

Do Rock Bass (*Ambloplites rupestris*) Induce Microhabitat Shifts in Mottled Sculpin (*Cottus bairdi*)?

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In Coweeta Creek, North Carolina, mottled sculpin (*Cottus bairdi*) co-occurred seasonally with a potential predator, rock bass (*Ambloplites rupestris*). We conducted experiments to determine whether rock bass affected microhabitat use by sculpin in an artificial stream. The general behavior and microhabitat use of both species in the artificial stream resembled those observed in Coweeta Creek. When all microhabitat observations were pooled, there was little evidence of predator-induced shifts by sculpin. However, at night in trials without predators, sculpin generally occurred farther from shelter, over greater amounts of gravel and lower quantities of erosional substrata. When we added predators, however, this response was obviated. Nonetheless, the lack of strong responses by sculpin to rock bass, coupled with their co-occurrence only during seasons of low metabolic activity, lead us to suspect that rock bass do not produce strong shifts in microhabitat use by most sculpin in the Coweeta drainage.

STREAM-DWELLING piscivorous fishes can induce shifts in habitat use by their prey (Fraser and Cerri, 1982; Power et al., 1985; Schlosser, 1987). These shifts may result in decreases in foraging efficiency and growth of prey species, even though they presumably increase survivorship (Dill and Fraser, 1984; Metcalfe et al., 1987; Fraser and Gilliam, 1992). Predator-induced microhabitat shifts by herbivorous fishes may even alter the trophic structure of stream reaches by releasing primary producers from grazing; thereby increasing production that can be utilized by higher trophic levels (Power, 1987). Because predators may have strong impacts on stream ecosystems, we were interested in quantifying a potential predator-prey interaction within a southeastern United States stream fish assemblage. At present, there is limited published information on the ecological relationships within fish assemblages from this region.

For the past 10 years, we have been studying the structural and functional organization of a fish assemblage occupying Coweeta Creek, a fifth order stream in western North Carolina. Coweeta

Creek contains a moderately diverse fish assemblage (14 species), dominated by cool water species such as rainbow trout (*Oncorhynchus mykiss*), mottled sculpin (*Cottus bairdi*), and long-nose dace (*Rhinichthys cataractae*; Freeman et al., 1988). The fauna is typical of many streams in the southern Appalachian Mountains. Much of our work in Coweeta Creek has focused on elucidating the effects of both biological and physico-chemical factors on microhabitat use by assemblage members (Facey and Grossman, 1990, 1992; Hill and Grossman, 1993). Our descriptive studies, however, have yielded few insights into the influence of piscine predators on microhabitat use by these species, because there are no resident predators in the system (Grossman and Freeman, 1987; Freeman et al., 1988; Freeman and Grossman, 1992). Nonetheless, piscine predators are present seasonally; in particular, rock bass (*Ambloplites rupestris*) have been collected from our sites between late autumn and early spring. Rock bass are known to consume fishes in both lotic and lentic environments (Schlosser, 1982; Probst et al. 1984; Keast, 1985). Consequently, we were interested in de-

termining the effects of rock bass on microhabitat use by mottled sculpin, the most common benthic fish in Coweeta Creek.

In this paper, we address the rock bass–mottled sculpin interaction by posing four questions: (1) What is the seasonal occurrence of rock bass in Coweeta Creek? (2) Do rock bass produce shifts in microhabitat use by sculpin in an artificial stream? (3) Are shifts affected by diel activity cycles (i.e., diurnal vs nocturnal)? and (4) Was mortality of sculpin in experiments related to predation intensity and subsequent microhabitat shifts?

METHODS

Seasonal occurrence of rock bass.—We sampled the Coweeta drainage to determine the seasonal presence of rock bass using two techniques: underwater observation and electrofishing. Underwater observations were conducted while snorkeling in a 37 m long site between summer 1983 and autumn 1992. We made between two and seven days of observations during each seasonal sample, with the exception of winter when fishes were inactive (GDG, pers. obs.). During each sampling period, we identified all species present in the site and made a series of microhabitat measurements on undisturbed individuals. Microhabitat measurements, sampling procedures, and the study site are described in greater detail in Grossman and Freeman (1987). We observed fishes during the following seasons: (1) spring—1984, 1988, 1990; (2) summer—1983, 1984, 1986, 1988, 1989, 1990, 1992; and (3) autumn—1983, 1984, 1986, 1989, 1990, 1992. We also electrofished two permanent sites, 30 m in length, between 1983 and 1992. These sites were sampled on a bimonthly (1984–1988) or seasonal (spring, late summer, and autumn 1989–1992) basis and represent sites 1 and 2 of Freeman et al. (1988). In addition, we began electrofishing a 100-m long permanent site in Coweeta Creek in autumn 1991. This site was sampled in autumn 1991 and 1992 and spring 1992 and 1993. In all sampling, we recorded the abundance of rock bass in the site. We also obtained water temperatures (± 0.5 C) from submerged thermographs placed near the sites.

