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Multi-scale effects of resource patchiness on foraging behaviour and habitat use by longnose dace, *Rhinichthys cataractae*

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SUMMARY

1. We examined the response of a predatory benthic fish, the longnose dace (*Rhinichthys cataractae*), to patchiness in the distribution of benthic macroinvertebrates on cobbles at three hierarchical spatial scales during summer and autumn 1996, and spring 1997 in a southern Appalachian stream.
2. At the primary scale (four to five individual cobbles separated by < 1 m), the intensity of foraging was not correlated with the biomass of benthic macroinvertebrates/cobble, regardless of season.
3. At the secondary scale (i.e. foraging patches < 5 m in diameter) we found that benthic macroinvertebrates were patchily distributed in summer, but not in autumn or spring. Concomitantly, in summer, longnose dace foraged on cobbles with a significantly higher biomass of benthic macronvertebrates than nearby, randomly selected cobbles with similar physical conditions (i.e. longnose dace tended to avoid low-prey foraging patches). In contrast, when benthic macroinvertebrates were distributed homogeneously (spring and autumn), dace did not select patches with a significantly higher biomass of benthic macroinvertebrates than that available on randomly selected cobbles.
4. At the tertiary scale (i.e. stream reaches 11–19 m long), the biomass of benthic macroinvertebrates (per cobble per reach) was patchily distributed (i.e. differed significantly among reaches) in all seasons. Among reaches with physical characteristics preferred by longnose dace, (i.e. erosional reaches dominated by cobble/boulder substratum and high current velocity), we detected a significant, positive correlation between the biomass of benthic macroinvertebrates/cobble and longnose dace density in all seasons.
5. Our results demonstrated that both spatial and temporal patchiness in resource availability influenced significantly the use of both foraging patches and stream reaches by longnose dace.

Keywords: foraging patch, habitat selection, predator–prey, spatial heterogeneity, stream fish

Introduction

Ecological systems are heterogeneous (i.e. patchy) over a range of spatial and temporal scales (Wiens, 1976, 1989; Levin, 1992; Cooper *et al.*, 1997). For example, habitats often contain many patch types differing in resource availability. Resource patchiness of this type may affect the behaviour of mobile species because these individuals often occupy microhabitats

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that yield the highest rates of net energy intake (and, consequently, increase their fitness) (Fretwell & Lucas, 1971; Charnov, 1976; Cowie, 1977; Hill & Grossman, 1993; Morgan, Brown & Thorson, 1997). Therefore, quantifying the effects of patchiness on resource use by animals should increase our understanding of how these organisms respond to environmental variation on both an individual and population level (Schneider & Piatt, 1986; Hodge, 1987a,b; Orians & Wittenberger, 1991; Ward & Saltz, 1994; Cooper *et al.*, 1998).

Quantifying patchiness and its effects on animals in natural habitats can be difficult, however, for two reasons. First, patches frequently occur on several hierarchical levels (i.e. larger patches contain several smaller patches) (Urban, O'Neill & Shugart, 1987; Kotliar & Wiens, 1990). Second, animals may not be able to differentiate among patches at all spatial scales (Pyke, 1981; Danell, Edenius & Lundberg, 1991; Fryxell & Doucet, 1993). Consequently, studies of the effects of resource patchiness on organisms must be linked to both the hierarchical distribution of patches in nature and their discriminatory capabilities (Kotliar & Wiens, 1990).

Due to their high level of spatial heterogeneity (Pringle *et al.*, 1988; Hildrew & Giller, 1994), temperate woodland streams are model systems for addressing how resource patchiness affects both resource use and the distribution of animals. Based on their physical characteristics, most temperate streams can be divided into several hierarchical spatial levels based on length, including: microhabitat (10^{-1} m), riffle-pool (10^{0} m) and reach (10^{1} m) (Frissel *et al.*, 1986). Patchiness in the distribution of physical factors at all hierarchical levels may affect the distribution and abundance of stream organisms, ranging from primary producers to tertiary consumers (Rabeni & Minshall, 1977; Culp, Walde & Davies, 1983; Kohler, 1984; Parker, 1989; Pringle, 1990). In fact, both spatial and temporal patchiness in resource availability are probably responsible for the patchy distribution of benthic macroinvertebrates at a variety of spatial scales (Hynes 1970; Wallace *et al.*, 1997) including: individual cobbles (Muotka & Penttinen, 1994; Downes *et al.*, 1998), groups of cobbles separated by < 1 m (Downes, Lake & Schreiber, 1993), and large aggregations of cobbles within stream reaches (Hynes, 1970; Downes *et al.*, 1993).

We examined the effects of spatial and temporal patchiness in resource availability on the foraging behaviour, patch choice and spatial distribution of a benthic stream fish (longnose dace, *Rhinichthys cataractae* Valenciennes) in a temperate woodland stream. We chose longnose dace for study because it is an abundant species with a broad geographic range (Jenkins & Burkhead, 1994). In the Coweeta drainage (NC, U.S.A.), longnose dace are active diurnal foragers, which facilitates direct observation of their behaviour and choice of foraging locations (A. Thompson & G. Grossman, pers. observ.). Furthermore, longnose dace exhibit relatively high site fidelity, remaining within the same stream reach (14 m) for up to 18 months (Hill & Grossman, 1987). Regardless of their geographic location, adult longnose dace consistently occupy riffles (i.e. erosional substrata and rapid current) (Gee & Northcote, 1963; Sheldon, 1968; Bartnick, 1970; Gibbons & Gee, 1972; Grossman & Freeman, 1987; Hubert & Rahel, 1989; Mullen & Burton, 1995, 1998; Grossman & Ratajczak 1998), where they typically prey on benthic macroinvertebrates captured from the surfaces of larger substratum particles (i.e. > 5 cm in diameter) (Gee & Northcote, 1963; Gerald, 1966; Gibbons & Gee, 1972; Barrett, 1989; Stouder, 1990). Intraspecific competition (mediated by food limitation), rather than interspecific competition or predation, is probably the major biotic factor influencing longnose dace populations in Coweeta Creek (Stouder, 1990; Grossman *et al.*, 1998).

