 cm/s higher for trout and 4.6 cm/s higher for dace. Thus net energy gain for trout at velocity x was calculated as $E_x = B_{x+5.6} - C_x$, and for dace $E_x = B_{x+4.6} - C_x$. Because costs (C_x) were primarily associated with the holding position focal point, these values were not adjusted.

Model results

We tested our model by comparing focal point velocities occupied by trout and dace in Coweeta Creek with the velocities predicted at E_{max} by the model. Hence it is first appropriate to describe the variation observed in the occupation of focal point velocities of the fishes in Coweeta Creek.

Velocity use varied with species, size, and season (Table 2). Focal point velocities differed significantly between small and medium trout ($t = 23.49$, df $= 276$, $P < .0001$) and between medium and large dace ($t =$
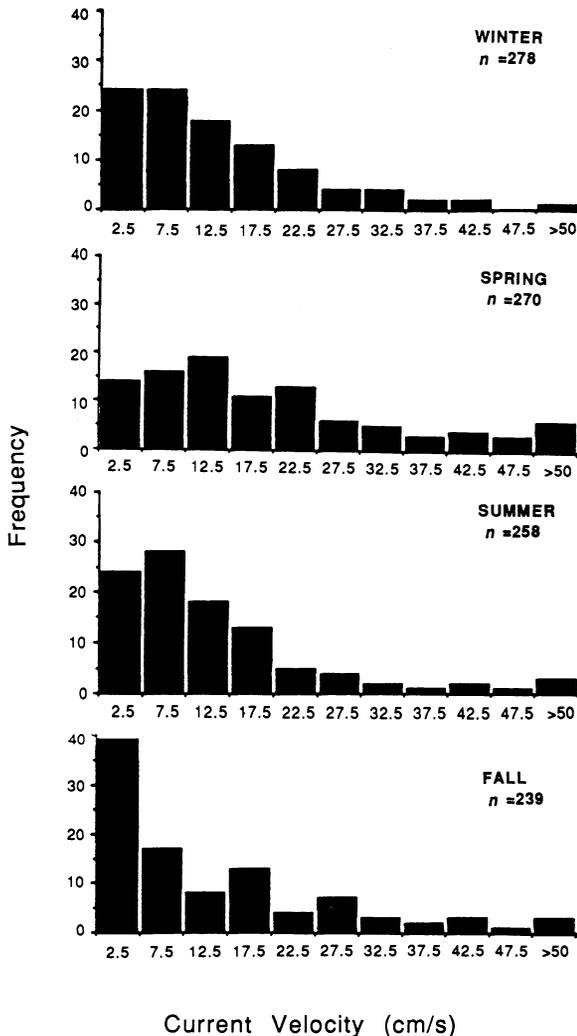

FIG. 5.   Current velocities present in the Coweeta Creek study sites.
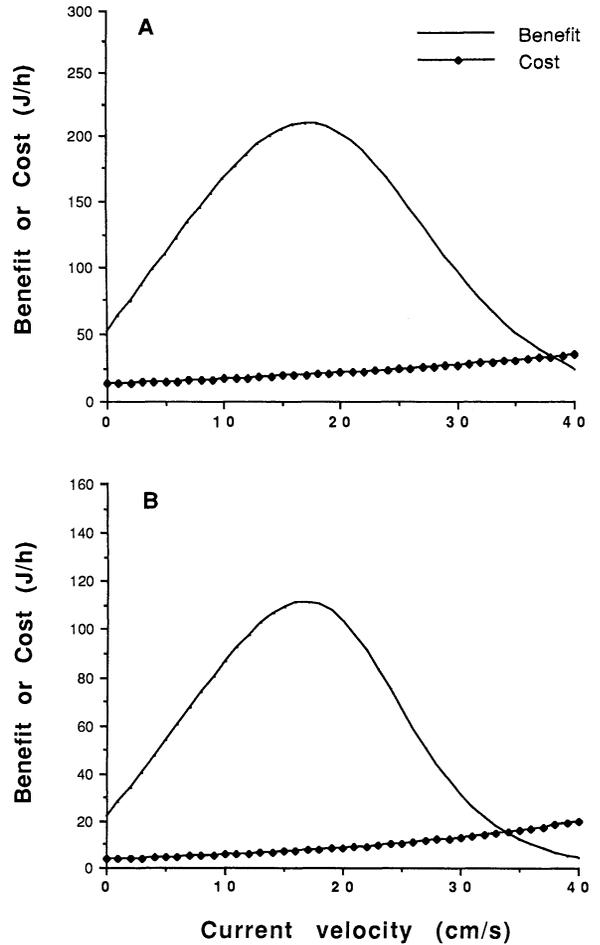

