Comparative microhabitat use of ecologically similar benthic fishes

Ellen van Snik Gray[a] & Jay R. Stauffer, Jr.
The Pennsylvania State University, School of Forest Resources, 2C Ferguson Building,
University Park, PA 16802, U.S.A.
[a]*Current address: U.S. Geological Survey, Leetown Science Center, 1700 Leetown Road, Kearneysville,*
WV 25430, U.S.A. (e-mail: ellen_gray@usgs.gov)

Synopsis

Although benthic insectivorous fishes such as darters and sculpins represent a significant component of riffle communities, few studies have compared the habitat use of these non-related but ecologically similar fishes. The objectives of this study were to examine the habitat use of *Etheostoma olmstedi* (tessellated darter) compared to *Cottus bairdi* (mottled sculpin) in Nescopeck Creek and *Cottus cognatus* (slimy sculpin) in Jack's Creek, Pennsylvania through underwater observation. *Etheostoma olmstedi* occupied habitats with significantly deeper waters than those available, whereas adult and young of the year *Cottus* occupied habitats with significantly faster water velocities than those available. Canonical discriminant analysis revealed microhabitat partitioning between *E. olmstedi* and each *Cottus* species. *Cottus bairdi* and *C. cognatus* occupied significantly shallower habitats with faster water velocities than *E. olmstedi*. Sculpin species were observed most frequently under substrate whereas *E. olmstedi* occurred most frequently on the top surface of the substrate. Hurlbert's standardized niche breadth values indicated that *C. bairdi* and *C. cognatus* were habitat specialists with regard to water velocity measures, but exhibited generalistic patterns of depth and substrate size use. *Etheostoma olmstedi* was a habitat specialist with respect to depth, but exhibited generalistic patterns of resource use for substrate size. Differential habitat use by these benthic fishes is consistent with the hypothesis that resource partitioning facilitates species coexistence among stream fishes.

Introduction

Benthic insectivorous fishes such as darters (Percidae) and sculpins (Cottidae) are relatively sedentary benthic fishes with small home ranges (Brown & Downhower 1982, Greenberg & Holtzman 1987, Hill & Grossman 1987, Freeman & Stouder 1989, Freeman 1995) and represent a significant component of riffle communities. Several studies have examined habitat use among species of darters (Englert & Seghers 1983, Schlosser & Toth 1984, Kessler & Thorp 1993, Stauffer et al. 1996) and among species of sculpins (Finger 1982, Matheson & Brooks 1983, Daniels 1987). Few studies have compared the habitat use of non-related but ecologically similar groups such as darters and

sculpins (Greenberg 1991) despite evidence that biotic interactions may be as great or greater among non-related feeding guild members than between congeners or species of the same family (Baltz et al. 1982, Resetarits 1995, Taylor 1996).

Underwater observation techniques are being used increasingly to examine stream fish habitat use because the habitat use of individual fish can be quantified (Fausch & White 1981, Brown & Moyle 1991, Greenberg 1991, Grossman & de Sostoa 1994, Stauffer et al. 1996). Stauffer et al. (1996) described a microhabitat quantification technique for stream fishes involving snorkeling observations. Variables measured included depth, bottom and mean water velocity, and substrate size. Stauffer et al. (1996) noted that the inclusion of

additional variables such as species use of vegetation and position with respect to the substrate (under, above, or between substrate) may improve their technique.

This study is a natural snapshot experiment (sensu Diamond 1986) of comparative habitat use between *Etheostoma olmstedi* Storer, the tessellated darter, and two sculpin species, *Cottus cognatus* Richardson, the slimy sculpin, and *Cottus bairdi* Girard, the mottled sculpin. Habitat use of stream fishes is examined to provide information on habitat requirements as well as to examine its potential role in competition. Niche characteristics such as breadth and overlap define the range of resources used by particular species as well as the degree to which different species utilize the same resources. By definition, competition is evident when reduced population size, growth, or production of one species in the presence of another is found. Measuring overlap in spatial resources does not demonstrate the existence of interspecific competition (Colwell & Futuyma 1971), however its results may be used to identify the relative importance of intraspecific vs. interspecific interactions, and may suggest that resource partitioning promotes species coexistence. The objectives of this study were to (1) examine the habitat use of *E. olmstedi* compared to *C. cognatus* in Jack's Creek and *C. bairdi* in Nescopeck Creek, Pennsylvania, (2) determine their populations sizes, and (3) refine the microhabitat quantification technique of Stauffer et al. (1996) through the inclusion of additional variables.

