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# Habitat use and feeding behavior of thirteen species of benthic stream fishes

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## Synopsis

The densities, habitat use, and feeding behaviors of 13 fish species belonging to the benthic invertebrate-feeding guild were studied by snorkeling at three localities in the Little River of eastern Tennessee, U.S.A. Resource partitioning occurred by habitat, feeding behavior and time of activity. Differences were also found at the generic level. *Cottus* was a nocturnal feeder, whereas *Percina* and *Etheostoma* were, for the most part, diurnally active. *Percina* moved about rapidly and spent most of its time above the bottom. In contrast, *Etheostoma* varied considerably in the amount of time spent under cover, spent little time above the bottom, and exhibited low levels of swimming activity. Nearly all species sought cover at night, suggesting they may be particularly sensitive to predation at night. Species with small adult sizes (*Etheostoma, Cottus* and *P. evides*) were concentrated in shallow water habitats, whereas species with large adult sizes (*Percina*) were more abundant in deep water habitats. The habitat use data are consistent with the hypothesis that size-selective predation by centrarchid bass may cause smaller fish to avoid deep water areas. Large species should have a lower risk of predation due to their size and behavior.

## Introduction

Members of a feeding guild have similar ecological requirements (sensu Root 1967), and if closely related, share similar evolutionary backgrounds. Consequently, intense interspecific competition for resources might be expected among guild species, and resource partitioning is a likely consequence of such competition (Paine et al. 1982). The ways in which guild members interact has been studied extensively. Relatively few studies, however, have related patterns of resource use among guild members to the threat of predation [but see Morin (1983) for predation's effect on guild structure]. One might expect that if guild members are

closely related their response to predation may be more similar than if they were not. However, if the predators are gape-limited, guild members that differ in body size may respond differently to the threat of predation. For example, Power (1987) and Schlosser (1987) suggested that small fish generally occur in shallow water because of swimming predators in deep water, whereas large fish occur in deep water because of wading and diving predators in shallow water.

The benthic invertebrate-feeding guild is one of the most speciose guilds of fishes in North American warm-water streams. Fishes from this guild are usually abundant, even if they typically comprise a small proportion of the total fish biomass in warm-

water streams (Moyle & Li 1979). Although often small in size, some benthic-invertebrate feeders are rather large, reaching sizes up to 168 mm standard length (SL) (Douglas 1968). Common members of this guild include dace, darter, madtom, and sculpin species belonging to the families Cyprinidae, Percidae, Ictaluridae, and Cottidae, respectively. Resource use in terms of habitat (Smart & Gee 1979, Paine et al. 1982), food (Wynes & Wissing 1982, Hlohowskyj & White 1983, Miller 1983) and time of activity (Cordes & Page 1980, Matthews et al. 1982) has been studied for this guild. Although segregation has been reported for depth (Fisher & Pearson 1987), current (Matthews 1985, Fisher & Pearson 1987), substrate particle size (Stiles 1972, Matheson & Brooks 1983, Hlohowskyj & Wissing 1986), vegetation (McCormick & Aspinwall 1983, White & Aspinwall 1984) and food (Smart & Gee 1979, Paine et al. 1982), the differences are usually small, and high resource overlap is common (Matthews et al. 1982, Wynes & Wissing 1982, Hlohowskyj & White 1983, Miller 1983, Hlohowskyj & Wissing 1986).

The objective of this study was to describe the density, habitat use, and feeding behavior of 13 species of benthic invertebrate-feeders in the Little River of eastern Tennessee, U.S.A. Underwater observations were used to study cover and water column use, movement rates, activity patterns, and the location of feeding bites. These data were then interpreted in light of potential competition and predation as well as taxonomic affinities. The study species were *Cottus carolinae* (banded sculpin) and *C. bairdi* (mottled sculpin) (hereafter referred to together as *Cottus*), *Etheostoma rufilineatum* (redline darter), *E. simoterum* (Tennessee snubnose darter), *E. blennioides* (greenside darter), *E. jessiae* (blueside darter), *E. zonale* (banded darter), *E. vulneratum* (spotted darter), *E. camurum* (bluebreast darter), *Percina aurantiaca* (tangerine darter), *P. evides* (gilt darter), *P. macrocephala* (longhead darter), *P. burtoni* (blotched logperch), and *P. caprodes* (logperch). Several of the species also belong to the same subgenus: *Etheostoma rufilineatum, E. vulneratum* and *E. camurum* are in *Nothonotus, P. caprodes* and *P. burtoni* are in *Percina, E. simoterum* and *E. zonale* are in *Nanostoma*

(according to Page 1981), and *E. blennioides* and *E. zonale* are in *Etheostoma* (according to Bailey & Gosline 1955).

## Materials and methods

### Study area

The study was conducted during the summers of 1980 to 1983 at three localities in the Little River of eastern Tennessee, U.S.A. Site 1, elevation 427 m a.s.l., was located in the Middle Prong of the Little River, approximately 4.0 km upstream of its confluence with the West Prong of the Little River in the Great Smoky Mountain National Park. Sites 2 (337 m a.s.l.) and 3 (270 m a.s.l.) were located in the Little River proper, 5.2 and 28.7 km downstream of site 1, respectively. The width of the stream was 7–14 m at site 1, 21–31 m at site 2 and 18–40 m at site 3. Three habitats were studied at each site: riffles-areas of rapid currents and shallow depths, pools-areas of slow currents and great depths, and runs-areas of intermediate current and depth.