Given the potential impact of spatial and temporal patchiness in prey availability on longnose dace in the Coweeta drainage, we attempted to characterize benthic macroinvertebrate patchiness within the system and to quantify the subsequent responses of longnose dace at three hierarchical scales during three seasons. We measured benthic macroinvertebrate patchiness at primary, secondary and tertiary scales following the hierarchical patch framework outlined by Kotliar & Wiens (1990). In this conceptualization, patchiness at the primary scale represents the lowest level at which an organism can differentiate individual patches. Scaling up, a secondary scale patch contains at least two primary scale patches, whereas a tertiary scale patch encompasses multiple secondary scale patches.

We tested three main predictions regarding the effects of prey patchiness on habitat use by longnose dace. First, we predicted that patchiness in the den-

sity of benthic macroinvertebrates on individual cobbles separated by < 1 m (primary scale) would result in longnose dace foraging with significantly greater intensity on cobbles with a higher density of benthic macroinvertebrates than cobbles with a lower density. Second, we predicted that when benthic macroinvertebrates were patchily distributed among foraging patches (i.e. cobbles separated by 0.5–5.0 m, the secondary scale), longnose dace would preferentially forage in high-prey patches (i.e. avoid low-prey patches). Finally, we tested the prediction that there would be a significant positive correlation between longnose dace density/reach and mean benthic macroinvertebrate density/reach (i.e. sections of stream 11–19 m long, separated by distinct physical breaks, the tertiary scale).

Methods

The study site

Our study site was a 100-m segment of Ball Creek, a fourth order stream situated on the USDA Forest Services Coweeta Hydrological Laboratory located within the Blue Ridge Province of the southern Appalachian mountains. Bankside vegetation along Ball Creek consisted primarily of rhododendron (*Rhododendron maximum* L.), mountain laurel (*Kalamia latifolia* L.) and dogwood (*Cornus florida* L.). During our study, Ball Creek had a mean annual temperature of 12 °C (range = 2–19 °C) and a mean wetted width of 5.2 m (range = 4.3–9.7 m). The major geomorphic features of the site were: 1) cobble-dominated riffles; 2) a shallow, silty run; and 3) a sandy pool. Resident fish include mottled sculpin (*Cottus bairdi* Girard), longnose dace (*Rhinichthys cataractae*) and rainbow trout (*Oncorhynchus mykiss* Walbaum). A weir directly below the site may have blocked upstream immigration of fish, although they were capable of moving downstream by traversing the weir. To facilitate spatial measurements within the site, we placed a permanent transect pole every 4 m along both banks.

Sampling regime

We quantified the physical characteristics of the site, patchiness in the densities of benthic macroinvertebrates and longnose dace foraging behaviour and habitat use in summer (14–21 August 1996), autumn (14–28 October 1996) and spring (11–19 June 1997). During each sampling period, we first observed fish by snorkelling during daylight hours and then measured physical habitat characteristics and collected samples of benthic macroinvertebrates. Although longnose dace may forage nocturnally in Alberta streams (Culp, 1989; Scrimgeour, Culp & Wrona, 1994), we regularly observe longnose dace foraging during the day at Coweeta (Grossman & Freeman, 1987; Grossman & Ratajczak 1998; A. Thompson, pers. obs.). In addition, dietary studies confirm that longnose dace forage diurnally in this system. (Stouder, 1990; G. Grossman, unpublished).

Primary scale patchiness and the foraging behaviour of longnose dace

Preliminary observations indicated that individual large substratum particles (i.e. cobbles and boulders) were the smallest 'patches' upon which dace foraged consistently, and we classified these particles as primary scale patches (A. Thompson & G. Grossman, pers. obs.). We will refer to these particles hereafter as cobbles (i.e. unembedded particles ≥ 5 cm in length). If patchiness at the primary scale influences foraging by longnose dace, we would expect a positive correlation between macroinvertebrate density on cobbles and the number of bites aimed at prey on cobbles by individual fish. We also predicted that this relationship would be strongest when macroinvertebrate patchiness among cobbles was greatest.

From the downstream end of the site, we snorkelled upstream to locate actively foraging adult longnose dace (> 45 mm standard length). Once a fish was located, we counted the number of bites it took from the next four or five cobbles. We used the number of bites taken by individual dace on each cobble (henceforth 'fish cobbles') as an estimate of foraging intensity. We used this metric rather than the time each fish spent foraging on a cobble because it was simpler to measure and the time increment between successive bites on cobbles appeared to be relatively constant (i.e. number of bites was positively correlated with the time spent on a cobble). After each fish completed a foraging bout, we placed a unique, coloured marker adjacent to each fish cobble for subsequent identification. Previous research has shown that the presence of a diver does not alter markedly the behaviour of longnose dace in this

system (Grossman & Freeman, 1987; Grossman & Ratajczak, 1998; A. Thompson, pers. obs.).

We collected foraging data for 20 adult longnose dace in each seasonal sample. This typically required three sampling passes through the site. In summer, we made three passes in a single day, but in autumn and spring we made one pass per day on three consecutive days. We reduced the probability of sampling the same fish on more than one pass by not taking measurements if, on the second or third pass, a similar-sized fish was seen within 2 m of a previously sampled location. After fish observations were completed, we determined the exact location of each fish cobble by triangulation with the two nearest transect posts on opposite banks.

Because fish cobbles were in close proximity (< 1 m), the general physical characteristics of these locations were similar. Therefore, we did not directly test whether physical patchiness at the primary scale influenced the foraging intensity of longnose dace. Nevertheless, we quantified the physical habitat characteristics associated with each fish cobble prior to sampling macroinvertebrates, for use in subsequent secondary and tertiary-scale analyses. We visually estimated substratum composition (percent bedrock, boulder, cobble, gravel, sand, silt and organic debris) in a 0.04-m^2 area surrounding each fish cobble using a plexiglass viewing box (Petty & Grossman, 1996). We categorized substrata other than debris on the basis of maximum linear particle size: bedrock (embedded material > 30 cm), boulder (unembedded material > 30 cm), cobble < 30 and > 2.5 cm, gravel < 2.5 cm and > 0.2 cm, sand < 0.2 cm, silt (material that could be suspended in the water column) and debris (organic material) (Grossman & Freeman, 1987; Grossman & Ratajczak 1998). We also measured bottom current velocity (i.e. the sensor was placed directly on the stream floor) and average (0.6 × water column depth, Bovee & Milhous, 1978) current velocity with an electronic velocity meter (Marsh-McBirney Model 201) accurate to ± 0.1 cm s^{-1}. We measured the depth of the water column with a metre stick.