FIG. 6.   An example of complete models for trout (A) and dace (B). The continuous line is the benefit curve and the dotted line is the cost curve. Data are for small trout and medium dace in summer.

3.18, df $= 777$, $P < .05$). Both trout and dace exhibited seasonal shifts in focal point velocities (trout, $F = 5.02$, df $= 276$, $P < .003$, dace, $F = 17.90$, df $= 777$, $P < .0002$). Trout and dace both occupied the lowest velocities in the fall: this may have been caused by a decrease in the mean velocity available in the study sites during this season (Fig. 5). The use of focal point velocities by trout and dace differed significantly ($P < .05$) from those available in our study sites in all tests but one. Hence, both species generally were utilizing velocities in a nonrandom manner.

The net energy gain (E_x) predicted by our model typically increased slowly with velocity to a flat peak and then declined (Hill 1989). The shape of these curves was similar to that of the benefit curves, because energetic costs were small relative to potential energetic benefits (Fig. 6). Net energy gain decreased to negative values at velocities ranging from 24 to 44 cm/s, depending upon species, size, and season.

Comparisons of focal point velocities of trout and dace from Coweeta Creek with those predicted by the

TABLE 3. Current velocity (cm/s) at the point of maximum deceleration of the capture success curves (i.e., predicted feeding velocity), and the focal point velocity used by trout and dace.

Species	Size	Season	Predicted feeding velocity (cm/s)	Predicted focal point velocity* (cm/s)	Observed focal point velocity (cm/s)†
Trout	Small	Winter	21.5	15.9	15.0 (21)
		Spring	21.0	15.4	17.7 (11)
		Summer	20.6	15.0	13.4 (8)
		Fall	21.0	15.4	12.8 (45)
Trout	Medium	Winter	24.2	18.6	18.0 (25)
		Spring	26.1	20.5	20.5 (31)
		Summer	28.0	22.4	21.2 (137)
		Fall	26.1	20.5	17.5 (40)
Dace	Medium	Winter	14.0	9.4	13.9 (33)
		Spring	17.3	12.7	12.8 (54)
		Summer	20.6	16.0	14.5 (236)
		Fall	17.3	12.7	11.4 (118)
Dace	Large	Winter	18.6	14.0	12.7 (73)
		Spring	20.1	15.5	15.2 (62)
		Summer	21.5	16.9	14.4 (29)
		Fall	20.1	15.5	10.4 (155)

* To obtain the predicted focal point (i.e., microhabitat) velocity, we subtracted the average difference between focal point and strike velocities for trout (5.6 cm/s) and dace (4.6 cm/s) from the velocity corresponding to the maximum deceleration in capture success.

† Numbers in parentheses refer to sample size.

model indicated that the model was a good descriptor of microhabitat use by dace and trout (Table 2). For trout, all seasonal mean focal point velocities produced a net energy gain within 10% of E_{max}, and seasonal focal point velocities for dace fell with the acceptance range for 6 of 8 cases. The average deviation in focal point velocity from the model was 2.8 cm/s for trout and 2.5 cm/s for dace (Table 2). The mean percentage of field focal point velocity observations within the acceptance range also was significantly greater than that expected by chance alone (Wilcoxon signed-ranks test, $n = 15$, $T = 12.5$, $P < .05$). Consequently, both trout and dace generally appear to be utilizing microhabitats that maximize their rate of energy intake.