### Species

The fish fauna was exceptionally diverse, comprised of at least 20 species of benthic invertebrate-feeders belonging to four families. Data were collected for thirteen of the species. Five of the remaining seven species, although occurring in the Little River, were not observed at the three sites. Very little behavioral data were collected for the other two species, *Rhinichthys cataractae* (occurs only at site 1) and *E. cinereum* (only seen at site 3 in the spring when they migrated upstream), and hence were not included in the analyses. All species are strictly invertebrate feeders (primarily insectivores) except *Cottus* which at large sizes includes fish in its diet. Adult sizes of *P. aurantiaca, P. burtoni, P. caprodes* and *P. macrocephala* generally range from 70–150 mm SL, whereas the other species generally range from 35–75 mm SL (Lee et al. 1980).

## Density and habitat use

The densities and habitat associations of each species were evaluated from a series of underwater dives (SCUBA and snorkeling) conducted at the three sites as well as more general observations conducted at numerous locations along the river. At each site, I divided the river into sixty to eighty 1.5 m wide transects that extended across the stream's width. Within each of the three habitats at each site, three (1981) or five or six (1982) randomly-selected transects were established by staking ropes across the stream. Each transect was completely divided into $1.5 \times 1.5$ m quadrats. During each dive, I recorded the numbers and lengths (SL) of individuals of each species as well as measured current velocity, substrate composition, and depth from each quadrat. Every large rock ($\approx > 0.15$ m), when possible, was jarred or flipped, and vegetation was disturbed in an attempt to count all fish. Each fish was directed to the sides or behind the observer (with the hand) in an attempt to prevent scoring the same fish more than once. Current velocity, estimated twice from each quadrat, was measured 5 cm above the bottom using a Pygmy-Gurley meter; this was as close to the bottom as one can get with this type of current meter. Four measurements of depth taken at each corner of the quadrat were used to calculate the mean depth of each quadrat. To determine substrate composition, I placed a $76 \times 76$ cm metal grid in the center of each quadrat. The grid was divided into sixteen $360$ cm$^2$ partitions and the dominant substrate type in each partition was recorded. Sometimes one type of substrate overlaid another; in all such cases except when silt was the material, the overlying substrate was recorded as the dominant substrate material. Substrate categories were bedrock, sand, gravel, pebble (Length (L) $< 0.095$ m), rubble ($0.095$ m $< L < 0.19$ m), cobble ($0.19$ m $< L < 0.38$ m), stone ($0.38$ m $< L < 0.76$ m), and boulder (L $> 0.76$ m). A mean substrate value was calculated for each quadrat by ascribing a value of one to eight (1 = bedrock, 2 = sand, 3 = gravel, ..., 8 = boulder) to each of the 16 partitions and then taking the average (Bain et al. 1988).

The dives were performed between 0900 and 1800 h from 31 July to 17 August 1981 and from 8 June to 6 July 1982. Previously, I tested whether fish number varied between these hours, and it did not (ANOVA, p $>$ 0.8), suggesting fish counts could be conducted throughout the day (Greenberg 1986). Analysis of the transect data was restricted to adults, defined as any fish at least one year old. Except for individuals of *E. rufilineatum* observed at site 3 in 1981, I experienced no difficulties distinguishing YOY from adults. For the *E. rufilineatum* at site 3 (1981), I defined an adult as being greater than 30 mm SL, as this roughly corresponded to the cut-off between adults and YOY.

To determine the density of each species at each site, I counted the number of individuals observed and divided this number by the area surveyed. As there were no obvious inter-year differences, despite the fact that dives were conducted in different parts of the summer, data were pooled from 1981 and 1982. There was an obvious bias in the density estimates (too high) for *Percina* in runs because these fishes were attracted to divers when sediments were disturbed. This was not a problem in other habitats as *Percina* were rarely present in riffles, and sediments were not disturbed when SCUBA diving in pools (bottom consisted of few rocks, mostly sand, silt, detritus, and bedrock).

The mean depth, current, substrate size, and percent cover of silt, *Podostemum ceratophyllum* (riverweed), woody debris, leafy debris, and *Justicia americana* (waterwillow) were computed for each species based on the habitat data from the quadrats in which individuals of each species occurred. A cluster analysis was performed on the ten most abundant species using the single linkage method with Euclidean distances (Systat program, Wilkinson 1987). The percent cover of woody debris, leafy debris, and *Justicia americana* was not included in the analysis as the values were mostly zero.

## Microhabitat use

Substrate composition appears to be the most important habitat feature influencing the distribu-

tions of darters (Page 1983), and presumably other benthic fishes as well. For this reason, residency under cover was quantified and compared using two methods. For the first method, I recorded the amount of time fish spent under cover (defined as rocks or vegetation) during two minute observation periods. Each observation was preceded by at least two minutes of unrecorded observations to ensure that the fish were not disturbed by the observer. If the behavior of a fish was obviously affected, the data were discarded. A fish was considered to be under cover if any part of its body was covered. Otherwise it was recorded as exposed. These observations were conducted between 22 July and 13 August 1981. All data were log transformed to stabilize variances. The data from each site were pooled before being analyzed by ANOVA and Scheffe's Multiple Contrast (SMC) procedure (Zar 1974).