We then quantified the abundance of macroinvertebrates on each fish cobble by gently lifting it into a Surber sampler and then transferring it to a pan. The cobble was then scraped vigorously to dislodge macroinvertebrates, which were collected using a 250-μm mesh sieve and preserved in a 10% formalin solution. We estimated the surface area of each fish cobble by multiplying its maximum length by its maximum width (perpendicular to length). This method yields accurate estimates of the surface area of cobbles with complex surfaces (McCreadie & Colbo, 1991).

In the laboratory, we identified macroinvertebrates to family whenever possible. However, mites, copepods, oligochaetes, metamorphosing and pupating insects and individuals with head capsule widths (HCW; total distance across the head at the level of the eyes) < 0.2 mm were identified only to order. We measured HCW or maximum body width (for mites) of specimens to the nearest 0.1 mm using a dissecting microscope and estimated volumes using family-specific regression models (i.e. length–volume) developed for the fauna of the Coweeta Creek drainage (Stouder, 1990). Samples containing large numbers of macroinvertebrates (i.e. those estimated to take > 4 h to analyze) were subsampled in the following manner. First, we divided these samples into two size fractions: 1) material retained on a 1-mm sieve and 2) material retained on a 270-μm sieve. We then estimated the volumes of all macroinvertebrates held on the 1-mm sieve, whereas we only calculated macroinvertebrate volumes for a one-eighth subsample of the 270-μm size fraction. The volume of the 270-μm size fraction was then multiplied by eight and added to the volume of the 1-mm size fraction to derive an estimate of total macroinvertebrate volume for the cobble (Thompson, 1998).

We used the total volume of macroinvertebrates on each cobble as an estimate of biomass because wet volume is strongly correlated with biomass for these taxa (Ciborowski, 1983). In addition, prey biomass is more representative of the energetic value of prey to a predator than prey abundance, so we standardized biomass by dividing total biomass by the surface area of a cobble. We also estimated the density of specific taxa that were known prey of longnose dace (Stouder, 1990). However, because results for taxon-specific data were identical to those for total macroinvertebrates, we only present results for the latter data set.

We determined the degree to which macroinvertebrate biomass was patchily distributed at the primary scale (i.e. among individual cobbles) by calculating a coefficient of variation (CV) for biomass data from each group of four to five fish cobbles. Large CV

values would indicate high primary scale patchiness and suggest that individual longnose dace encountered a wide range of prey biomass/cobble. Although CV values for macroinvertebrate biomass on groups of fish cobbles cannot strictly be used to estimate quantitatively whether macroinvertebrates were patchily distributed on cobbles, these values should be useful for characterizing the degree of macroinvertebrate patchiness among groups of fish cobbles (Palmer, Hakenkamp & Nelson-Baker, 1997). To determine whether longnose dace experienced significantly different levels of primary scale patchiness among seasons, we compared CV values for each seasonal sample of fish cobbles using ANOVA and *post hoc* pairwise Tukey tests (Palmer *et al.*, 1997).

We tested the prediction that primary scale patchiness in macroinvertebrate biomass affected the foraging intensity of longnose dace by testing for significant correlations between macroinvertebrate biomass/cobble and the number of bites each fish took from a fish cobble, using linear regression. If primary scale prey patchiness affected the foraging intensity of longnose dace, then this should have produced significantly more positive correlation coefficients then expected by chance alone. We tested this prediction with a χ^2 test (Ho: frequencies do not differ significantly from a 50:50 positive:negative distribution; Zar, 1996). We also tested the hypothesis that longnose dace would respond to primary patchiness in macroinvertebrate biomass most strongly when patchiness among fish cobbles was high. If true, then we would expect a positive correlation between the CV of macroinvertebrate biomass and values for correlation coefficients from correlation analyses between number of bites fish cobble and macroinvertebrate biomass fish cobble. We evaluated this possibility by performing a correlation analysis (using linear regression) between CV values for macroinvertebrate biomass fish cobble and the correlation coefficient (see Palmer *et al.*, 1997 for discussion of the use of CV as an independent variable).

Secondary scale patchiness and patch use by longnose dace

Our primary goal was to evaluate the effects of patchiness in prey on patch use by longnose dace. Prior to this assessment, however, we needed to determine whether the physical characteristics of a patch (i.e. groups of fish cobbles) affected patch selection. Hence, we tested for significant differences in the physical characteristics of foraging patches and nearby randomly selected locations. We began this analyses by placing permanent transect markers at 4-m intervals along both banks of the stream (total = 25 transect lines). We then established transects across the stream (i.e. between permanent transect markers at the same metre mark) and collected physical habitat data at 1-m intervals. At each cross-stream metre mark, we placed a 1-m^2 grid divided into 25 equal quadrats (0.04 m^2 each) and then used a random number table to select one quadrat. We quantified the physical habitat characteristics of the quadrat as previously described for primary scale patches. If cobbles were present, we collected macroinvertebrates from the cobble closest to the centre of the quadrat. We obtained physical microhabitat measurements for 111, 116 and 118 random locations and macroinvertebrates from 87, 100 and 107 random cobbles in summer, autumn and spring, respectively. As with fish cobbles, we used triangulation to locate the exact position of each random quadrant.

To determine whether the physical characteristics of a location influenced foraging patch use by longnose dace, we performed separate principle component analyses (PCA) on each seasonal set of physical data from both random locations and fish cobbles. We used the partitioned χ^2 technique of Grossman & Freeman (1987) and Grossman & Ratajczak (1998) to test for significant differences between PC scores for fish cobbles and random locations. Because fish cobbles were not independent (i.e. they represented groups of four to five cobbles that dace had foraged on), we did not treat them as independent points in the analysis. Instead we calculated a mean component score for each group of fish cobbles and compared this score to the scores from random locations. We transformed data (linear–ln, percentage–arcsine squareroot) to reduce heteroscedasticity and kurtosis.