Upon examining the model it became clear that one element, prey capture success, contributed disproportionately to the predictions of the model. Because we were also interested in identifying the most influential components of the model, we attempted to predict focal point velocity use, based solely on prey capture success. Capture success curves (Figs. 3 and 4) generally were asymptotic until a critical velocity was reached, and then, prey capture success declined rapidly. It seemed reasonable to assume that selection might act on trout and dace so that they would choose the fastest velocity possible (recall that prey availability is positively correlated with velocity) that still yielded a high capture success. As an apriori test criterion, we cal-

culated the third derivative of prey capture success curves, which is the point of maximum deceleration of the curve. We then compared the velocity at the third derivative to focal point velocities occupied by trout and dace in Coweeta Creek, using the same correction factor for the difference between focal point and strike positions (see *Focal point and strike velocities* above). These comparisons produced even smaller differences between predicted and observed velocities than did the complete model (Table 3). The mean deviations between predicted and observed values for trout and dace, respectively, were 1.5 and 1.9 cm/s. Hence, the third derivative of prey capture success curves appears to be a more accurate predictor of microhabitat use by trout and dace, than the complete energy maximization model.

DISCUSSION

The model

Our energetic maximization model generally was able to predict microhabitat use for trout (100% success) and dace (75% success). Hence, it is likely that habitat use in Coweeta Creek for these species has been strongly affected by selective pressures leading to the maximization of net energy intake. The maximum deviation for any given model was 6.2 cm/s for medium dace in winter, which produced an E_x at the mean velocity utilized that was 29% lower than E_{max}. Our results corroborate those of other investigators, who have found great predictive value in models that explain habitat use on the basis of energy maximization principles (see Stephens and Krebs 1986, Dill 1987, Pulliam 1989).

Surprisingly, the use of the third derivative of prey capture success curves provided a better fit to field focal point velocities than did the complete model. Velocities predicted by the third derivative were very close to velocities that maximized net energy gain in the complete model (compare Tables 2 and 3). Energetic costs or variation in food availability changed E_{max} only slightly, implying that prey capture success was the major factor influencing model predictions. In part, the better fit of the model based solely upon capture success may be due to the fact that capture success was less variable than other model components. This result is not unexpected, because the ability to capture drifting prey must have a profound effect on the fitness of these fishes. In contrast, the addition of food availability as a model component may have added more error than predictive power to the model. This is a real possibility, because the availability of drifting invertebrates in streams exhibits considerable spatial and temporal variation for any given velocity.

Many other stream-dwelling salmonids are potentially subjected to the same selective pressures as rosyside dace and rainbow trout. In fact, other researchers have shown that several salmonid species behave in a manner consistent with the energy maximization pre-

cept (Fausch 1984, Godin and Rangeley 1989, Hughes and Dill 1990). Recognition of the power of this concept occurred as early as 1956 (Newman 1956). Our study differs from previous attempts to test this hypothesis, however, in that we have empirical data for all aspects of the model. In addition, our model makes a precise numerical prediction regarding the velocities to be occupied by trout and dace in Coweeta Creek. Nonetheless, the predictions of our model are limited to a specific 18-mo period, in a specific stream. Rainbow trout densities are relatively low in Coweeta Creek, in comparison to more favorable western habitats, and intraspecific competition for space typically may not be as strong (G. D. Grossman, *unpublished data*) as that reported for other areas. Despite these shortcomings, we hope that our model is sufficiently general to be of use to other investigators.

The two cases in which the model failed to accurately predict velocity use both involved dace (medium dace: winter, large dace: fall). We were only able to capture one group of medium dace for winter capture success experiments and this, coupled with a relatively low number of seasonal microhabitat measurements ($n = 33$), may have affected the model's predictive power. We were able to obtain adequate sample sizes ($n = 118$) for fall microhabitat measurements, however, and it is possible that dace truly occupied velocities that were significantly lower than those at E_{max} during this season. This difference could have been caused by a limitation in the availability of high velocity microhabitats during fall (Fig. 5). This limitation may have induced competition between small trout and large dace (i.e., those of equal size) for velocities at or near their energetic optima and ultimately caused a shift in microhabitat (i.e., velocity) use by large dace. However, further experimentation will be necessary to test this hypothesis.