For the second method, I recorded the location of fish (frequency under rocks) while diving in riffle, run, and pool habitats at the three sites (described above). For each transect, the location of every fish was recorded as being under rocks or exposed (the exposed category included the few fish occurring in vegetation). These behavioral observations were conducted between 8 June and 6 July 1982. The data from each site were pooled. To look for diel variation in activity, the frequency of fish under rocks was also measured at night using underwater flashlights. These data were derived from 22 h of observations and were compared with the frequency under rocks data obtained during the day (Zar 1974).

Observations of the position of the fish in the water column were performed to look for different vertical distributions. Although darters spend most of their time close to the bottom, some species, particularly *Percina*, tend to inhabit the midwaters of streams (Smart & Gee 1979, Page 1983, Page & Swofford 1984). I recorded the amount of time individuals of each species spent within 2.5 cm of the bottom during four minute observation periods. Each observation, made from 1 July to 5 August 1981, was preceded by at least two minutes of unrecorded observations to ensure that the fish was not disturbed by the observer. If the behavior of a fish

was obviously affected, the data were discarded. All data, which were square root transformed (sqrt of (mean + 0.5)) to stabilize variances, were pooled before analyzing with ANOVA and SMC (Zar 1974).

## Movement patterns

Mobility in the stream was studied to examine whether differences in manner of space utilization could be identified. Studies of residency rate, a short-time measure of the amount of time a fish spent in a localized area, were conducted. For the residency rate study, a portable gridwork was set up on the river bottom at least 30 min before observations commenced. The grid, which did not appear to affect the behavior of the fishes, was constructed from 2 mm diameter wires and consisted of about 90 square quadrats (0.16 m² each). The amount of time a fish spent in each quadrat was recorded for fifteen minutes or until the fish swam out of the grid, whichever came first. These observations were carried out from 31 May to 12 July 1981. Because all fish were not observed the same amount of time, the data were expressed as the average amount of time a fish spent in each quadrat. ANOVA and SMC were used to test for differences between genera. Data from sites were pooled. Because means were correlated with variances, data were log transformed (Zar 1974).