For analyses, we have presented rock bass abundance data in presence/absence format for two reasons. First, our main purpose in quantifying the occurrence of rock bass was to identify seasons in which this species co-occurred with sculpin in the natural habitat. Second, all sampling was either nondestructive or conducted with replacement. Hence, if four rock

bass were observed in the microhabitat site on both days one and two of sampling, it was unclear whether these were the same individuals, different individuals, or a mixture of both. Thus, accurate enumeration of rock bass abundances was problematical. Finally, because actual abundances were not essential for our analyses, it seemed more appropriate to present these data in the more conservative format of presence/absence.

Artificial stream.—We conducted experiments using the artificial stream of Grossman and Boulé (1991). In brief, the stream is a 10-m long oval, built from fiberglassed plywood with plexiglass viewing ports. Stream width ranges from 50–75 cm and depth varies from 32 cm (pools) to 5 cm (riffles). Pools are located in the curved portions of the oval, whereas riffles and runs occur in the straight areas of the tank. Both rock bass and sculpins freely crossed pools and riffles. We suspended either pieces of plywood or small logs in pools to provide overhead cover for rock bass. After the addition of overhead cover, rock bass occupied positions in the water column and did not appear to be agitated, behavior concordant with that observed in the stream. Several investigators also have noted that rock bass are associated with cover in natural habitats (Probst et al. 1984; Pajak and Neves, 1987).

Although Grossman and Boulé (1991) demonstrated that the artificial stream was a reasonable approximation of the habitats occupied by fishes in Coweeta Creek, we conducted several analyses to ascertain the suitability of the artificial stream as an experimental habitat. First, to assess whether sculpins or rock bass were stressed physiologically during trials, we compared both mean weights and standard lengths of these species before and after trials using a Wilcoxon two-sample test. These analyses detected no significant differences in either mean weight or length for any trial (all $P_s \gg 0.05$). We observed a similar pattern for rock bass (i.e., all either gained or maintained body weight), but statistical testing was precluded by sample size constraints ($n = 2$ per trial).

Second, to assess the constancy of conditions, we compared microhabitat availability measurements made both before and after each trial and among all trials using the principal component technique of Grossman and Freeman (1987). These analyses indicated that there were no significant changes in microhabitat availability measurements made before and after any trial. Nor did we detect any significant differences in microhabitat availability among trials.

These data, coupled with extensive comparisons between the artificial stream and Coweeta Creek of both microhabitat availability and microhabitat use data for sculpins and rock bass (GDG, unpubl. data), led us to conclude that the artificial stream was conducive to eliciting behaviors in sculpins and rock bass that were comparable to those observed in Coweeta Creek.

Experimental design and methods.—We conducted two types of experiments (i.e., control trials and predator trials) to assess whether sculpin shifted microhabitat use in the presence of rock bass. Both types of trials began with a two-day acclimation period for sculpins followed by three five-day observation periods (termed, C1, T, and C2). During control trials, we made microhabitat observations of sculpins in the absence of predators. In predator trials, we first completed five days of observations on sculpins alone (C1) and then introduced two rock bass into the tank during the second five-day observation period (T). Rock bass were removed at the end of this period, and we then conducted a final five-day series of observations (C2). We used 12 sculpin per trial, and previous field observations indicate that similar densities of sculpin are found in portions of Coweeta Creek (GDG, pers. obs.). The density of rock bass in trials (i.e., $n = 2$) may have been higher than those normally encountered in Coweeta Creek, where we commonly captured zero to one rock bass in sites ranging from 30–100 m in length. Nonetheless, when we observed multiple rock bass in this drainage, their distribution frequently was clumped and restricted to areas similar in size to the artificial stream. Rock bass were acclimated for one week prior to being used in trials. Specimens used in experiments were collected from the Coweeta Creek drainage.

Prior to their use in trials, we held fishes in fiberglass tanks at experimental temperatures. Rock bass and sculpins were fed a mixture of ground chicken liver, brine shrimp, and commercial flake fish food, supplemented with cod liver oil and vitamins C and E. We added gelatin to this mixture to produce semisolid masses which we then fed to fishes in holding tanks and the artificial stream. Both sculpins and rock bass consumed this mixture readily. Ration sizes during trials ranged from 17–24% of the body weight of fishes per day. These high rates were used because food particles dissipated quickly in the artificial stream. The mean standard length of sculpin used in trials ranged from 57–62 mm, whereas the standard lengths of rock bass ranged from 133–190 mm. All specimens were used in only one trial.

Our field observations indicated that rock bass only occurred in the study sites from late Aug. to May, at water temperatures between 3 and 17 C (see Results). However, in a habitat with a similar thermal regime, rock bass ceased feeding at temperatures approximating 8.5 C (Keast, 1968). Consequently, we conducted trials at two temperatures: 12 C and 15 C (henceforth low and high). We believed these temperatures would elicit behaviors that would be displayed at 11–13 C and 14–17 C, when most rock bass would be actively feeding. In addition, such temperatures approximate spring and late summer/early autumn stream temperatures; and hence, we used a 12L:12D photoperiod for trials. We conducted three predator trials and two control trials at each temperature, and trials were conducted between March 1986 and March 1992.