Methods

Two sites were selected for sampling in the Susquehanna River drainage of Pennsylvania: Nescopeck Creek, a third order stream located in Luzerne County, and Jack's Creek, a fourth order stream located in Mifflin County; both are part of the Ridge and Valley physiographic province (Guilday 1985). The spring-fed study streams were 15–20 m wide and temperatures ranged from 12–16°C during the sampling period. Each site was sampled during low flows once in August and September 1995.

Each site contained a 40 m long riffle, run, and pool sequence that was snorkeled during daytime hours with good visibility. Typically two investigators each spent two hours snorkeling at each visit. The investigators would begin at the downstream end of the site and make their way slowly upstream so that fishes were not disturbed. An observation was excluded if the fish was startled by the observer. Rocks were turned over as snorkeling proceeded so that observations were not biased against hidden fishes. Following a darter or sculpin observation, a numbered flag was secured in the stream bed at the specific locality of the fish, and the following variables were recorded by the observer: flag number, species, age group (adult or young of the year, yoy, visually estimated), orientation to the current (subsequently referred to as direction; 1 – snout facing the current, 2 – left side facing the current, 3 – snout facing downstream, and 4 – right side facing the current), orientation to the substrate (subsequently referred to as position), and the type of vegetation present, if any. Each fish was classified into one of the following four categories for the position variable: under substrate, on the top surface of substrate (subsequently referred to as above), between substrate, and suspended in the water column.

Following a snorkeling session, the following abiotic variables were recorded at each flag: depth (to the nearest 0.5 cm), water velocity at the substrate level (subsequently referred to as bottom water velocity, m sec^{-1}), water velocity at 6/10 depth or mean water velocity (Bovee 1986), and substrate size. Water velocity measures were determined with a Marsh-McBirney digital flow meter with a bulb sensor. Substrate size was quantified using a 25 × 25 cm acrylic sheet marked with a grid of 25, 5 × 5 cm squares. The center of the grid was placed over the flag's location, and the number of 5 × 5 cm squares covered by each rock was recorded. Twenty-five categories of rock size were possible (R); each category is a unique number of squares that a given rock occupies (i.e. range = one square to twenty-five squares, representing 5 × 5 cm rock to 25 × 25 cm rock). In this manner the substrate size in the 25 × 25 cm area around each fish's locality was quantified. A substrate index (I) was determined by the sum of the number of rocks (n) observed in each category multiplied by the category squared: $I = \sum nR^2$. The index therefore ranges from 25–625 and increases with substrate size.

Relationships have been discovered between the species or size of fish occurring under rocks for shelter and the diameter of the rock (Rimmer et al. 1984, Cunjak 1988). Therefore, for fishes that were found under substrate, the length, width, and height of the rock were measured (to the nearest 0.5 cm). Two-tailed T tests were used to determine if the three species used rocks of different area or volume for cover. Differences were considered statistically significant if p ≤ 0.05 for all statistical tests.

Habitat availability at each site and date was measured so that fish habitat preferences could be evaluated and differences among collections could be assessed. Six transects were established at equally-spaced intervals over the section of stream snorkeled. Five equidistant points across each transect were sampled for the four abiotic variables as previously described. Type of vegetation, if any, was also recorded.