Several researchers have demonstrated that habitat choice, and associated energy gain, can be strongly affected by the presence of predators (Werner et al. 1983, Mittelbach 1984, Gilliam and Fraser 1987, Abrahams and Dill 1989). Our experiments did not include predators, and their effect on microhabitat use of trout and dace is unknown. Inferential evidence suggests, however, that predators did not have a strong impact on microhabitat use by these species in Coweeta Creek. First, Grossman and Freeman (1987), G. D. Grossman et al. (*unpublished data*), and Freeman (1990) failed to detect predator-induced shifts in microhabitat use in Coweeta Creek fishes. Second, the sole common predator in Coweeta Creek, rockbass (*Ambloplites interruptus*), is only present in our study sites during fall and winter (Freeman et al. 1988). When rockbass were captured during these seasons for dietary studies, they all had empty stomachs (Stouder 1990). Nonetheless, it is possible that large dace were shifting away from optimal focal point velocities in fall to avoid rockbass. For most models, however, there was little evidence

that a lack of predators in experiments substantially compromised our results.

Microhabitat use (i.e., focal point velocity) by trout and dace varied with fish size and season, although trout and dace of similar size utilized similar velocities, as predicted by the model. Velocity use may be species specific (Symons 1976, Heggenes and Traaen 1988) or guild specific (Grossman and Freeman 1987). Due to the similarities in predicted velocity use by large dace and small trout, velocity use may be guild specific in Coweeta Creek. In addition, because trout consistently occupy velocities close to their energetic optima, it does not appear that dace are affecting microhabitat use of trout in our sites. This corresponds with the results of Grossman and Boulé (1991) who found that the presence of rosyside dace did not produce microhabitat shifts in rainbow trout in laboratory studies. Density-independent factors, or intraspecific competition typically may be maintaining populations of these species at levels below which interspecific competition occurs (Freeman et al. 1988). However, it is possible that trout caused a shift in microhabitat use by similar-sized dace in fall, as mentioned previously.

Past research has shown that a variety of factors, including velocity, influence microhabitat use in rainbow trout (Lewis 1969, Smith and Li 1983, Moyle and Baltz 1985) and other stream fishes (Everest and Chapman 1972, Symons 1976, Moyle and Vondracek 1985, Grossman and Freeman 1987, Hillman et al. 1987, Bain et al. 1988, Heggenes and Traaen 1988, Taylor 1988). As in our study, other investigators have found that microhabitat use is temperature dependent, in that stream fishes tend to occupy higher velocities at higher temperatures (Smith and Li 1983, Sheppard and Johnson 1985, Baltz et al. 1987, Heggenes and Traaen 1988, Taylor 1988). Our data suggest that this response may be caused by an increased ability to capture prey at higher temperatures, coupled with a concomitant increase in prey availability at higher velocities.

This argument is supported by physiological evidence for rainbow trout. Barron et al. (1987) demonstrated that increases in ambient temperature produced an increase in the distribution of blood flow to white muscle mass in rainbow trout, which may enable trout to respond faster to drifting prey. Hence, it is possible that microhabitat use in other lotic, drift-feeding fishes, is affected by selective pressures to maximize net energy intake.

Trout and dace fed consistently in Coweeta Creek during daylight hours, with no obvious diurnal periodicity. We only observed nocturnal activity and feeding in trout and dace when artificial illumination was present for more than momentary time spans. These findings are consistent with those of other researchers (Elson 1942, Hoar 1953, Newman 1956, Kalleberg 1958, Edmundson et al. 1968). Although some salmonids can apparently feed at night using natural light (Elliott 1967, Jenkins 1969a, Mason 1969) this did not

occur in Coweeta Creek. Perhaps the considerable canopy coverage in this system limited nocturnal activity by trout and dace. It is also possible that genetic differences exist in foraging behavior within strains of rainbow trout.

Energetic costs did not play a strong role in net energy gain models; energetic benefits were much more important to the determination of E_{max}. Although energetic costs appeared to have little influence on the determination of E_{max}, we did observe that trout and dace maintained position at velocities lower than those where they fed. This phenomenon also has been noted by other researchers (Jenkins 1969b, Mundie 1969, Everest and Chapman 1972, Griffith 1972, Fausch and White 1981, Smith and Li 1983, Fausch 1984). One possibility is that there are other unmeasured costs to maintaining position at velocities where feeding occurs. For example, visibility may be lower at higher velocities due to greater turbulence or turbidity. Maintaining position at high velocities also may render a fish more vulnerable to injury from debris or predators. These factors may be responsible for this phenomenon in trout and dace.