During each trial, we observed specimens through viewing ports and made a visual estimate of their position using x (longitudinal position), y (distance from the stream side), and z (distance from the substrate) coordinates (Grossman and Boulé, 1991). We recorded these coordinates and, after examining the entire stream, returned to the location of each observation and collected the following data: (1) longitudinal position, (2) distance from shelter, (3) shelter size, (4) depth, (5) average velocity, (6) focal point velocity, and (7) the percent composition of between four and seven substrate categories [i.e., bedrock (bare wood), boulder, cobble, gravel, sand, silt, and debris] in a 400-cm² area directly underneath the fish. By convention, we will call silt, sand, and debris depositional substrata, whereas cobble, boulder, and bedrock will be referred to as erosional substrata. Fish observations were made twice daily in a staggered schedule which provided coverage of morning, afternoon, and nocturnal time periods. We made night observations using a narrow-beamed flashlight covered with a dark red filter.

We made distance, depth, and size measurements (± 1 cm) using either a scale on the outside of the stream or a meter stick. Shelter was defined as any object capable of concealing at least 50% of the fish's body, and shelter size was the maximum length of the object. Velocity measurements (± 1 cm/sec) were made using a Marsh McBirney Model 201 velocity meter. We estimated substratum composition visually. In our first series of trials (15 C treatment trials and one control), we placed a simplified set of substrata in the stream and, hence, only recorded data on the percent composition of bedrock (= exposed stream bottom), cobble, gravel,

and silt. However, our second set of trials (12 C treatment and control trials and one 15 C control) were conducted with a more diverse substratum; and thus, we also were able to collect data on boulder, sand, and debris substrata. These techniques have been utilized in a variety of other habitats and studies (Grossman and Freeman, 1987; Grossman et al., 1987; and Grossman and Boulé, 1991).

Through comparisons of microhabitat use both among periods within a trial (i.e., C1, T, C2) and between trials (control vs predator), we were able to detect a variety of effects: (1) no effect (all trials: C1 = T = C2), (2) shifts due to acclimation (all trials: C1 \neq T and C2, C1, and T \neq C2, C1 \neq T, or C1 \neq C2, etc.), (3) simple predator effects (control trials: C1 = T = C2, treatment trials: C1 and C2 \neq T), and (4) predator plus experience effects (control trials: C1 = T = C2, treatment trials: C1 \neq T and C2). (For a more elaborate presentation of this experimental design see Grossman and Boulé, 1991.) We performed principle component analyses (PCA) on microhabitat use data of sculpins during each trial and then applied Kruskal-Wallis tests ($P = 0.05$) to mean PCA scores for sculpins to test for significant differences among periods (i.e., C1, T, and C2; Grossman and Boulé, 1991). If a significant difference was obtained, we then used Tukey-Kramer tests to identify significant pairwise differences.

Rock bass appear to be active throughout the diel cycle, although this may vary across habitats (Keast and Welsh, 1968; Helfman 1981; Gerber and Haynes, 1988). In addition, Greenberg and Holtzman (1987) have shown that a congeneric sculpin (*Cottus caroliniae*) is nocturnally active, as has been suggested for *Cottus bairdi* in lakes (Emery, 1973; Hoekstra and Janssen, 1985). Consequently, we also examined whether microhabitat use by sculpins differed between diurnal and nocturnal observation periods. To test this hypothesis, we compared mean PCA scores using a Wilcoxon sum of ranks test, for the three observation times (i.e., diurnal = morning and afternoon; nocturnal = night) for each experimental period (C1, T, and C2) in each trial. Although the data for these periods were not independent, it was necessary to conduct tests for each experimental period separately to differentiate potential predator-induced shifts from those present in normal diel activity cycles.

RESULTS

Rock bass in Coweeta Creek.—Rock bass were not particularly common in our sites; and out of 155 days of sampling (1983–1992), this species was

observed on only 29 days. Rock bass exhibited a distinct seasonal pattern of occurrence, with the first observation of the year typically occurring in autumn and the last observation varying between late autumn and spring (Table 1). In 10 years of sampling, we never observed rock bass during April, June, or July. In addition, we only recorded one observation of this species during either May or Sept., and only observed rock bass twice in Aug. (Table 1). Because rock bass are not found upstream of our study sites (GDG, unpubl. data), this species appears to be migrating from downstream areas to our sites during autumn and returning the following winter or spring.

We also recorded the temperatures at which rock bass were present in our site. Of the 29 days on which we observed rock bass, 14 records occurred at temperatures of 10 C or less (48%), nine observations at temperatures between 11 and 13 C (31%), and six at temperatures between 14 and 17 C (21%). Consequently, almost half of our observations of rock bass in the Coweeta drainage occurred at temperatures near those at which this predator would not be actively feeding (i.e., 8.5 C). Nonetheless, rock bass and sculpin did co-occur at temperatures used in our laboratory experiments (52% of observations).