Population estimates were obtained using the sequential removal method (Zippin 1956, 1958) on 26 July 1995 for Nescopeck Creek and 25 August 1995 for Jack's Creek. A 2 × 15 m transect was sampled using backpack electrofishing techniques (220–250 volts, DC current) at each site. Four passes were made at Nescopeck Creek and three were made at Jack's Creek. We estimated population densities (and 95% confidence intervals) of darters and sculpins using a maximum likelihood method and software developed by Van Deventer & Platts[1]. When the computed lower 95% confidence interval was less than the total number caught, we used the total catch as the lower confidence interval.

Principal components analysis (PCA, Minitab 10 for Windows) was used to determine whether collections had similar habitat availability, and therefore could be pooled. Transformation of variables was conduced to stabilize variances when necessary as determined by Levene's test for all statistical tests. Analysis of variance (ANOVA, SAS 6.07, Proc ANOVA) of the principal component scores was used to determine if a significant difference existed among minimum polygon clusters (MPCs) on a PCA axis so that the possibility of pooling data could be objectively assessed. For both multivariate techniques, only axes with eigenvalues greater than one were examined (Cliff 1988). If there was a significant difference among MPCs, the Tukey-Kramer multiple comparison method (SAS 6.07, Day & Quinn 1989) was used to identify which species and age groups differed on a particular axis.

Two-tailed T tests were used to determine whether the habitats occupied by the three species were significantly different from habitat availability. Canonical Discriminant Analysis (CDA, SAS 6.07, Proc CANDISC) was used to examine differences in habitat use between *E. olmstedi* and each *Cottus* species. The variables analyzed were: depth, bottom water velocity, mean water velocity, substrate index, direction, position, and vegetation. Direction, position, and vegetation were categorical variables recorded as shift variables (Digby & Kempton 1987). ANOVA of the canonical scores and the Tukey-Kramer multiple comparison method were used to test for significant differences among the clusters as previously described.

Hurlbert's standardized niche breadth was calculated for each species (Hurlbert 1978). This niche breadth measure takes into account the variability in abundance of different resources, and indicates where species fall on the continuum from generalist to specialist resource use. The index ranges from 0–1, with high niche breadth values indicating habitat generalization (values greater than 0.66) and low niche breadth values indicating habitat specialization (values smaller than 0.33).

Results

Habitat availability

Analysis of the habitat availability data produced two principal component axes with eigenvalues greater than one (Table 1, Figure 1). ANOVA of PCA scores indicated a significant difference in available habitat among MPCs based on the first principal component (F = 6.84; 3, 116 df; p = 0.0003), however there were no statistically significant differences on the second principal component (F = 2.57; 3, 116 df; p = 0.0575). The Tukey-Kramer multiple comparison method indicated that there were significant differences in habitat availability between Jack's and Nescopeck creeks, however within a stream, there were no significant differences in habitat availability in August and September collections. Therefore, all data were pooled for each stream. PCA 1 was highly loaded on bottom and mean water velocity. Nescopeck Creek had microhabitats with significantly higher water velocities (mean bottom and mean water velocity = 0.11, 0.19 m sec^{-1}) than Jack's Creek (mean bottom and mean water velocity = 0.04, 0.12 m sec^{-1}, Table 2). Aquatic vegetation was not observed at either study site during the sampling period.

Table 1. Percent of variance explained, eigenvalues, and variable loadings of the principal components analysis of habitat availability and canonical discriminant analysis of species habitat use in Nescopeck and Jack's creeks.