CONCLUSION

Temperate streams are temporally heterogeneous environments with varying temperatures, flow regimes, and prey abundances. Our data suggest that microhabitat use in two common stream fishes can be explained as behavior that maximizes net energy intake. Furthermore, a single component of our model, prey capture success, appeared to be the most important variable determining the velocity associated with maximizing net energy intake. It seems probable that prey capture success is an important component of habitat use for many drift-feeding stream fishes. In conclusion, we suspect that energy-based, mechanistic approaches to the study of microhabitat use in stream fishes will yield substantial insights when employed in other systems. Such models may ultimately be useful in predicting how species respond, intra- and interspecifically, to both natural and anthropogenic changes in flow regimes.

ACKNOWLEDGMENTS

LITERATURE CITED

Abrahams, M. V., and L. M. Dill. 1989. A determination of the energetic equivalence of the risk of predation. Ecology 70:999–1007.

Alley, D. W., Jr. 1974. The energetic significance of microhabitat selection by fishes in a foothill Sierra stream. Thesis. University of California, Davis, California, USA.

Andrassy, I. 1956. The determination of volume and weight of nematodes. Acta Zoologica Hungarica 2:1–5.

Angermeier, P. L. 1987. Spatiotemporal variation in habitat selection by fishes in small Illinois streams. Pages 52–60 in W. J. Matthews and D. C. Heins, editors. Community and evolutionary ecology of North American stream fishes. University Oklahoma Press, Norman, Oklahoma, USA.

Antonelli, A. L., R. A. Nussbaum, and S. D. Smith. 1972. Comparative food habits of four species of stream-dwelling vertebrates (Dicamptodon ensatus, D. copei, Cottus tenuis, Salmo gairdneri). Northwest Science 46:277–289.

Bain, M. B., J. T. Finn, and H. E. Booke. 1988. Streamflow regulation and fish community structure. Ecology 69:382–392.

Baker, J. A., and S. T. Ross. 1981. Spatial and temporal resource utilization by southeastern cyprinids. Copeia 1981: 178–189.

Baltz, D. M., and P. B. Moyle. 1984. Segregation by species and size class of rainbow trout (Salmo gairdneri) and Sacramento sucker (Catastomus occidentalis) in three California streams. Environmental Biology of Fishes 10:101–110.

Baltz, D. M., B. Vondracek, L. R. Brown, and P. B. Moyle. 1987. Influence of temperature on microhabitat choice by fishes in a California stream. Transactions of the American Fisheries Society 116:12–20.

Barrett, J. C., and G. D. Grossman. 1988. Effects of direct current electrofishing on the mottled sculpin. North American Journal of Fisheries Management 8:112–116.

Barron, M. G., B. D. Tarr, and W. L. Hayton. 1987. Temperature-dependance of cardiac output and regional blood flow in rainbow trout, Salmo gairdneri Richardson. Journal of Fish Biology 31:735–744.

Beamish, F. W. H. 1972. Ration size and digestion in largemouth bass, Micropterus salmoides Lacepede. Canadian Journal of Zoology 50:153–164.

———. 1974. Apparent specific dynamic action of largemouth bass, Micropterus salmoides. Journal of the Fisheries Research Board of Canada 31:1763–1769.

Bisson, P. A. 1978. Diet food selection by two sizes of rainbow trout (Salmo gairdneri) in an experimental stream. Journal of the Fisheries Research Board of Canada 35:971–975.

Bovee, K. D., and R. J. Milhous. 1978. Hydraulic simulation in instream flow studies: theory and technique. Instream Flow Paper Number 5, U.S. Fish and Wildlife Service/Office of Biological Services 78/33.

Breder, C. M., Jr., and D. R. Crawford. 1922. The food of certain minnows. Zoologica 2:287–327.

Cummins, K. W., and J. C. Wuycheck. 1971. Caloric equivalents for investigations in ecological energetics. Internationale Vereinigung für theoretishe und angewandte Limnologie, Verhandlungen 18:1–58.