Microhabitat use in experimental trials.—Regardless of temperature regime, analyses including all data indicated that rock bass did not produce strong shifts in microhabitat use by sculpins during trials (Table 2). In fact, the significant differences observed were common to both control and predator trials (Table 2). Most of these shifts involved minor microhabitat components (i.e., variance explained ranged from 9–15%) and can be attributed to acclimation effects. Of the six predator trials, only results for both High and Low Temperature Predator Trials 3 could not be unambiguously attributed to acclimation effects.

Dividing results into diurnal and nocturnal periods, however, provided some evidence for both a diel shift in microhabitat use and inhibition of this response when rock bass were present (Table 3). For example, during control experiments sculpins exhibited relatively consistent nocturnal shifts to microhabitats that were farther from shelter (1.4 vs 3.6 cm), over more gravel (35% vs 50%), and on less erosional substrata (Table 3). We observed such shifts in nine of 12 periods during control trials. In addition, at night in low temperature control trials, when sculpins occupied shelters, these shelters generally were smaller (five of six periods)

TABLE 1. SEASONAL OBSERVATIONS OF ROCK BASS IN THE COWEETA CREEK DRAINAGE. Sampling techniques include microhabitat observations (M) and electrofishing (E).

Year	Sampling (# days)	Technique (M or E)	# Days absent	# Days present	First observed	Last observed
1983	17	M	17	0	not observed	not observed
	4	E	4	0		
1984	15	M	15	0	Nov. 1984	Feb. 1985
	10	E	8	2		
1985	12	E	8	4	Sept. 1985	March 1986
1986	7	M	7	0	Nov. 1986	March 1987
	12	E	8	4		
1987	4	M	4	0	Sept. 1987	Nov. 1987
	12	E	10	2		
1988	5	M	5	0	Sept. 1988	Sept. 1988
	10	E	9	1		
1989	12	M	9	3	Oct. 1989	Nov. 1989
	4	E	3	1		
1990	8	M	5	3	Oct. 1990	Nov. 1990
	6	E	4	2		
1991	8	E	3	5	Aug. 1991	May 1992
1992	5	M	4	1	Aug. 1992	Oct. 1992
	7	E	6	1		
Totals	158		129	29		

and in shallower water (22.1 cm vs 27.3 cm; four of six periods). However, this response was not observed during high temperature control trials. In contrast, when we recorded shifts in predator trials, they typically were observed prior to the introduction of the predator (i.e., in C1; five of six cases). The responses of sculpins during predator trials were less consistent than those recorded in control trials (Table 3). In low temperature predator trials, the shifts generally matched those recorded during control trials; however, results from high temperature predator trials were markedly different. The origin of these disparities is problematical, because they were observed prior to the introduction of rock bass and, hence, should not have differed from control trials. Nonetheless, the data suggest that sculpin tended to exhibit diel shifts in microhabitat use in control trials and that this response may have been inhibited by the presence of the predator.

We recorded mortality events during trials, in an effort to elucidate the factors affecting our results (Table 4). Mortality could be ascribed to the following: (1) predation (presence of a prey in a predator's stomach or buccal cavity), (2) stress (carcass found in the stream), or (3) unknown (fish missing). Because all fish were recovered from control trials, even when mortalities occurred, it is reasonable to assume that some of the sculpins missing from predator trials were consumed by rock bass. However, can-

nibalism also occurred in one trial (Table 4). Nevertheless, there was no apparent relationship between the intensity or type of mortality in trials and microhabitat use by sculpins (Tables 2, 4). In addition, an examination of the sizes of sculpins used in trials suggested that the lack of predator response probably was not an effect of unusually large mean sizes of sculpins used in experiments (Table 4).

DISCUSSION

Our examination of the effects of rock bass on microhabitat use by mottled sculpin identified an interaction that was subtle in expression. When all microhabitat observations were pooled, there was little evidence of a predator-induced shift in microhabitat use. In contrast, when we examined microhabitat use on a diel basis in control trials, sculpin generally occurred farther from shelter over greater amounts of gravel and lower quantities of erosional substrata at night. This response was not observed when we added predators. Our analysis was conducted separately for each period during a trial, and as a consequence, we reanalyzed the data for each trial using only nocturnal observations. Results from this analysis were equivocal, perhaps because of small sample sizes. Hence, our findings regarding the presence of a microhabitat shift by sculpin in the presence of rock bass remain suggestive,

TABLE 2. RESULTS FROM CONTROL AND PREDATOR TRIALS. Presented are treatment differences and the variable loadings ($\geq |0.40|$) from principle components on which sculpins exhibited significant interperiod differences. Results are based on Kruskal-Wallis tests ($P = 0.05$) on mean PCA scores for sculpin during each period, followed by Tukey-Kramer a posteriori tests for pairwise differences. For clarity, trials have been reordered so that Trial 1 exhibited the simplest results, whereas those of Trial 3 were the most complex (i.e., their order does not represent the actual temporal sequence of trials).