## Feeding habits

Feeding behavior and feeding locations were compared among species. During two minute periods conducted between 22 July and 13 August 1981, I recorded the site of bites and the orientation of the fish's body during each bite. The site of bites was classified as either on the bottom or in the water column. The orientation of the fish's body when biting (only the first bite taken by each fish was analyzed), which might reflect differences in feeding microhabitats, was divided into two components, a vertical component, pitch, and a horizontal component, yaw (Smart & Gee 1979). Pitch was recorded
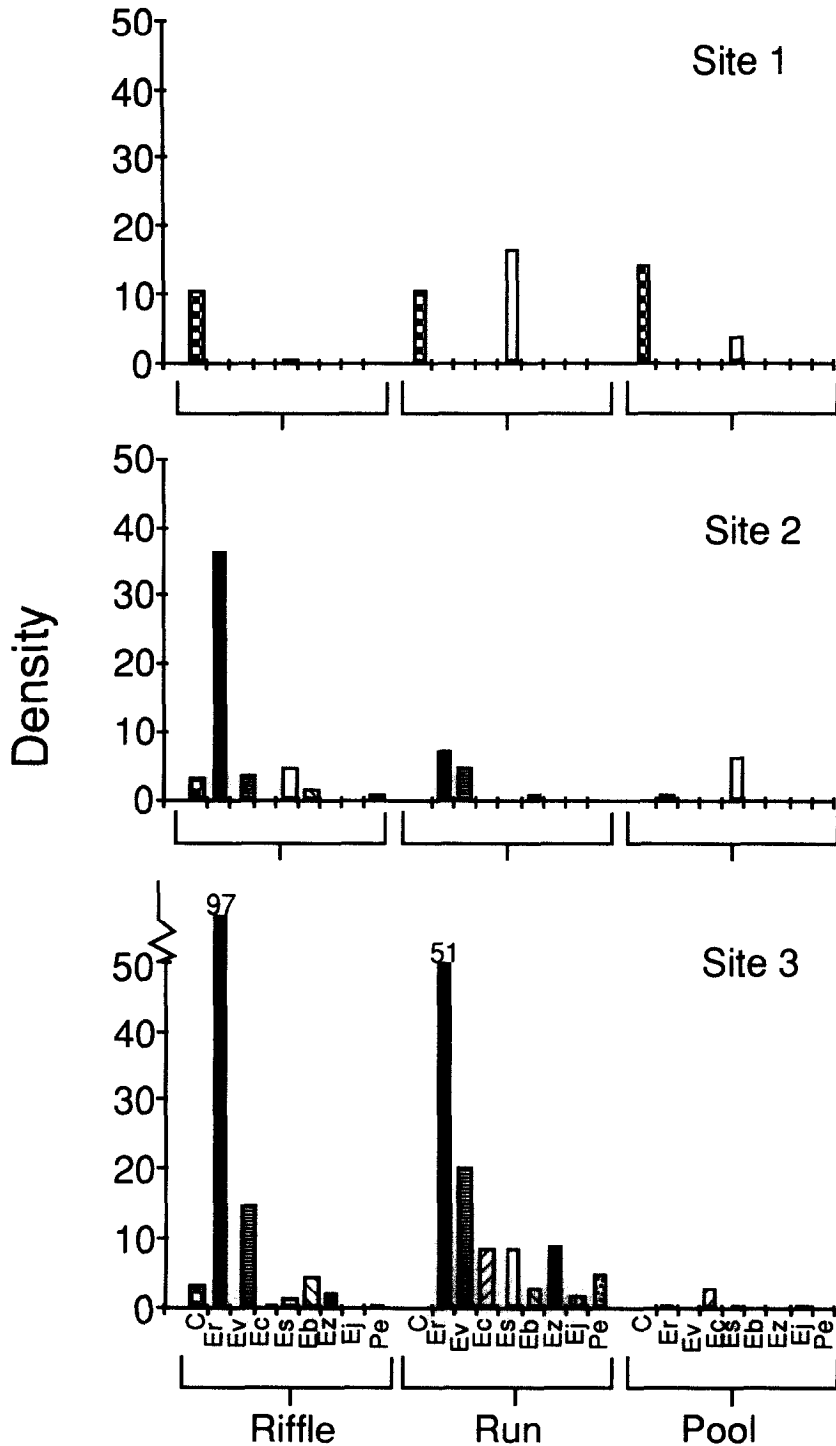
*Fig. 1.* Density of the nine small-sized adult fish species (number per 100 m²) by habitat and site averaged for 1981 and 1982. Note break in ordinate axis for site 3. C = *Cottus*, Er = *E. rufilineatum*, Ev = *E. vulneratum*, Ec = *E. camurum*, Es = *E. simoterum*, Eb = *E. blennioides*, Ez = *E. zonale*, Ej = *E. jessiae*, Pe = *P. evides*.
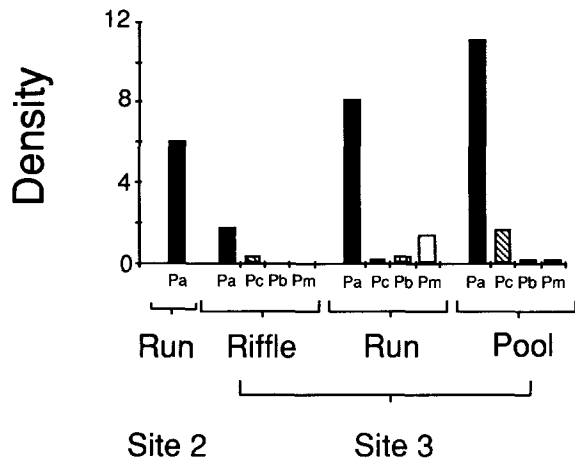
Fig. 2. Density of the four large-sized adult fish species (number per 100 m²) by habitat and site averaged for 1981 and 1982. Pa = *P. aurantiaca*, Pc = *P. caprodes*, Pb = *P. burtoni*, and Pm = *P. macrocephala*.
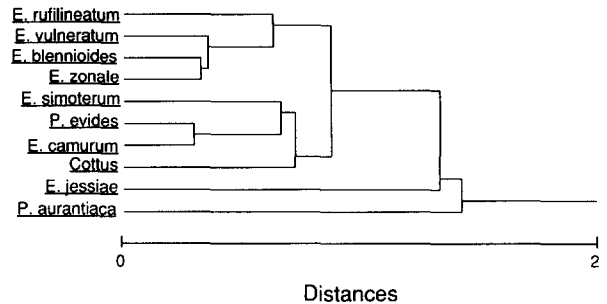


Fig. 3. Cluster analysis of the ten most common benthic fishes based on depth, current, percent cover silt, percent cover *Podostemum* and substrate size.

## Results

### Densities

Density of all species combined increased from site 1 to site 3 (Fig. 1–2). In terms of habitat, the increase occurred in riffles and runs, but not in pools. At sites 2 and 3, species of small adult size were most dense in riffles and runs (Fig. 1), whereas species of large adult size were most dense in runs and pools (Fig. 2). The dominant species at sites 2 and 3 was *E. rufilineatum*, and it was more dense in riffles than in runs. *Etheostoma vulneratum* was the second most abundant species and its density was similar in riffles and runs. For species of large adult size, all species except *P. aurantiaca* had low densities.

as the number of upward-directed, downward-directed or straight bites. Yaw was classified as angles either greater than or less than 30°. Observations for each species were pooled over all habitats and sites and then tested using $X^2$ tests.

In addition, the proportion of bites taken from various substrate surfaces was determined during the residency rate observations. Each fish (only those taking at least five bites) received equal weight when calculating the average proportions for each substrate type. Data for each species were pooled over all sites. No statistical analyses were conducted.