Dill, L. M. 1987. Animal decision making and its ecological consequences: the future of aquatic ecology and behavior. Canadian Journal of Zoology 65:803–811.

Edmundson, E. H., F. H. Everest, and D. W. Chapman. 1968. Permanence of station in juvenile chinook salmon and steelhead trout in two Idaho streams. Journal of the Fisheries Research Board of Canada 25:1453–1469.

Elliott, J. M. 1967. The food of trout (Salmo trutta) in a Dartmoor stream. Journal of Applied Ecology 4:59–71.

———. 1973. The food of brown and rainbow trout (Salmo trutta and S. gairdneri) in relation to the abundance of

drifting invertebrates in a mountain stream. Oecologia (Berlin) 12:329–347.

Elliott, J. M., and W. Davison. 1975. Energy equivalents of oxygen consumption in animal energetics. Oecologia (Berlin) 19:195–201.

Elson, P. F. 1942. Behavior and survival of planted Atlantic salmon fingerlings. Transactions of the North American Wildlife Natural Resources Conference 7:202–211.

Everest, F. H., and D. H. Chapman. 1972. Habitat selection and spatial interaction by juvenile chinook salmon and steelhead trout in two Idaho streams. Journal of the Fisheries Research Board of Canada 29:91–100.

Facey, D. E. 1987. Metabolic constraints and microhabitat selection in four stream fishes. Dissertation. University of Georgia, Athens, Georgia, USA.

Facey, D. E., and G. D. Grossman. 1990. A comparative study of oxygen consumption by four stream fishes: the effects of season and velocity. Physiological Zoology 63: 757–776.

Facey, D. E., and G. D. Grossman. 1992. The relationship between water velocity, energetic costs, and microhabitat use on four North American stream fishes. Hydrobiologia 239:1–6.

Fausch, K. D. 1984. Profitable stream positions for salmonids: relating specific growth rate to net energy gain. Canadian Journal of Zoology 62:441–451.

Fausch, K. D., and R. J. White. 1981. Competition between brook trout (Salvelinus fontinalis) and brown trout (Salmo trutta) for positions in a Michigan stream. Canadian Journal of Fisheries and Aquatic Sciences 38:1220–1227.

Feldmeth, C. R., and T. M. Jenkins, Jr. 1973. An estimate of energy expenditure by rainbow trout (Salmo gairdneri) in a small mountain stream. Journal of the Fisheries Research Board of Canada 30:1755–1759.

Flemer, D. A., and W. S. Wolcott. 1966. Foot habits and distribution of the fishes of Tuckahoe Creek, Virginia, with special emphasis on the bluegill, Lepomis macrochirus Rafinesque. Chesapeake Science 7:75–89.

Freeman, M. C. 1990. Foraging behavior of the rosyside dace, Clinostomus funduloides: the importance of social interactions. Dissertation. University of Georgia, Athens, Georgia, USA.

Freeman, M. C., M. K. Crawford, J. C. Barrett, D. E. Facey, M. G. Flood, J. Hill, D. J. Stouder, and G. D. Grossman. 1988. Fish assemblage stability in a southern Appalachian stream. Canadian Journal of Fisheries and Aquatic Sciences 45:1949–1958.

Gatz, A. J., Jr. 1981. Morphologically inferred niche differentiation in stream fishes. American Midland Naturalist 160:10–21.

Gilliam, J. F., and D. F. Fraser. 1987. Habitat selection under predation hazard: test of a model with foraging minnows. Ecology 68:1856–1862.

Godin, J.J.-G., and R. W. Rangeley. 1989. Living in the fast lane: effects of cost of locomotion on foraging behaviour in Atlantic salmon. Animal Behaviour 37:943–954.

Griffith, J. S., Jr. 1972. Comparative behavior and habitat utilization of brook trout (Salvelinus fontinalis) and cutthroat trout (Salmo clarki) in small streams in Northern Idaho. Journal of the Fisheries Research Board of Canada 29:265–273.

Grossman, G. D., and V. Boulé. 1991. An experimental study of competition for space between rainbow trout (Oncorhynchus mykiss) and rosyside dace (Clinostomus funduloides). Canadian Journal of Fisheries and Aquatic Sciences 48:1235–1243.