Trial	Component (PC) and loadings (r)	Variance explained	Result	Interpretation
<i>Low Temperature Trials</i>				
Control Trial 1	PC4 Debris (-0.71) Boulder (0.62)	11%	C2 > T ^a	Acclimation
Control Trial 2	PC5 Debris (0.82)	9%	C1 > C2	Acclimation
Predator Trial 1	All components	71%	C1 = T = C2	No effect
Predator Trial 2	PC3 % Boulders (0.67) % Bedrock (0.52) % Debris (-0.46)	12%	T > C2	Acclimation
Predator Trial 3	PC1 Focal point velocity (-0.73) % Gravel (-0.68) Ave. velocity (-0.65) % Silt (0.63) Dist. from shelter (-0.54) % Sand (0.54) Shelter size (0.51) % Cobble (0.47)	27%	C2, T > C1	Acclimation, or predator + experience
	PC4 % Boulder (0.78) % Debris (-0.51) Shelter size (0.48)	11%	C1 > T	Acclimation
<i>High Temperature Trials</i>				
Control Trial 1	All components	64%	C1 = T = C2	No effect
Control Trial 2	PC1 % Gravel (0.93) % Cobble (-0.82) Dist. from shelter (0.60) Depth (0.55) % Bedrock (-0.42) Shelter size (-0.40)	35%	C1 > C2	Acclimation
	PC3 Ave. velocity (0.80) Focal point velocity (0.46)	14%	C1, C2 > T	Acclimation ^b
Predator Trial 1	All components	56%	C1 = T = C2	No effect
Predator Trial 2	PC2 Focal point velocity (0.65) Ave. velocity (0.59) Depth (-0.54)	15%	C1, T > C2	Acclimation
Predator Trial 3	PC1 % Gravel (0.86) % Cobble (-0.79) Dist. from shelter (0.69) % Silt (0.64) Depth (0.64) Focal point velocity (0.55) Shelter size (-0.55) Ave. velocity (-0.51) % Bedrock (-0.41)	37%	C1 > T, C ₂	Acclimation or predator + experience
	PC3 Dist. from substrate (0.88)	10%	T > C1	Acclimation ^c

^a This result is interpreted as follows: during segment C2 sculpin occurred over less debris and more boulder than in segment T.

^b This result may have been produced by the overnight failure of a pump during segment T which caused temperatures to rise to 20 C.

^c Produced by one sculpin that was 1 cm of the substrate during segment T.

rather than conclusive. Nonetheless, it is reasonable to assume that potential prey will experience an increase in fitness if they remain closer to shelter in the presence of a predator.

Several points, however, lead us to conclude that the general fitness consequences of this predator-prey interaction probably are not strong. First, although sculpin densities were similar to those observed in many habitats in Coweeta Creek (GDG, pers. obs.), rock bass densities were at the high end of those recorded from Coweeta Creek (Grossman and Freeman 1987; Freeman et al. 1988; GDG, unpubl. data). In fact, in one 30-month period (March 1987–Sept. 1989), we only observed three rock bass in our three study sites. However, when we did observe multiple rock bass in a site (approximately nine of 29 observations in 10 years), they frequently exhibited a clumped distribution (GDG, unpubl. data). Hence, our results should accurately represent microhabitat use by sculpins remaining in close proximity to rock bass, yet most sculpin in the Coweeta drainage clearly do not meet this criterion. Second, our experiments were conducted at temperatures that should have increased the likelihood of obtaining a strong response to the predator (i.e., 11–17 C); yet almost half our field observations (48%) of rock bass occurred at temperatures (i.e., ≤ 10 C) at which this predator probably was not feeding very actively (Keast, 1968). Third, because sculpins have low metabolic rates from fall through early spring (Facey and Grossman, 1990), this species probably is not particularly active during the very periods in which rock bass typically are present. Thus, the threat of rock bass predation on mottled sculpin in Coweeta Creek generally may be low, which may obviate the need for strong shifts in microhabitat use. Nonetheless, when rock bass are in close proximity, sculpin appear to possess the behavioral plasticity necessary to respond in a manner which should increase their fitness (i.e., stay close to shelter at night).

Our results differ slightly from those of other researchers who have observed strong shifts in microhabitat use by stream fishes in the presence of piscine predators (Schlosser, 1988a; Schlosser and Ebel, 1989; Harvey 1991). Several of these investigators used centrarchids as predators, which stimulated our original interest in the rock bass–sculpin interaction. In addition, the predatory efforts of rock bass may cause prey, including mottled sculpin, to shift into shallower (Anderson, 1983; Angermeier, 1992) and more structurally complex habitats (Anderson, 1983). These investigators concluded that such shifts increased the fitness of prey

by reducing the efficiency of the predator. The responses of sculpin to rock bass in our experiments were more subtle than those observed by either Anderson (1983) or Angermeier (1992) and, possibly, are attributable to differences in experimental design. For example, both of these investigators utilized relatively small experimental chambers (i.e., lengths and widths of 1–2 m) with relatively high densities of prey (i.e., between 7 and 20 prey/m²; Anderson, 1983; Angermeier, 1992). It is not clear how these densities compare to actual field densities, nor how environmental conditions in the aquaria (e.g., velocities, substratum composition, etc.) compare with the natural habitats occupied by either predator or prey. Consequently, it is possible that the differential responses obtained in these studies are due to disparities in both experimental design and the aquaria within which experiments were conducted.