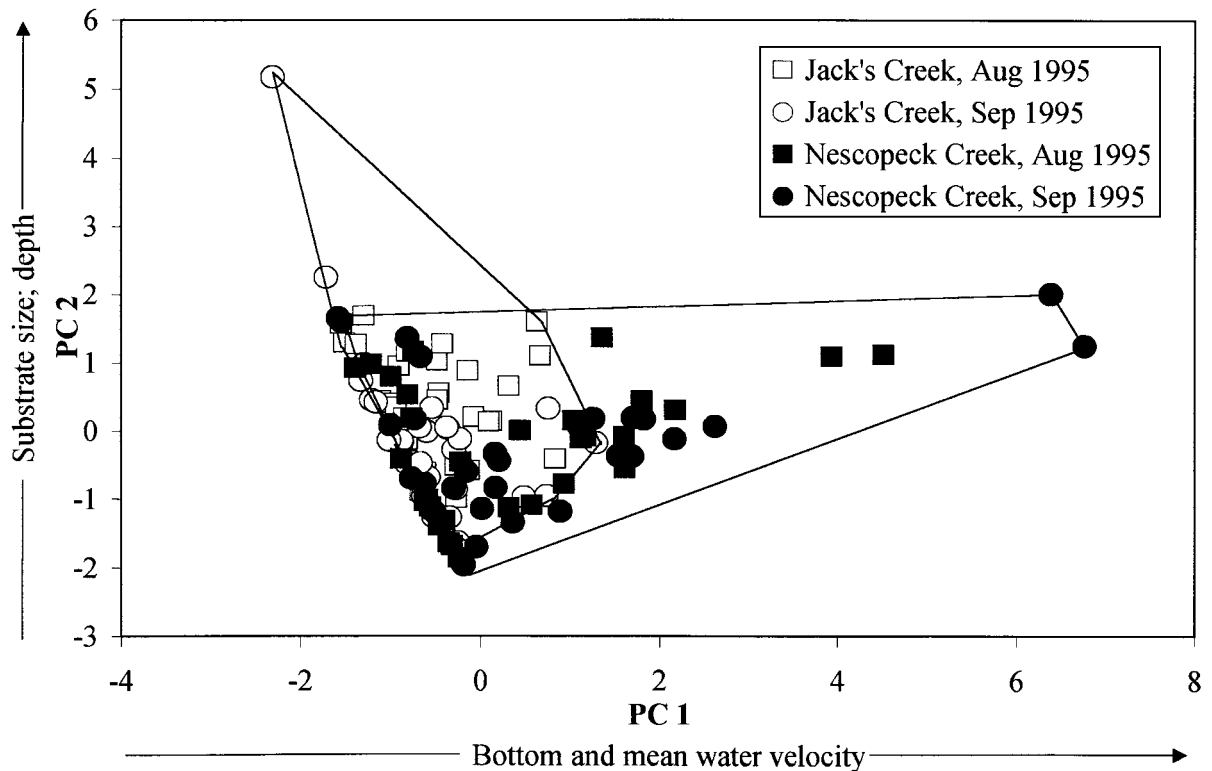| Variable	Habitat availability		Nescopeck Creek		Jack's Creek	
	PC 1	PC 2	Canonical 1	Canonical 2	Canonical 1	Canonical 2
Percent of variance explained	48.68	26.87	93.10	6.90	93.32	6.68
Eigenvalue	1.9472	1.0748	2.3050	0.1708	2.4371	0.1746
Biotic variables						
Position 1	—	—	0.6753	0.0601	0.6320	−0.6171
Position 2	—	—	0.1348	0.4844	−0.0433	0.4464
Direction 1	—	—	0.2678	−0.0640	0.1218	−0.1204
Direction 2	—	—	−0.0922	0.2700	−0.1022	0.6436
Direction 3	—	—	−0.0832	0.4004	−0.0299	−0.3277
Abiotic variables						
Depth	−0.2815	0.6181	0.7218	−0.2966	0.8539	−0.0060
Bottom water velocity	0.6696	0.2105	−0.6914	0.4919	−0.6334	0.2608
Mean water velocity	0.6515	0.2864	−0.6952	0.4583	−0.6208	0.1335
Substrate index	−0.2190	0.7012	−0.3434	0.1196	−0.2259	0.4070

Figure 1. Plot of the first and second principal components of the habitat availability data for Nescopeck and Jack's creeks.

Table 2. Mean and standard deviation (in parentheses) of depth, bottom and mean water velocity, and substrate size utilized by darters and sculpins in Nescopeck and Jack's creeks. For position and direction, modes and percent of individuals at the mode are given. For direction, the categories are 1 – snout facing the current, 2 – left side facing the current, 3 – tail facing the current, and 4 – right side facing the current. For fishes that were found under substrate, the average length, width, and height of the rock are given. Average and standard deviation (in parentheses) of habitat availability data are given in bold. Asterisks indicate significant differences (p ≤ 0.05) between species habitat use and habitat availability.