Grossman, G. D., A. de Sostoa, M. Freeman, and J. Lobón-Cerviá. 1987a. Microhabitat selection in a Mediterranean riverine fish assemblage. I. Fishes of the lower Matarraña. Oecologia (Berlin) 73:490–500.

Grossman, G. D., A. de Sostoa, M. Freeman, and J. Lobón-Cerviá. 1987b. Microhabitat selection in a Mediterranean riverine fish assemblage: II. Fishes of the lower Matarraña. Oecologia (Berlin) 73:501–512.

Grossman, G. D., and M. C. Freeman. 1987. Microhabitat use in a stream fish assemblage. Journal of Zoology (London) 212:151–176.

Heggenes, J., and T. Traaen. 1988. Downstream migration and critical water velocities in stream channels for fry of four salmonid species. Journal of Fish Biology 32:717–727.

Hill, J. 1989. The energetic significance of microhabitat use in two stream fishes. Dissertation. University of Georgia, Athens, Georgia, USA.

Hill, J., and G. D. Grossman. 1987a. Effects of subcutaneous marking on stream fishes. Copeia 1987:492–495.

Hill, J., and G. D. Grossman. 1987b. Home range estimates for three North American stream fishes. Copeia 1987:376–380.

Hillman, T. W., J. S. Griffith, and W. S. Platts. 1987. Summer and winter habitat selection by juvenile chinook salmon in a highly sedimented Idaho stream. Transactions of the American Fisheries Society 116:185–195.

Hoar, W. S. 1953. Control and timing of fish migration. Biological Reviews of the Cambridge Philosophical Society 28:437–452.

Hughes, N. F., and L. M. Dill. 1990. Position choice by drift-feeding salmonids: models and test for Arctic grayling (Thymallus arcticus) in subarctic mountain streams, interior Alaska. Canadian Journal of Fisheries and Aquatic Sciences 47:2039–2048.

Jenkins, T. M., Jr. 1969a. Night feeding of brown and rainbow trout in an experimental stream channel. Journal of the Fisheries Research Board of Canada 26:3275–3278.

———. 1969b. Social structure, position choice and microdistribution of two trout species (Salmo trutta and Salmo gairdneri) resident in mountain streams. Animal Behavior Monographs 2:57–123.

Kalleberg, H. 1958. Observations in a stream tank of territoriality and competition in juvenile salmon and trout (Salmo salar L. and S. trutta L.). Report of the Institute of Freshwater Research Drottningholm 39:55–98.

Leuven, R. S. E. W., T. C. M. Brock, and H. A. M. van Druten. 1985. Effects of preservation on dry- and ash-free dry weight biomass of some common aquatic macro-invertebrates. Hydrobiologia 127:151–159.

Lewis, S. L. 1969. Physical factors influencing fish populations in pools of a trout stream. Transactions of the American Fisheries Society 98:14–19.

Mason, J. C. 1969. Hypoxial stress prior to emergence and competition among coho salmon fry. Journal of the Fisheries Research Board of Canada 26:63–91.

McClintock, J. B. 1986. On estimating energetic values of prey: implications in optimal diet models. Oecologia (Berlin) 70:161–162.

Mittelbach, G. G. 1984. Predation and resource partitioning in two sunfishes (Centrarchidae). Ecology 65:499–513.

Moyle, P. B., and D. M. Baltz. 1985. Microhabitat use by an assemblage of California stream fishes: developing criteria for instream flow determinations. Transactions of the American Fisheries Society 114:695–704.

Moyle, P. B., and B. Vondracek. 1985. Structure and persistence of the fish assemblage in a small California stream. Ecology 66:1–13.

Mundie, J. H. 1969. Ecological implications of the diet of juvenile coho in streams. The University of British Columbia Institute of Fisheries, H. R. MacMillan Lectures. Pages 135–152 in Fisheries, Symposium on Salmon and Trout in Streams 1968. University of British Columbia Press, Vancouver, British Columbia, Canada.

Newman, M. A. 1956. Social behavior and interspecific

competition in two trout species. Physiological Zoology **29**: 64–81.