Although there can be little doubt that predators can affect microhabitat use in stream fishes, the presence and magnitude of this response will depend upon a multitude of factors. For example, Schlosser (1988a, 1988b) demonstrated that the intensity of the response by a prey species may depend upon the efficacy of the predator. Similarly, McLean and Godin (1988) provided evidence that behavioral responses of four potential prey species to a model predator were inversely correlated with morphological adaptations that differentially reduced the probability of predation. Harvey and Stewart (1991) also noted that descriptive studies of microhabitat use in streams with either high or low mean velocities suggest that predator-induced microhabitat shifts may not be as common in the former as in the latter. They attribute this difference to the reduced efficacy of predators in systems with high environmental heterogeneity (e.g., substratum, velocity, depth). The lack of a strong response manifested by sculpin in our experiments provides indirect support for this hypothesis.

In northern lakes, mottled sculpin exhibit greater activity at night than during the day (Emery, 1973; Hoekstra and Janssen, 1985). Greenberg (1991) also suggested that mottled sculpin in a Tennessee river were nocturnally active, although he was unable to distinguish *Cottus bairdi* from *C. carolinae* while under water. Previous observation by Greenberg and Holtzman (1987) demonstrated that the latter of these morphologically similar species spends more time in the open at night than during the day. Our data suggest that, in the absence of rock bass, mottled sculpin occur farther from shelter at night. Although it appears that sculpin do

TABLE 3. ANALYSIS OF MICROHABITAT USE BY DIEL OBSERVATION PERIOD (N = NOCTURNAL OBSERVATIONS, D = DIURNAL OBSERVATIONS). Presented are treatment differences and variable loadings ($\geq |0.40|$) for principle components upon which sculpins exhibited significant diel differences in microhabitat use. Results are based on Wilcoxon tests ($P = 0.05$) for mean PCA scores for each time period. Only significant results are reported.

Trial	Component (PC) and loadings (r)	Variance explained	Period	Result
<i>Low Temperature Trials</i>				
Control Trial 1	PC1 % Gravel (0.78) Dist. from Shelter (0.64) % Cobble (-0.60) Shelter size (-0.58) Depth (-0.44)	21%	C1	N > D*
	PC3 % Silt (0.66) % Boulder (-0.50) Shelter size (-0.44) Depth (-0.42)	12%	C2	N > D
Control Trial 2	PC1 % Sand (-0.68) % Silt (-0.67) Ave. velocity (0.61) Focal point velocity (0.58) % Gravel (0.58) Depth (-0.53) Shelter size (-0.46)	24%	C1 T	N > D N > D
	PC2 Dist. from Shelter (0.80) % Cobble (-0.77) Ave. velocity (-0.41)	15%	C1 T C2	N > D N > D N > D
	PC3 % Bedrock (-0.74) % Gravel (0.55) % Boulder (0.44)	13%	C1	N > D
	PC4 % Boulder (-0.70) Shelter size (-0.51) % Bedrock (-0.42)	11%	C2	N > D
	PC5 % Debris (-0.82)	9%	C1 T	N > D N > D
Predator Trial 1	PC1 % Sand (-0.79) Ave. velocity (0.74) % Silt (-0.72) Focal point velocity (0.67) % Debris (-0.57) Depth (-0.46) % Bedrock (0.42)	26%	T	N > D
	PC2 % Cobble (-0.78) % Gravel (0.78) Dist. from Shelter (0.57)	16%	C1	N > D
Predator Trial 2	PC1 Ave. velocity (-0.76) Focal point velocity (-0.75) % Sand (0.70) Depth (0.57) % Bedrock (-0.51) Shelter size (0.49) % Silt (0.45) % Cobble (-0.40)	26%	C1	N > D

TABLE 3. CONTINUED.

Trial	Component (PC) and loadings (r)	Variance explained	Period	Result
	PC2 % Gravel (0.86) % Cobble (-0.75) Dist. from Shelter (0.58) % Silt (-0.54)	19%	C1	N > D
Predator Trial 3	none			
<i>High Temperature Trials</i>				
Control Trial 1	PC2 Cobble (-0.81) Gravel (0.77) Dist. from shelter (0.72)	19%	C1 T C2	N > D N > D N > D
Control Trial 2	PC1 % Gravel (0.93) % Cobble (-0.82) Dist. from Shelter (0.60) Depth (0.55) % Bedrock (-0.42)	34%	C1 T	N > D N > D
	PC2 % Bedrock (0.69) Depth (-0.67) Focal point velocity (0.53) % Cobble (-0.41)	21%	C1	N > D
Predator Trial 1	PC2 % Silt (-0.80) Depth (0.78) Ave. velocity (-0.56) % Bedrock (-0.49)	21%	C1	N > D
Predator Trial 2	PC2 Focal point velocity (0.65) Ave. velocity (0.59) Depth (-0.54)	15%	C1	N > D
	PC3 Dist. from substrate (-0.65) % Bedrock (-0.50) Shelter (-0.44)	11%	C1	N > D
Predator Trial 3	PC1 % Gravel (0.86) % Cobble (-0.79) Dist. from Shelter (0.69) Depth (0.64) % Silt (0.64) Shelter size (-0.55) Focal point velocity (0.55) Ave. velocity (-0.51) % Bedrock (-0.41)	37%	C1	N > D
	PC2 % Bedrock (0.62) Ave. velocity (0.46) % Cobble (-0.45) Focal point velocity (0.44)	15%	C1	N > D