We quantified secondary scale patchiness of macroinvertebrates within the site by using spatial autocorrelation analysis to test the null hypothesis of no significant correlation in the macroinvertebrates biomass values of randomly selected cobbles separated by varying distances (Sarnelle, Kratz & Cooper, 1993; Lovvorn & Gillingham, 1996; Cooper *et al.*, 1997). This analysis not only allowed the detection of secondary scale patches (i.e. significant correlation in

biomass among random cobbles), it also enabled us to estimate the size of secondary patches (maximum distance between significantly correlated cobbles). Using the X–Y coordinates of each random cobble, we calculated the distance between cobbles to the nearest 0.05 m. We then calculated Pearson's product-moment correlation coefficients (r) for biomass values of pairs of cobbles separated by 0–1, 1–2, 2–3 and 3–5.4 m along transect lines. We chose these distances because we observed that longnose dace never moved more than 5 m during a foraging bout (A. Thompson and G. Grossman, pers. observ.). Finally, we created a correlelogram for each seasonal data set by plotting correlation coefficients (Y) versus distance class (X) for all pairs of random cobbles. To avoid violating the assumption of independence, cobbles were used once only for each distance class analysis (Underwood & Chapman, 1996).

We tested the null hypothesis that secondary scale patchiness had no effect on foraging patch use by longnose dace by ascertaining whether macroinvertebrate biomass on fish cobbles (i.e. in foraging patches) differed significantly from that on random cobbles with similar physical characteristics. For each fish, we chose the nearest random cobble that was >1 m from its foraging patch. Because our results indicated that longnose dace in Coweeta Creek avoid depositional areas, we chose only random cobbles found in erosional locations. As with the physical data, we did not treat individual fish cobbles as independent points, but calculated an average macroinvertebrate biomass value for each fish from the four to five cobbles in a foraging patch. We then used a paired t-test to test for significant differences between the fish and random data sets.

Tertiary scale patchiness and longnose dace abundance

We examined the distribution of longnose dace at the tertiary scale by dividing the site into seven reaches bounded by either natural barriers (i.e. where $>70\%$ flow was diverted) or distinct geomorphological changes (e.g. shifts from pool to riffle). Mean reach length (i.e. tertiary patch) was 12 m (range = 11–19 m) and mean reach area was 81 m^2 (range = 51–133 m^2). The length of tertiary patches also corresponded to mean home range size of longnose dace, which averaged 13.4 m over an 18-month period in a portion of the drainage slightly downstream from our study site (Hill & Grossman, 1987).

We estimated longnose dace density in each reach by dividing the number of longnose dace observed in a reach by its area. We minimized the probability that individual longnose dace were counted repeatedly by deleting individuals of similar size observed within 2 m of a previously identified fish. Nonetheless, this only resulted in the elimination of a small number of fish (0 in summer, 1 in autumn and 1 in spring). In order to validate visual estimates of fish density, we electrofished each reach after all samples had been collected in spring (we did not electrofish in other seasons to avoid disturbing fish). Visual observations of fish number were either exactly the same (reaches 1–4) or differed by one (reach 7) or two (reach 6) fish from electrofishing estimates. In reach 5, however, electrofishing accounted for five fish, while snorkelling observations failed to identify any fish. This discrepancy was caused either by post-snorkelling fish movement or our inability to observe fish accurately in reach 5. We believe that the latter explanation is not entirely correct because we observed longnose dace in reach 5 in summer and autumn. Consequently, some longnose dace probably moved into reach 5 following disturbances associated with data collection. In spite of the incongruity associated with reach 5, linear regression indicated that visual estimates of dace abundance reach were highly correlated with estimates derived from electrofishing ($r = 0.76$, $P = 0.04$, d.f. = 6), suggesting that visual observations were effective at determining dace abundance within the site.

If tertiary scale (i.e. among reach) patchiness in macroinvertebrate biomass affected the distribution of longnose dace, then we would expect a significant positive correlation between the biomass of macroinvertebrates and abundance of longnose dace across reaches. However, given that adult longnose dace are often under-represented in depositional microhabitats (Grossman & Freeman, 1987; Grossman & Ratajczak, 1998), physical differences among reaches may have also affected distribution patterns. Consequently, we first assessed whether the physical characteristics of reaches differed and whether these differences were correlated (using linear regression) with dace density. Second, we quantified patchiness in macroinvertebrate biomass among reaches (see below) and then tested the prediction that reaches phys-

ically suitable for dace would also display a significant positive correlation (using linear regression) between macroinvertebrates biomass and the abundance of longnose dace.

To quantify third order patchiness in the physical environment, we tested the hypothesis that mean principal component 1 (PC 1) scores generated separately for each seasonal data set (see above) differed significantly among reaches. We were unable to meet normality assumptions necessary for standard parametric analysis, so we utilized Kruskal–Wallis analysis to test for overall differences and an *a posteriori* Nemenyi test (Zar, 1996) to evaluate pairwise differences. Once the physical nature of each reach was identified, we used χ^2 analysis to test the hypothesis that longnose dace abundances in depositional reaches were lower than those expected by chance alone (Zar, 1996).

We quantified third order patchiness by testing the hypothesis that mean macroinvertebrate biomass varied significantly among reaches. As with physical data, we were unable to meet normality assumptions and, consequently, utilized a Kruskal–Wallis analysis to test for overall differences, followed by a Nemenyi test of pairwise differences (Zar, 1996). Using linear regression, we tested the null hypothesis of no significant correlation between macroinvertebrate biomass and fish abundance among reaches using regression analysis. Because longnose dace apparently avoided depositional reaches irrespective of food availability (see Results), we restricted the regression analyses to erosional reaches. All statistical calculations were made using Microsoft Excel and SAS (SAS Institute, Cary, NC).