Table 1. The mean depth (cm), current speed (cm sec⁻¹), percent cover *Podostemum*, percent cover silt and substrate size of the 13 benthic species recorded at three sites in the Little River. Habitat data for those species with N > 9 are averaged for the two years. The remaining data are pooled and then averaged (Pc, Pb, Pm). Mean substrate size for each fish was computed as the average substrate size value for sixteen 360 cm² partitions, where 1 = bedrock, 2 = sand, 3 = gravel, 4 = pebble, 5 = rubble, 6 = cobble, 7 = stone, 8 = boulder. These values were then averaged for each species. See Figures 1–2 for species abbreviations.

| Variable | C | $E_r$ | $E_v$ | $E_c$ | $E_s$ | $E_b$ | $E_z$ | $E_j$ | $P_e$ | $P_a$ | $P_c$ | $P_b$ | $P_m$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Depth | 50.2 | 44.6 | 63.5 | 65.3 | 58.3 | 53.1 | 56.9 | 47.4 | 68.1 | 143.1 | 84.3 | 71.3 | 65.0 |
| Current | 31.4 | 38.9 | 21.8 | 20.7 | 13.4 | 27.9 | 23.2 | 4.1 | 17.2 | 9.9 | 5.2 | 15.2 | 0.0 |
| % *Podostemum* | 11.3 | 48.4 | 70.6 | 15.9 | 30.9 | 48.4 | 71.6 | 7.2 | 29.1 | 28.1 | 14.4 | 16.9 | 3.9 |
| % silt | 3.1 | 0.9 | 1.6 | 6.6 | 13.1 | 0 | 0.1 | 42.5 | 7.2 | 23.1 | 77.5 | 0 | 46.9 |
| Substrate size | 5.1 | 4.0 | 4.0 | 4.4 | 3.6 | 3.7 | 3.4 | 2.4 | 4.5 | 3.2 | 2.7 | 2.7 | 4.5 |
| N | 74 | 675 | 172 | 57 | 119 | 37 | 50 | 10 | 30 | 110 | 9 | 3 | 8 |

## Microhabitat associations

Cluster analysis of the ten most abundant species showed that the species could be separated into five groups (Fig. 3). The first group consisted of one species, *P. aurantiaca*. It was found in much deeper water than the other species, often associated with a silty bottom and a low substrate index (Table 1). The second group consisted of *E. jessiae*, which was found in shallow water with very slow currents, high amounts of silt and a low substrate index (mostly sand). The third group consisted of *E. rufilineatum, E. vulneratum, E. blennioides* and *E. zonale,* species associated with rapid currents and *Podostemum*. In contrast to the third group, the fourth group, consisting of *E. simoterum, P. evides, E. camurum* and *Cottus* was generally associated with slow currents, large rock sizes, and was not strongly associated with *Podostemum*. The other species of *Percina* (*P. caprodes, P. burtoni* and *P. macrocephala*), which were not included in the cluster analysis due to small sample sizes, were found in areas of low current velocities and deep water, though not as deep as *P. aurantiaca*.

## Behavior

When cover was used, it usually consisted of rocks. In a few instances, *E. rufilineatum* (8%), *E. blennioides* (8%), *E. simoterum* (1%), and *P. evides* (2%) resided under thick mats of *Podostemum cer-*

*atophyllum*. Only *E. zonale* used *Podostemum* to a great extent (6 of 7 fish). Time under cover varied greatly among the species, ranging from 0 to 80% of the time (Table 2). *Etheostoma rufilineatum* and *E. vulneratum* spent the most time under rocks, followed by *E. camurum* and *E. zonale. Etheostoma* species, which varied greatly in the amount of time spent under cover, spent more time under cover than did *Percina* species (SMC, $p < 0.00005$), which rarely resided under cover ($< 5\%$). All species found in riffles spent considerable amounts of time under cover.

The results obtained from the frequency under rocks data compare well with the residency time data (Table 2). *Etheostoma rufilineatum, E. vulneratum, E. blennioides,* and *Cottus* were usually observed under rocks, whereas *E. camurum* and *E. zonale* were not observed under rocks as frequently. The major discrepancy between these two data sets concerns *E. blennioides*. The time spent under cover was 16%, whereas the frequency under rocks was 63%. Additional observations indicated that large individuals usually occurred under rocks, whereas smaller individuals did not (Greenberg & Stiles unpublished data). The remaining species, particularly *Percina*, were rarely observed under rocks.

Fewer data are available for nocturnal habits. *Etheostoma rufilineatum, E. vulneratum,* and *E. simoterum* showed no obvious diel change in their occurrence under rocks, whereas *Percina* increased its frequency under rocks at night (Table 2). *Cot-*

*Table 2.* Time spent under cover and number of fish found under cover during transect dives (expressed as a percentage) during the day and night. The data were pooled over all sites. See Figures 1–2 for species abbreviations. All species of *Percina* were pooled due to low mean and variance and low sample sizes at night. Numbers in parentheses are sample sizes. Standard deviations are shown for time under rocks.

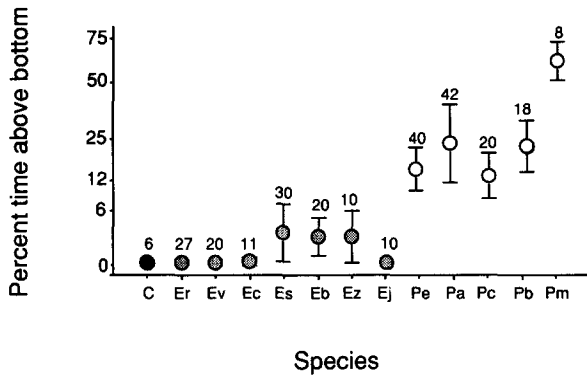| Time | Cover | Species | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | C | $E_r$ | $E_v$ | $E_c$ | $E_s$ | $E_b$ | $E_z$ | $E_j$ | *Percina* |
| Day | % time | – | 69.8 ± 32 | 79.5 ± 27 | 40.6 ± 36 | 4.7 ± 15 | 15.6 ± 33 | 32.3 ± 36 | 0 ± 0 | 1.5 ± 5 |
| | (N) | (0) | (161) | (85) | (22) | (118) | (52) | (6) | (15) | (170) |
| | % number | 70.9 | 81.3 | 91.6 | 48.7 | 11.1 | 62.5 | 48.6 | 0 | 0 |
| | (N) | (55) | (396) | (95) | (39) | (72) | (16) | (37) | (3) | (105) |
| Night | % number | 9.4 | 84.6 | 100 | – | 14.3 | 8.0 | – | 50 | 42.9 |
| | (N) | (106) | (26) | (6) | (0) | (63) | (25) | (0) | (2) | (14) |