* The interpretation of this result is as follows: in C1 at night, sculpin occurred over more gravel, farther from shelter, over less cobble, in smaller shelters, and in shallower water than during the day.

TABLE 4. STANDARD LENGTHS (SL) AND MORTALITY OF SCULPINS USED IN TRIALS. The mortality source is identified (RB = rock bass, MS = mottled sculpin) as is the effect detected in the experiment.

Trial	n	Starting SL $\bar{x} \pm SD$	n	Final SL $\bar{x} \pm SD$	Mortality	Effect
<i>Low Temperature Trials</i>						
Control Trial 1	12	60.8 \pm 6.3	12	61.3 \pm 6.5	none	Acclimation
Control Trial 2	12	60.2 \pm 4.8	12	60.1 \pm 4.8	none	Acclimation
Predator Trial 1	12	59.8 \pm 4.2	11	59.4 \pm 4.2	1 eaten by RB	No effect
Predator Trial 2	12	58.5 \pm 5.6	8	57.6 \pm 5.4	1 eaten by RB 3 missing	Acclimation
Predator Trial 3	12	62.1 \pm 5.8	12	62.1 \pm 5.9	none	Acclimation or predator and experience
<i>High Temperature Trials</i>						
Control Trial 1	12	58.1 \pm 5.6	9	61.6 \pm 3.6	3 stress (all gravid)	No effect
Control Trial 2	12	56.5 \pm 9.9	11	56.0 \pm 8.8	1 stress	Acclimation
Predator Trial 1	12	58.1 \pm 12.1	5	69.4 \pm 8.9	3 stress 4 missing	No effect
Predator Trial 2	12	60.6 \pm 17.4	9	66.9 \pm 16.6	2 eaten by MS 1 missing	Acclimation
Predator Trial 3	12	58.8 \pm 3.6	4	59.0 \pm 4.3	2 stress 6 missing	Acclimation

not display diel microhabitat shifts in the presence of rock bass, such shifts may occur when rock bass are absent.

Our study suggests that rock bass generally do not have a strong impact on microhabitat use by sculpin in the Coweeta drainage. This result is similar to previous descriptive studies which indicate that predation does not appear to have a marked effect on microhabitat use by other assemblage members in Coweeta Creek (Grossman and Freeman, 1987; GDG, unpubl. data). Hence, the Coweeta drainage appears to differ in this characteristic from many warm water streams in North America. Nonetheless, similar streams probably are common throughout the southern Appalachian Mountains, as are ecologically similar assemblages and habitats in the western United States (Moyle, 1976; Moyle and Cech, 1988). Consequently, continued efforts are needed to elucidate the general relationship between predators, microhabitat use and assemblage organization in stream fishes.

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LITERATURE CITED

- ANDERSON, C. S. 1983. The influence of stream size on sculpin population dynamics. Unpubl. Ph.D. diss. Univ. of Michigan, Ann Arbor.
- ANGERMEIER, P. L. 1992. Predation by rock bass on other stream fishes: experimental effects of depth and cover. *Environ. Biol. Fishes* 34:171-180.
- DILL, L. M., AND A. H. G. FRASER. 1984. Risk of predation and the feeding behavior of juvenile coho salmon (*Oncorhynchus kisutch*). *Behav. Ecol. Sociobiol.* 16:65-71.
- EMERY, A. R. 1973. Preliminary comparisons of day and night habits of freshwater fish in Ontario lakes. *J. Fish. Res. Board Canada* 30:761-774.
- FACEY, D. E., AND G. D. GROSSMAN. 1990. A comparative study of oxygen consumption by four stream fishes: the effects of season and velocity. *Physiol. Zool.* 63:757-776.
- , AND ———. 1992. The relationship between water velocity, energetic costs, and microhabitat use on four North American stream fishes. *Hydrobiologia* 239:1-6.
- FRASER, D. F., AND R. D. CERRI. 1982. Experimental evaluation of predator-prey relationships in a patchy