Results

Primary scale patchiness and the foraging behaviour of longnose dace

Primary scale patchiness in the biomass of macroinvertebrates within foraging patches varied among seasons. Summer coefficients of variation (CV) for macroinvertebrate biomass on fish cobbles (0.48 ± 0.05, mean $\pm$ SE) were significantly lower than values for both autumn (0.94 ± 0.09) and spring (0.78 ± 0.06) ($F = 10.9$, $P < 0.001$, d.f. = 59). Despite high CV values for macroinvertebrate biomass in autumn and spring, there was no evidence that the foraging intensity of longnose dace was influenced by primary scale patchiness in macroinvertebrate densities on fish cobbles in any season. First, the frequency of positive correlation coefficients between macroinvertebrate biomass and foraging intensity (i.e. the number of bites taken) by individual fish did not differ from that expected by chance alone (number of fish displaying positive r's in summer = 8/20, autumn = 9 20, spring = 10 20, all χ^2 P's > 0.10). Second, the CV of macroinvertebrate biomass was not correlated with the correlation coefficient between macroinvertebrate biomass and foraging intensity (summer $r = 0.24$, autumn $r = 0.25$, spring $r = 0.20$, all P's > 0.10). These results suggest that patchiness in macroinvertebrate biomass among fish cobbles (i.e. primary scale patchiness) had little impact on the foraging behaviour of longnose dace.

Secondary scale patchiness and patch use by longnose dace

Principal component analysis and partitioned χ^2 tests demonstrated that the physical characteristics of patches significantly affected foraging patch use by longnose dace in all seasons. Principal component analysis extracted three to four components with eigenvalues greater than 1 from each seasonal set of habitat availability data. However, we retained only PC 1 because it explained the greatest amount of total variance within the data (26% in summer, 32% in autumn and 31% in spring), and also depicted the major habitat gradient (erosional–depositional) present in the site. Partitioned χ^2 analyses demonstrated that longnose dace were significantly underrepresented in patches with low velocity and depositional substrata in all seasons (summer $\chi^2 = 15.4$ $P = 0.008$, autumn $\chi^2 = 0.026$ $P = 0.026$, spring $\chi^2 = 15.3$ $P = 0.018$, Fig. 1).

The presence of secondary scale patchiness in the biomass of macroinvertebrates varied among seasons. In summer, macroinvertebrate biomass was positively correlated for cobbles within 3 m of each other (Fig. 2). In autumn and spring, however, we failed to detect significant autocorrelation at any distance class (Fig. 2).

When secondary scale patchiness in macroinvertebrate density was present (i.e. summer), longnose dace foraged in patches with significantly greater macroinvertebrate biomass than that observed on random cobbles with similar physical characteristics (Table 1). In contrast, when secondary scale patchiness in macroinvertebrate biomass was not observed

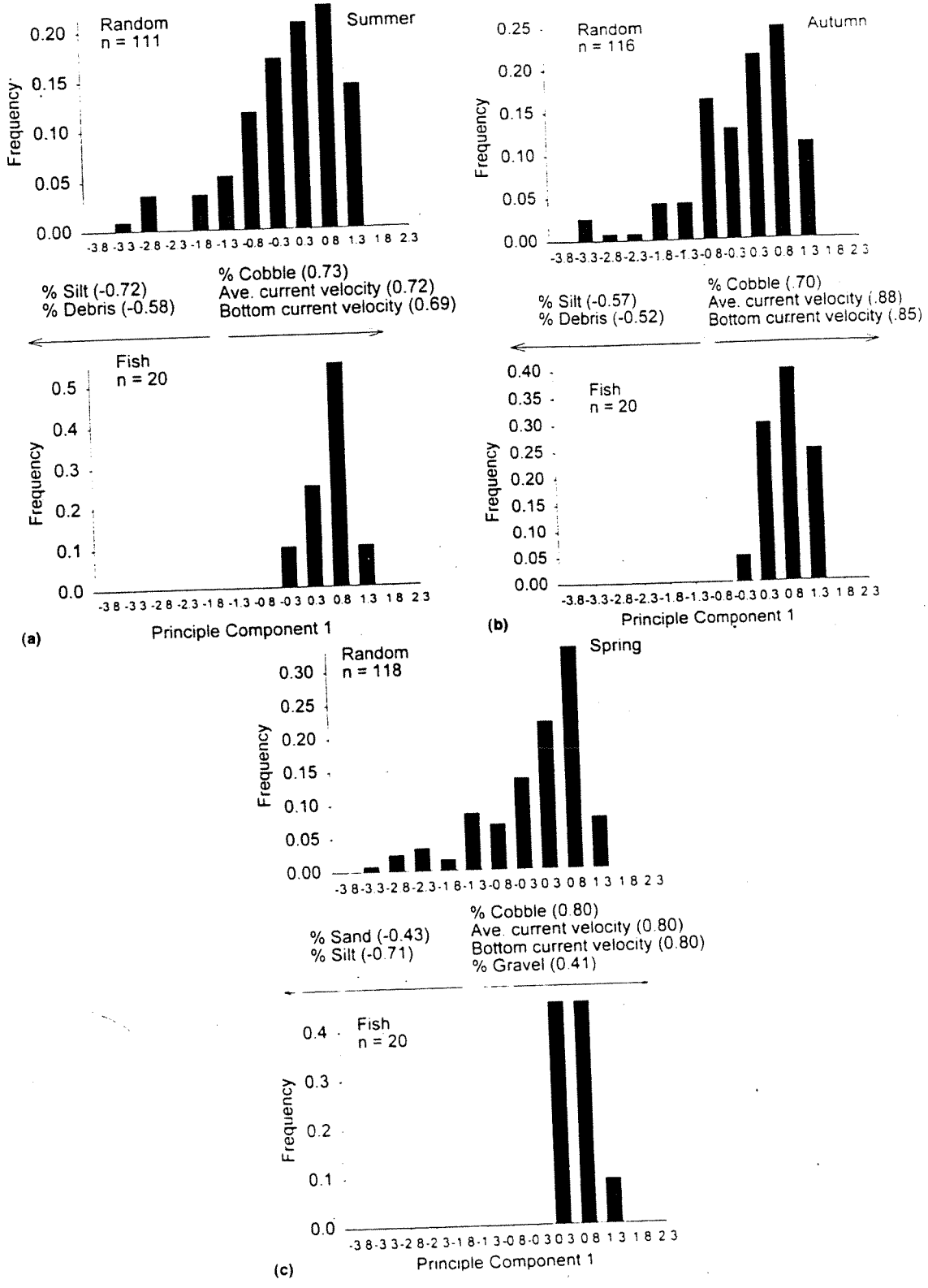

Fig. 1 Patch use on PC 1 in summer (a), autumn (b) and spring (c). Histograms represent frequency distributions of PC 1 scores for random and fish locations. Variables with component loadings > |0.4| are listed.