Niimi, A. F., and F. W. H. Beamish. 1974. Bioenergetics and growth of largemouth bass (*Micropterus salmoides*) in relation to body weight and temperature. Canadian Journal of Zoology **52**:447–456.

Pulliam, H. R. 1989. Individual behavior and the procurement of essential resources. Pages 25–38 *in* J. Roughgarden, R. M. May, and S. A. Levin, editors. Perspectives in ecological theory. Princeton University Press, Princeton, New Jersey, USA.

Rao, G. M. M. 1968. Oxygen consumption of rainbow trout (*Salmo gairdneri*) in relation to activity and salinity. Canadian Journal of Zoology **46**:781–786.

Rice, J. A., J. E. Breck, S. M. Bartell, and J. F. Kitchell. 1983. Evaluating the constraints of temperature, activity and consumption on growth of largemouth bass. Environmental Biology of Fishes **9**:263–275.

Rogers, L. E., R. L. Buschbom, and C. R. Watson. 1977. Length–weight relationships of shrubsteppe invertebrates. Annals of the Entomological Society of America **70**:51–53.

Rudstam, L. G., and J. J. Magnuson. 1985. Predicting the vertical distribution of fish populations: analysis of cisco (*Coregonus artedii*) and yellow perch (*Percy flavesceus*). Canadian Journal of Fisheries and Aquatic Sciences **42**:1178–1188.

Sheppard, J. D., and J. H. Johnson. 1985. Probability-of-use for depth, velocity, and substrate by subyearling coho salmon and steelhead in Lake Ontario tributary streams. North American Journal of Fisheries Management **5**:277–282.

Smith, J. J., and H. W. Li. 1983. Energetic factors influencing foraging tactics of juvenile steelhead trout, *Salmo gairdneri*. Pages 173–180 *in* D. Lindquist, G. Helfman, and J. Ward, editors. Predators and prey in fishes. Dr. W. Junk, The Hague, The Netherlands.

Smock, L. A. 1980. Relationships between body size and biomass of aquatic insects. Freshwater Biology **10**:375–383.

Stefanich, F. A. 1952. The population and movement of fish in Prickley Pear Creek, Montana. Transaction of the American Fisheries Society **81**:260–274.

Stephens, D. W., and J. R. Krebs. 1986. Foraging theory. Princeton University Press, Princeton, New Jersey, USA.

Stouder, D. J. 1990. Dietary fluctuations in stream fishes and the effects of benthic species interactions. Dissertation. University of Georgia, Athens, Georgia, USA.

Symons, P. E. K. 1976. Behavior and growth of juvenile Atlantic salmon (*Salmo salar*) and three competitors at two stream velocities. Journal of the Fisheries Research Board of Canada **33**:2766–2773.

Taylor, E. B. 1988. Water temperature and velocity as determinants of microhabitat of juvenile chinook and coho salmon in a laboratory stream channel. Transactions of the American Fisheries Society **117**:22–28.

Tebo, L. B., Jr., and W. W. Hassler. 1963. Food of brook, brown and rainbow trout in streams in western North Carolina. Journal of the Elisha Mitchell Scientific Society **79**: 44–53.

Tippets, W. E., and P. B. Moyle. 1978. Epibenthic feeding by rainbow trout (*Salmo gairdneri*) in the McCloud River, California. Journal of Animal Ecology **47**:549–559.

Webb, P. W. 1978. Partitioning of energy into metabolism and growth. Pages 184–214 *in* S. D. Gerking, editor. Biology of freshwater fish production. John Wiley & Sons, New York, New York, USA.

Werner, E. E., J. F. Gilliam, D. J. Hall, and G. G. Mittelback. 1983. An experimental test of the effects of predation risk on habitat use in fish. Ecology **64**:1540–1548.

Whitworth, W. E., and R. J. Strange. 1983. Growth and production of sympatric brook and rainbow trout in an Appalachian stream. Transactions of the American Fisheries Society **112**:469–475.

Yeates, G. W. 1972. Nematoda of a Danish beech forest. II. Production estimates. Oikos **23**:178–189.

———. 1979. Soil nematodes in terrestrial ecosystems. Journal of Nematology **11**:213–229.