- environment: consequences for habitat use patterns in minnows. *Ecology* 63:307-313.
- , AND J. F. GILLIAM. 1992. Nonlethal impacts of predator invasion: facultative suppression of growth and reproduction. *Ibid.* 73:959-970.
- FREEMAN, M. C., AND G. D. GROSSMAN. 1992. Group foraging by a stream minnow: shoals or aggregations? *Anim. Beh.* 44:393-403.
- , M. K. CRAWFORD, J. C. BARRETT, D. E. FACEY, M. G. FLOOD, J. HILL, D. J. STOUDE, AND G. D. GROSSMAN. 1988. Fish assemblage stability in a southern Appalachian stream. *Can. J. Fish. Aquat. Sci.* 45:1949-1958.
- GERBER, G. P., AND J. M. HAYNES. 1988. Movements and behavior of thirteen species of benthic stream fishes. *Environ. Biol. Fish.* 31:389-401.
- , AND D. A. HOLTZMAN. 1987. Microhabitat utilization, feeding periodicity, home range and population size of the banded sculpin, *Cottus caroliniae*. *Copeia*: 1987:19-25.
- GROSSMAN, G. D., AND V. BOULÉ. 1991. An experimental study of competition for space between rainbow trout (*Oncorhynchus mykiss*) and rosieside dace (*Clinostomus funduloides*). *Can. J. Fish. Aquat. Sci.* 48:1235-1243.
- , AND M. C. FREEMAN. 1987. Microhabitat use in a stream fish assemblage. *J. Zool. (London)* 212: 151-176.
- , A. DE SOSTOA, M. FREEMAN, AND J. LOBÓN-CERVIÀ. 1987. Microhabitat selection in a Mediterranean riverine fish assemblage. I. Fishes of the lower Matarraña. *Oecologia* 73:490-500.
- HARVEY, B. C. 1991. Interactions among stream fishes: predator-induced habitat shifts and larval survival. *Ibid.* 87:29-36.
- , AND A. J. STEWART. 1991. Fish size and habitat depth relationships in headwater streams. *Ibid.* 87:336-342.
- HELPMAN, G. S. 1981. Twilight activities and temporal structure in a freshwater fish community. *Can. J. Fish. Aquat. Sci.* 38:1405-1420.
- HILL, J., AND G. D. GROSSMAN. 1993. An energetic model of microhabitat use for rainbow trout and rosieside dace. *Ecology* 74:685-698.
- HOEKSTRA, D., AND J. JANNSEN. 1985. Nonvisual foraging behavior of the mottled sculpin *Cottus bairdi* in Lake Michigan. *Environ. Biol. Fish.* 12:111-117.
- KEAST, A. 1968. Feeding of some Great Lakes fishes at low temperatures. *J. Fish. Res. Bd. Canada* 25: 1199-1218.
- . 1985. The piscivore feeding guild of fishes in small freshwater ecosystems. *Environ. Biol. Fish.* 12:119-129.
- , AND L. WELSH. 1968. Daily feeding periodicities, food uptake rates, and dietary changes with hour of day in some lake fishes. *J. Fish. Res. Board Canada* 25:1133-1144.
- MCLEAN, E. B., AND J.-G. J. GODIN. 1989. Distance to cover and fleeing from predators in fish with different amounts of defensive armour. *Oikos* 55: 281-290.
- METCALFE, N. B., F. A. HUNTINGFORD, AND J. E. THORPE. 1987. The influence of predation risk on the feeding motivation and foraging strategy of juvenile Atlantic salmon. *Anim. Behav.* 35:901-911.
- MOYLE, P. B. 1976. Inland fishes of California. Univ. of California Press, Berkeley.
- , AND J. J. CECH. 1988. Fishes: an introduction to ichthyology, Prentice Hall, Englewood Cliffs, New Jersey.
- PAJAK, P., AND R. J. NEVES. 1987. Habitat suitability and fish production: a model evaluation for rock bass in two Virginia streams. *Trans. Am. Fish. Soc.* 116:839-850.
- POWER, M. E. 1987. Predator avoidance by grazing fishes in temperate and tropical streams: importance of stream depth and prey size, p. 333-353. *In: Predation: direct and indirect impacts on aquatic communities.* W. C. Kerfoot and A. Sih (eds.). Univ. Press of New England, Hanover, England.
- , W. J. MATTHEWS, AND A. J. STEWART. 1985. Grazing minnows, piscivorous bass, and stream algae: dynamics of a strong interaction. *Ecology* 66: 1448-1456.
- PROBST, W. E., C. F. RABENI, W. G. COVINGTON, AND R. E. MARTENEY. 1984. Resource use by stream-dwelling rock bass and smallmouth bass. *Trans. Am. Fish. Soc.* 113:283-294.
- SCHLOSSER, I. J. 1982. Fish community structure and function along two habitat gradients in a headwater stream. *Ecol. Monogr.* 52:395-414.
- . 1987. The role of predation in age- and size-related habitat use by stream fishes. *Ecology* 68: 651-659.
- . 1988a. Predation rates and the behavioral response of adult brassy minnows (*Hybognathus hankinsoni*) to creek chub and smallmouth bass predators. *Copeia* 1988:691-697.
- . 1988b. Predation risk and habitat selection by two size classes of a stream cyprinid: experimental test of a hypothesis. *Oikos* 52:36-40.
- , AND K. EBEL. 1989. Effects of flow regime and cyprinid predation on a headwater stream. *Ecol. Monogr.* 59:41-57.

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