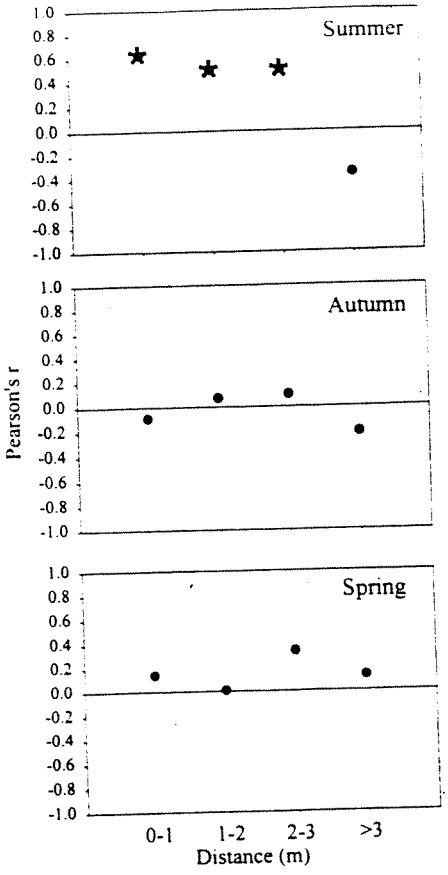

Fig. 2 Correlogram of benthic macroinvertebrate biomass in summer, autumn and spring. Distance class represents the range of distances separating pairs of cobbles. Significant regressions ($P < 0.05$) are depicted by *.

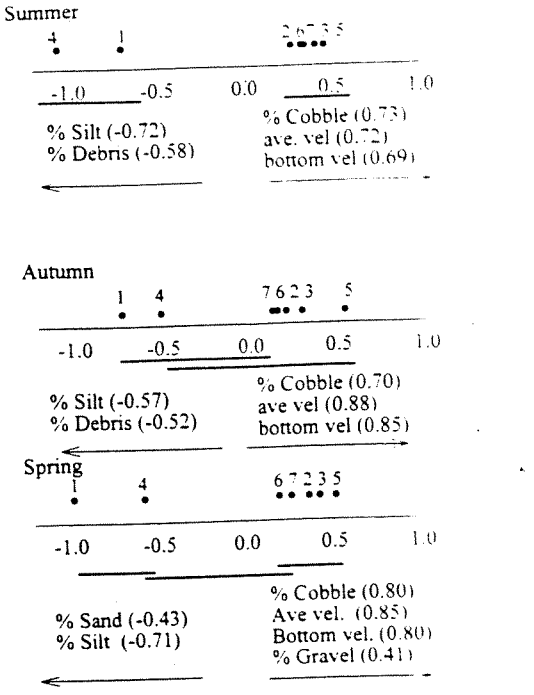

Fig. 3 Mean PC 1 score per reach in summer, autumn and spring. Horizontal bars depict reaches that did not differ based on a Nemenyi test. Reaches are identified by the numbers above the symbols. Only variables with component loadings $> |0.4|$ are listed.

(autumn and spring, Fig. 2), there were no significant differences in the biomass of macroinvertebrates between paired fish and random cobbles (Table 1).

Tertiary scale patchiness and the abundance of longnose dace

Reaches within the study site displayed tertiary scale patchiness in physical characteristics during all seasons (Kruskal–Wallis tests on PC 1 scores — summer $\chi^2 = 31.4$ $P < 0.01$, autumn $\chi^2 = 22.3$ $P < 0.001$, spring $\chi^2 = 36.1$ $P < 0.001$, Fig. 3). These analyses indicated that the site was comprised of two significantly different groups of reaches (erosional reaches with high current velocity and cobble-dominated substratum [reaches 2, 3, 5, 6 and 7]; and depositional reaches with a low current velocity, sand, silt and debris-dominated substratum [reaches 1 and 4]).

Chi-square tests indicated that significantly fewer longnose dace were found in the depositional reaches (1 and 4) in each season than was expected by chance alone (summer $P < 0.025$, autumn $P < 0.10$ and spring

Table 1 Pair-wise comparisons of macroinvertebrate biomass ($\mu L\ cm^{-2}$) and PC 1 scores between foraged-upon ($n = 20$) and random cobbles ($n = 20$). Only random cobbles with similar PC 1 scores to fish cobbles were selected for the analysis

Season	Macroinvertebrate biomass fish cobbles (2SE)	Macroinvertebrate biomass random cobbles (2SE)	t	P	PC 1 score fish cobbles (2SE)	PC 1 score random cobbles (2SE)	t	P
Summer	0.28 (0.04)	0.20 (0.07)	2.05	0.03	0.61 (0.17)	0.57 (0.17)	0.40	0.35
Autumn	0.23 (0.07)	0.21 (0.09)	0.28	0.39	0.69 (0.17)	0.63 (0.18)	0.55	0.29
Spring	0.32 (0.10)	0.26 (0.11)	0.78	0.22	0.55 (0.10)	0.63 (0.17)	0.83	0.21

$P < 0.025$). In summer and spring, no fish were observed in reaches 1 or 4, while in autumn one fish was observed in reach 4.

Tertiary scale patchiness in the biomass of macroinvertebrates was present in all seasons (Kruskal–Wallis test — all P's < 0.01). In summer, Nemenyi tests demonstrated that reaches 1, 2, 3 and 5 had significantly higher macroinvertebrate biomass than reaches 4 or 7 (Fig. 4). In addition, reach 2 also had significantly higher macroinvertebrate biomass than reach 6 (Fig. 4). In autumn, reaches 1 and 2 had significantly higher macroinvertebrate biomass than reaches 4 and 6 (Fig. 4). Finally, in spring, reaches 1, 2 and 3 had significantly higher macroinvertebrate biomass than reaches 4 and 7 (Fig. 4).

Tertiary scale patchiness in macroinvertebrate biomass influenced the spatial distribution of longnose dace across reaches. There were strong positive correlations between macroinvertebrate biomass and longnose dace density within erosional reaches in every season (summer $r = 0.98$ $P = 0.003$, autumn $r = 0.96$ $P = 0.008$ and spring $r = 0.86$ $P = 0.059$, Fig. 5).