Fig. 4. Interspecific comparisons (pooled over all sites) of the time spent above the bottom. Data were analyzed by ANOVA after square root transformed. Vertical lines represent the mean plus or minus one SD. Numbers above the vertical lines are the sample sizes. Gray circles represent *Etheostoma*, white circles represent *Percina*, and black circle *Cottus*. See Figures 1–2 for species abbreviations.
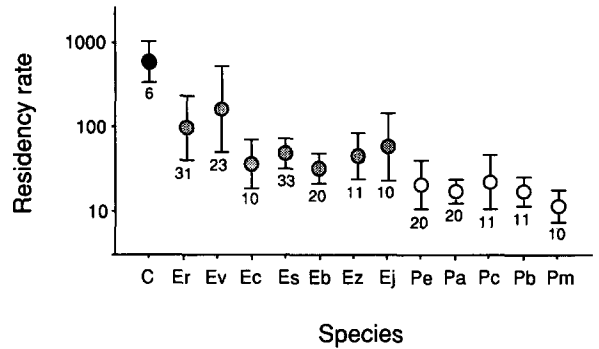


Fig. 5. Interspecific comparisons (pooled over all sites) of residency rates. Log transformed data were analyzed by ANOVA. Vertical lines represent the mean plus or minus one SD. Numbers below the vertical lines are the sample sizes. Gray circles represent *Etheostoma*, white circles represent *Percina*, and black circle *Cottus*. See Figures 1–2 for species abbreviations.

*tus*, which is nocturnally active (Greenberg & Holtzman 1987), occurred on tops of rocks more frequently at night. *Etheostoma blennioides* is more difficult to characterize, but additional nighttime observations indicated that the very largest individuals were resting on tops of boulders, often a few centimeters from the surface. The smaller individuals, which were not observed as frequently, were under rocks (Greenberg & Stiles unpublished data).

There was an obvious difference in water column use by *Percina* and *Etheostoma* (Fig. 4). *Percina* spent significantly more time off the bottom (13–61%) than *Etheostoma* (<4%) did (SMC, p < 0.00005). Of the five species of *Percina* studied, *P. macrocephala* (61%) and *P. aurantiaca* (25%) utilized the water column the most. *Etheostoma rufilineatum*, *E. vulneratum*, *E. jessiae* and *Cottus* (*E. camurum* only 0.2%) were never observed off the bottom.

Mean residency rates, which ranged from 12 to 713 sec quadrat$^{-1}$, also exhibited striking generic differences (Fig. 5). *Percina* were the most mobile species (12–29 sec quadrat$^{-1}$), followed by *Etheostoma* (35–334 sec quadrat$^{-1}$) and *Cottus* (713 sec quadrat$^{-1}$) (SMC between *Percina* and *Etheostoma* and between *Cottus* and *Etheostoma*, p < 0.00005). *Percina macrocephala*, which spent the most time

in the water column, had the lowest residency rate. Similarly, *E. rufilineatum*. *E. vulneratum*, and *Cottus*, which spent the most time under cover, had the highest residency rates.

## Feeding habits

Except for *Cottus* (Greenberg & Holtzman 1987) and possibly the larger *E. blennioides*, all of the species examined were diurnal feeders (Page 1983, personal observations). In addition, all thirteen species fed on invertebrates located on rock surfaces or on aquatic vegetation attached to the bottom. Of the observed feeding bites, only 7% of those taken by *P. evides* (N = 54), 4% of those taken by *E. rufilineatum* (N = 25), and 1% of those taken by *P. aurantiaca* (N = 101) and *E. simoterum* (N = 143) occurred off the bottom in the water column. The pitch and yaw of feeding bites, which were only recorded for darters, did not differ much between species, suggesting feeding microhabitats (e.g. the location on rocks where feeding occurs) were probably similar (Table 3). Exceptions were *E. rufilineatum* and *P. evides*, which had a significantly higher proportion of upward-directed bites than the other species, and *E. rufilineatum* and *P. caprodes*, which had a greater proportion of bites with yaw angles greater than 30°.

The types of surfaces that feeding occurred upon

were similar for most species; nine species took most of their feeding bites on rubble and cobble surfaces (Table 4). However, *P. aurantiaca* took bites on stone and boulder surfaces, *E. jessiae* on sand, and *E. zonale* on *Podostemum*. The location of *E. zonale* and *E. jessiae's* feeding bites corresponded with their microhabitat use (Table 2) as *E. jessiae* was usually observed over sandy bottoms and *E. zonale* generally occurred in areas containing dense growths of *Podostemum ceratophyllum*. *Percina caprodes* and *P. burtoni* fed primarily on rubble surfaces, the same rocks that they usually turned over with their pronounced snouts (about 25% of their bites occurred under flipped rocks). On several occasions, *P. aurantiaca* was also observed rolling stones (as reported by Howell 1971) and gastropod shells over and feeding on prey underneath these objects. *Percina evides* was often observed following *P. caprodes* or *P. burtoni*. When these species flipped stones over, several *P. evides* would dash under the stones, take several nibbles and leave.

## Discussion

### Phylogenetic comparisons

Patterns of resource use and behavior are often very similar to each other within subgenera of darters (Page 1983, Page & Swofford 1984). For example, the logperch, *P. burtoni* and *P. caprodes*, both

members of the subgenus *Percina*, often fed by turning over stones [Keast & Webb (1966) have reported this for *P. caprodes*]. *Etheostoma rufilineatum*, *E. vulneratum*, and *E. camurum*, members of the subgenus *Nothonotus*, were also similar as all three species, but especially *E. rufilineatum* and *E. vulneratum*, spent substantial amounts of time under cover, had similar residency rates and time spent on the bottom. *Etheostoma zonale* and *E. blennioides* were more similar to each other than to *E. simoterum*, which corresponds to the classification system proposed by Bailey & Gosline (1955) in which they placed *E. zonale* and *E. blennioides* in the subgenus *Etheostoma* and *E. simoterum* in the subgenus *Ulocentra*. Page (1981) placed *E. zonale* and *E. simoterum* in the subgenus *Nanostoma*, leaving *E. blennioides* in the subgenus *Etheostoma*.

Resource use and behavior can also be compared at the generic level. In general, *Percina* occurred in deep water habitats, spent little time under cover, spent large amounts of time above the bottom, and had low residency rates. In contrast, *Etheostoma* was found in shallow water habitats, varied considerably in the time spent under cover, spent little time above the bottom, and had high residency rates. *Cottus*, like *Etheostoma*, was in shallow water habitats, spent little time above the bottom, had a high residency rate, and spent most of its time under cover. However, unlike *Etheostoma* or *Percina*, *Cottus* was more active at night than during the day (Greenberg & Holtzman 1987). Thus there

*Table 3.* Pitch and yaw of feeding bites of the different species with N > 9. Numbers represent number of bites (one bite per fish). R × C chi-square tests were used to test for species differences. Significantly different species are indicated by different superscripts (pitch: a versus b, yaw: c versus d).

| Species | Pitch | | Yaw | |
| --- | --- | --- | --- | --- |
| | Straight or downward | Upward | < 30° | > 30° |
| E rufilineatum | [a]12 | 7 | 13 | 6[c] |
| E. simoterum | [b]78 | 1 | 76 | 2[d] |
| E. blennioides | [b]31 | 1 | 32 | 0[d] |
| P. evides | [a]33 | 6 | 37 | 2[d] |
| P. aurantiaca | [b]47 | 5 | 47 | 5[d] |
| P. caprodes | [b]14 | 0 | 11 | 3[c] |
| P. burtoni | [b]15 | 0 | 15 | 0[d] |

were clear ecological affinities within each genus as has been reported by Page & Swofford (1984).

*Resource partitioning*

Habitat and food partitioning are generally regarded as more important than time partitioning (Schoener 1974, Ross 1986). I found evidence of partitioning by habitat, feeding behavior and time of activity, although differences were more pronounced for habitat than for the other two. Thus, these data support Schoener's (1974) finding that habitat partitioning is more important than food partitioning, in contrast with Ross (1986) who reported the opposite. However, as Werner (1986) points out, Schoener's and Ross's results must be treated with caution because of the types of investigations that fish ecologists have conducted. To evaluate the importance of different types of partitioning requires investigation of the mechanisms responsible for the observed patterns. The mechanisms can be broadly classified as: (1) factors that determine a species' use of resources independently of other species (i.e. physiological tolerances) and (2) biotic interactions (i.e. competition and predation) (Toft 1985). Most studies have interpreted patterns of resource partitioning solely in terms of competition, although when the mecha-

nisms are actually studied, several are usually involved, often simultaneously (Toft 1985). Little experimental work exists that examines the mechanisms responsible for patterns of resource partitioning for benthic invertebrate-feeders. Exceptions include studies by Baltz et al. (1982) on a sculpin and dace and Greenberg (1988) on darters (two species in the Little River), both of which implicated physical factors (1 above) and competition (2 above) to explain differential resource use. Another potentially important factor, predation, has received less attention.