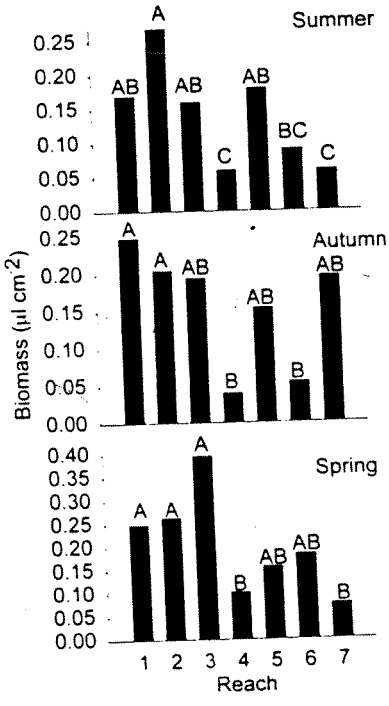

Fig. 4 Mean macroinvertebrate biomass per reach in summer, autumn and spring. Letters depict reaches that differed significantly based on a Nemenyi test ($P < 0.05$).

Discussion

The capability of many animals to select foraging locations that maximize their rate of energy gain (Charnov, 1976; Hill & Grossman, 1993; Morgan *et al.*, 1997) is dependent upon an ability to recognize and to evaluate resource patches over a range of spatial scales (Schmidt & Brown, 1996). We found that resource patchiness (i.e. spatial variation in resource availability) significantly affected the distribution of longnose dace both within and among reaches. The presence and magnitude of this response, however, was strongly influenced by spatial and temporal patchiness in resource availability during the course of our study. At the primary spatial scale (i.e. individual cobbles), we detected no relationship between macroinvertebrate biomass and the foraging intensity of longnose dace in any season. At the secondary scale (i.e. foraging patches within reaches), when macroinvertebrates were patchily distributed within the site (i.e. summer), longnose dace preferentially occupied patches with significantly higher prey biomass. In contrast, this result was not obtained when macroinvertebrates were not patchily distributed (i.e. autumn and spring). Finally, we detected tertiary scale patchiness (i.e. among reaches) in the biomass of macroinvertebrates in all seasons, and longnose dace densities were consistently correlated with this patchiness.

Given that both secondary and tertiary scale patchiness in the biomass of macroinvertebrates significantly influenced patch choice and the spatial distribution of longnose dace, we were surprised that longnose dace did not respond to prey patchiness at the primary scale. Our findings are not unique, however, for Ives, Kareiva & Perry (1993) also found that predatory lady beetles, *Coccinella 7-punctata* Linnaeus and *Hippodamia variegata* Goeze, responded to patchiness of their aphid prey *Macrosiphum euphorbiae* Thomas at secondary (individual plants) and tertiary (groups of plants) scales but not at the primary scale (individual leaves). In addition, Fryxell & Doucet (1993) found that beaver, *Castor canadensis* Kuhl, actively selected high-quality sapling stands but, once within a stand, did not differentiate among individual saplings. One potential explanation for these findings is that the behaviour of individuals in complex environments may be highly variable over short periods of time (Gray, 1987), and that short-term sam-

pling simply is incapable of detecting the subtle responses of some animals to patchiness at the primary scale. Our findings, as well as those of Ives *et al.* (1993) and Fryxell & Doucet (1993), suggest that responses to environmental patchiness by animals may often not be evident unless examined at multiple spatial scales.

The ability of animals to forage in patches with high prey density can be influenced strongly by the level of patchiness present in the local environment. In environments where patch boundaries are vague, animals are less likely to forage in locations of high prey (Gilinsky, 1984; Tokeshi & Pinder, 1985; Kareiva, 1987; Tokeshi, 1994; Schmidt & Brown, 1996). For example, Grand & Grant (1994) found that convict cichlids, *Cichlasoma nigrofasciatum* Guenther, do not forage consistently in patches with high prey availability when the spatial distribution of prey is unpredictable. However, when the location of prey patches is predictable, convict cichlids typically forage in high-prey patches (Grand & Grant, 1994). Similarly, the failure of longnose dace to choose more profitable foraging patches in autumn and spring may have been affected by a lack of clear patch boundaries (i.e. no significant prey patchiness) in the site during these seasons.

Our finding of seasonal variation in secondary scale patchiness in macroinvertebrates may be related to seasonal variation in the availability of benthic organic matter in this system. The macroinvertebrate assemblage in the Coweeta Creek drainage is dominated by detritivores (collector–gatherers and shredders), whose distribution and abundance are strongly affected by seasonal variations in resource availability (Wallace, Webster & Meyer, 1995). In autumn, when leaf litter is ubiquitous, detritus tends to be more uniformly distributed in southern Appalachian streams than in other seasons (J. Hutchens, unpublished data). After leaf fall, however, high flow events and decomposition tend to produce aggregations of detritus (i.e. patches) (Webster *et al.*, 1994). Therefore, as the year progresses from autumn to late summer, it is likely that the distribution of detritus becomes less homogeneous and increasingly patchy in the Coweeta drainage. Because collector–gatherer distributions are strongly affected by food availability (Culp *et al.*, 1983), it follows that both detritus patches and patches of benthic macroinvertebrates would be most discrete in late summer (Webster *et al.*, 1994).

In contrast to macroinvertebrate patchiness at the secondary scale, we detected patchiness in the density of macroinvertebrates at the tertiary (i.e. reach) scale in all seasons. Furthermore, tertiary scale patchiness in prey distributions explained the vast majority of variance in dace abundance among reaches (i.e. 74–96%). Therefore, although longnose dace did not choose foraging patches with high prey biomass in all seasons, they did preferentially occupy reaches with high prey biomass throughout the study.

Tertiary scale (reach scale) patchiness in benthic macroinvertebrate biomass has been detected in temperate streams other than Ball Creek (Downes *et al.*, 1993). Working in an Australian stream, Downes *et al.*, (1993) found that benthic macroinvertebrate density differed significantly between adjacent riffles. They cautioned investigators against assuming reaches are homogenous based on physical characteristics because the biotic environment can be highly variable. Our results reinforce this *caveat*, as do the findings of Grossman, Hill and Petty (1995).