*Size-related resource use*

Fish of the sizes most vulnerable to predation are often found in the most protected habitats (Mittelbach & Chesson 1987). Recently, Power and Schlosser (Power 1987, Schlosser 1987, 1988a, b, Power et al. 1989) hypothesized that small species and size classes avoid deep water because of swimming predators and large fish avoid shallow water because of diving or wading predators. In the Little River, species with large adult body sizes (most *Percina*) were more abundant in deep water habitats than species with small adult body sizes (*Etheostoma*, *Cottus* and *P. evides*). Centrarchid bass (*Micropterus* and *Ambloplites*) were quite numer-

*Table 4.* Location of feeding bites (percent occurrence) pooled over all sites. Sa = sand, Gr = gravel, Ru = rubble, Co = cobble, SB = stone and boulder, Be = bedrock, Po = *Podostemum ceratophyllum*, N = number of fish, Nb = number of bites. Numbers in boldface represent surfaces where most feeding bites occurred. * = feeding bites summed over individuals instead of weighted by individuals as few bites were observed per individual. + = most bites taken by one fish.

| Species | N | Nb | Be | Sa | Gr | Ru | Co | SB | Po |
|---|---|---|---|---|---|---|---|---|---|
| E. rufilineatum | 20* | 36 | 3 | 0 | 21 | **40** | 36 | 0 | 0 |
| E. vulneratum | 6* | 10 | 10 | 0 | 10 | 0 | **70** | 0 | 10 |
| E. camurum | 7* | 30 | 0 | 0 | 10 | 27 | **63** | 0 | 0 |
| E. simoterum | 26 | 404 | 14 | 9 | 2 | 8 | **37** | 31 | 1 |
| E. blennioides | 9 | 159 | 10 | 8 | 3 | 9 | **50** | 18 | 0 |
| E. zonale | 3 | 57 | 0 | 0 | 0 | 0 | 0 | 0 | **100** |
| E. jessiae | 3 | 81 | 0 | **80** | 10 | 4 | 1 | 3 | 0 |
| P. evides | 10 | 83 | 0 | 7 | 9 | 33 | **45** | 6 | 0 |
| P. aurantiaca | 15 | 558 | 0 | 12 | 3 | 14 | 13 | **55** | 0 |
| P. caprodes | 7 | 139 | 0 | 4 | 8 | **62** | 25 | 1 | 0 |
| P. burtoni | 7* | 44+ | 0 | 0 | 18 | **66** | 16 | 0 | 0 |
| P. macrocephala | 6* | 15 | 7 | 0 | 0 | 13 | **67** | 13 | 0 |

ous and appear to be the dominant fish predators in the Little River. On several occasions I observed *Micropterus* preying on darters, as has been reported previously (Page 1983). Furthermore, centrarchid bass have been shown to affect the depth distribution of small fish in both field and laboratory experiments (Power et al. 1985, Schlosser 1987, 1988a, b). Thus, the habitat use of small and large benthic-invertebrate feeders in the Little River is consistent with the predation hypothesis proposed by Power (1987) and Schlosser (1987).

Further evidence of predation's potential effects comes from the behavior of the darters and sculpins, which, for other species has been shown to reduce susceptibility to predation (e.g. Dill & Fraser 1984, Wolf 1985). *Percina* were presumably more exposed to predators than were *Etheostoma* or *Cottus* because of their higher position in the water column. However, *Percina's* cryptic color patterns, larger adult size, and presumed greater swimming abilities should reduce susceptibility to predation (Page 1983, Page & Swofford 1984). In addition, large *Percina*, especially *P. aurantiaca*, may further reduce predation risk by occurring in small aggregations or shoals (as defined by Pitcher 1986). Nighttime may be particularly dangerous, even for the large *Percina*, as nearly all species were found under cover at night; centrarchids, *Cottus*, and the hellbender salamander, *Cryptobranchus allegaaniensis* are potential predators at this time. As a group, darters are regarded as diurnal visual foragers (Roberts & Winn 1962, Page 1983), and thus are probably less effective at avoiding predation at night than during the day. In contrast, *Cottus, E. blennioides,* and *E. simoterum* did not use cover much at night. It is not clear why *E. simoterum* did not use cover, except that most nocturnal observations occurred at site 1 where few fish predators occurred. *Cottus* probably relies heavily on its lateral line when feeding (Hoekstra & Janssen 1985, Greenberg & Holtzman 1987), and large *E. blennioides* were restricted to extremely shallow water in riffles (Greenberg & Stiles unpublished data). Thus, the behavioral data are consistent with the notion that the benthic-invertebrate feeding guild is sensitive to predation, and this is expressed in terms of both behavior and habitat use.

Habitat use of benthic invertebrate-feeders should also be affected by food availability. Riffles are generally regarded as areas of high food availability and pools as areas of low availability (Kuehne & Barbour 1983, Schlosser 1987). If this is true in the Little River, this would suggest that the fish should prefer riffles. However, the cost of foraging in riffles may be prohibitive for most species. Runs may represent a compromise, with relatively high densities of food and moderate currents. Still some species, particularly *P. aurantiaca*, were found in pools (site 3). *Percina aurantiaca's* occurrence in pools may relate to its low total food requirements from this habitat, due to its low density, and to its large size, which presumably affords it protection from predators in deep water. Further study of foraging gains and predation risk are needed to be able to assess the mechanisms behind habitat use of this guild.

In summary, members of the benthic feeding guild exhibited diverse patterns of microhabitat use, feeding behavior, and diel activity pattern. Such patterns of resource partitioning are often presented as evidence of competition, which is undoubtedly occurring (e.g. Greenberg 1988). However, the patterns of habitat use and behavior are also consistent with the predation hypothesis of Power (1987) and Schlosser (1987) in which they state that small species are found in shallower water than large species due to their vulnerability to predation by large fish predators. Furthermore, the data indicate that body size may be important to understanding the nature of biotic interactions in streams. Future research should be directed at elucidating the mechanisms, both in terms of physiological constraints and biotic interactions, affecting resource use of this guild.

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