Although food availability was undoubtedly an important factor influencing habitat-use patterns of longnose dace, the physical characteristics of habitat patches also affected habitat use by this species at several spatial scales. Our results indicated that longnose dace consistently avoided both depositional (i.e. low current velocity, high amounts of sand, silt and debris) patches and reaches. If the physical characteristics of a reach did not provide adequate habitat for longnose dace, it was not used even if food was abundant. For example, although reach 1 (a depositional reach) had high mean benthic macroinvertebrate density in all seasons (Fig. 3), we failed to observe a single adult longnose dace in this reach during our study. Similarly, Wallace *et al.* (1995) found that habitat use by stream macroinvertebrates could be constrained by abiotic factors even when food levels were high.

Our conclusion that adult longnose dace avoided depositional habitats is consistent with other studies (Hubert & Rahel, 1989; Mullen & Burton, 1995, 1998). For example, Grossman & Freeman (1987) and Grossman & Ratajczak (1998) found that adult longnose dace (i.e. >5 cm SL) occupied habitats with high current velocity and erosional substrata. In addition, longnose dace from streams in Alberta and British Columbia, Canada also occupied riffle habitats with high current velocities (Gee & Northcote, 1963; Gib-

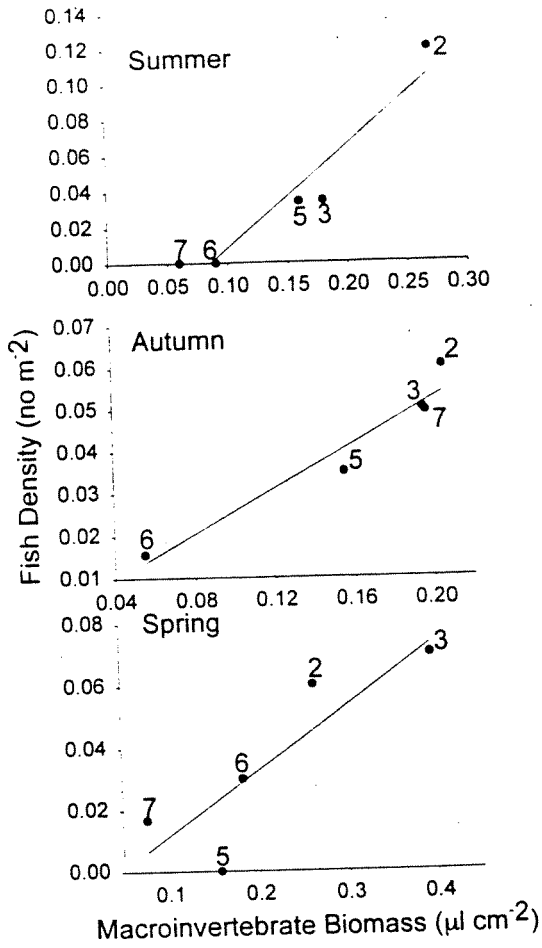

Fig. 5 Regression of mean macroinvertebrate biomass and longnose dace density in summer, autumn and spring including best-fit regression line. Data are presented only for erosional reaches. Reach numbers are represented next to each symbol.

bons & Gee, 1972). Furthermore, Sheldon (1968) found that longnose dace were obligate riffle dwellers in a third order stream in New York.

Our general findings also underscore the importance of quantifying the effects of both physical and biological resources on habitat use in stream fish. Although many investigators have examined the relationship between physical habitat characteristics and habitat use/abundance of stream fish (Gorman & Karr, 1978; Ross, 1986; Grossman & Freeman, 1987; Fausch, Hawkes & Parsons, 1988; Gorman, 1988; Greenberg, 1991; Grossman *et al.*, 1998), fewer studies have examined habitat use or abundance of stream fish in relation to prey distributions (Fausch, 1984; Hughes & Dill, 1990; Hill & Grossman, 1993; Petty & Grossman, 1996). Failure to quantify the effects of prey availability on habitat use by stream fish, however, may lead to erroneous results. For example, Fraser & Sise (1980) attempted to predict the abundance of blacknose dace (*Rhinichthys atratulus* Hermann) among stream reaches based on the physical characteristics of these reaches. They hypothesized that reaches with high-quality physical characteristics also would have a high food level and, consequently, high blacknose dace density. However, the model of Fraser & Sise (1980) failed to predict accurately the abundance of blacknose dace among reaches, a result they attributed to an insufficiently precise habitat quality rating system. Had we attempted to use the availability of cobble-riffle habitat within reaches to predict longnose dace abundance, our results would also have been problematical. For example, reach 6 had adequate physical characteristics (i.e. high current velocity, erosional substrata), but relatively low prey density. Therefore, in terms of physical conditions, reach 6 could be classified as a 'high-quality tertiary scale patch', whereas in terms of prey density, it represented a 'low-quality tertiary scale patch'. Low-prey density in reach 6 probably accounted for the low abundance of longnose dace in this reach (Fig. 5).

The identification of tertiary scale patches that had adequate physical characteristics for longnose dace, but inadequate biological resources, has important implications both for fish conservation and management. A common finding in studies of fish–habitat relationships is that, although fish abundance is consistently low in habitats with inadequate physical conditions, the abundance of fish in areas with apparently suitable physiognomy varies substantially (Fausch *et al.* 1988). Terrell *et al.* (1996) termed this relationship a 'wedge-shaped curve'. A likely explanation for the high variability in fish abundance in locations with suitable physical habitat characteristics is that prey abundance also varies considerably among these locations. It is possible that the inclusion of prey abundance in models of habitat suitability will greatly increase our ability to predict fish abundance within reaches of a stream.

Our study is one of the first to address how patchiness in both physical and biological habitat characteristics at multiple spatial scales affected the behavior, patch choice and spatial distribution of a common stream fish. Longnose dace in the Coweeta drainage responded to resource patchiness at both

secondary and tertiary scales, but failed to respond at the primary scale. These results suggest that a hierarchical approach to habitat use and environmental patchiness will increase our understanding of how organisms respond to their environment.

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