Species	Sample size	Direction	Position	Depth (cm)	Bottom velocity (m sec^{-1})	Mean velocity (m sec^{-1})	Substrate index	Rock length (cm)	Rock width (cm)	Rock height (cm)
Nescopeck Creek	**30**	—	—	**15.04**	**0.11**	**0.19**	**41.47**	—	—	—
habitat availability				**(7.47)**	**(0.13)**	**(0.20)**	**(15.78)**	—	—	—
E. olmstedi	38	1	above	27.87*	0.07	0.12*	36.05*	—	—	—
		47%	84%	(5.74)	(0.09)	(0.15)	(14.49)			
C. bairdi	21	1	under	16.48	0.26*	0.40*	45.10	14.00	9.22	2.56
		57%	76%	(5.75)	(0.11)	(0.17)	(12.89)	(3.02)	(2.29)	(1.44)
C. bairdi yoy	22	1	above	18.48	0.25*	0.37*	46.74	13.67	8.89	3.44
		41%	45%	(6.58)	(0.18)	(0.23)	(25.34)	(3.61)	(2.32)	(2.13)
Jack's Creek	**30**	—	—	**20.69**	**0.04**	**0.12**	**48.20**	—	—	—
habitat availability				**(6.31)**	**(0.05)**	**(0.09)**	**(26.84)**	—	—	—
E. olmstedi	39	1	above	30.23*	0.06	0.16*	45.62	17.67	14.33	5.33
		44%	85%	(4.38)	(0.07)	(0.10)	(17.81)	(2.08)	(2.08)	(3.06)
C. cognatus	18	1	under	21.33	0.19*	0.31*	57.56	16.32	11.82	5.00
		39%	61%	(6.11)	(0.15)	(0.15)	(27.96)	(6.12)	(4.33)	(2.36)
C. cognatus yoy	7	1	under	17.64	0.20*	0.34*	49.00	18.50	12.50	5.63
		43%	57%	(4.20)	(0.14)	(0.22)	(17.24)	(3.00)	(3.79)	(2.56)

Cottus bairdi *and* Etheostoma olmstedi *in Nescopeck Creek*

The population estimate for *E. olmstedi* was 0.40 fish m^{-2} in Nescopeck Creek (Table 3). *Cottus bairdi*

adults were present at higher densities, 0.77 fish m^{-2}, and the abundance of *C. bairdi* yoy was 0.33 fish m^{-2}.

In Nescopeck Creek, the habitat use of *C. bairdi* (N = 43, including 22 young of the year (yoy) and both sampling months) and *E. olmstedi* (N = 38) was evaluated (Table 2). Comparison of the habitat availability and species habitat use data indicated that *E. olmstedi* and adult and yoy *C. bairdi* exhibited habitat selection and utilized significantly different habitats from those available for most variables. *Etheostoma olmstedi* occupied significantly deeper waters (t = 8.38; 98 df; p = 0.0000), slower mean water velocities (t = −2.00; 97 df; p = 0.0488), and smaller substrates (t = −1.96; 89 df; p = 0.0532) than those available, whereas adult and yoy *C. bairdi* occupied significantly faster bottom (adult: t = 4.49; 79 df; p = 0.0000; yoy: t = 4.15; 80 df; p = 0.0000) and mean water velocities (adult: t = 4.14; 79 df; p = 0.0000; yoy: t = 3.84; 80 df; p = 0.0002) than those available. There was no significant difference between the area or volume of rocks adult and yoy *C. bairdi* used for cover (area: t = 0.26; 15 df; p = 0.8000; volume: t = −0.97;

Table 3. Estimated densities (number of fish m^{-2}) of darters and sculpins in Nescopeck and Jack's creeks, with 95% confidence intervals in parentheses.

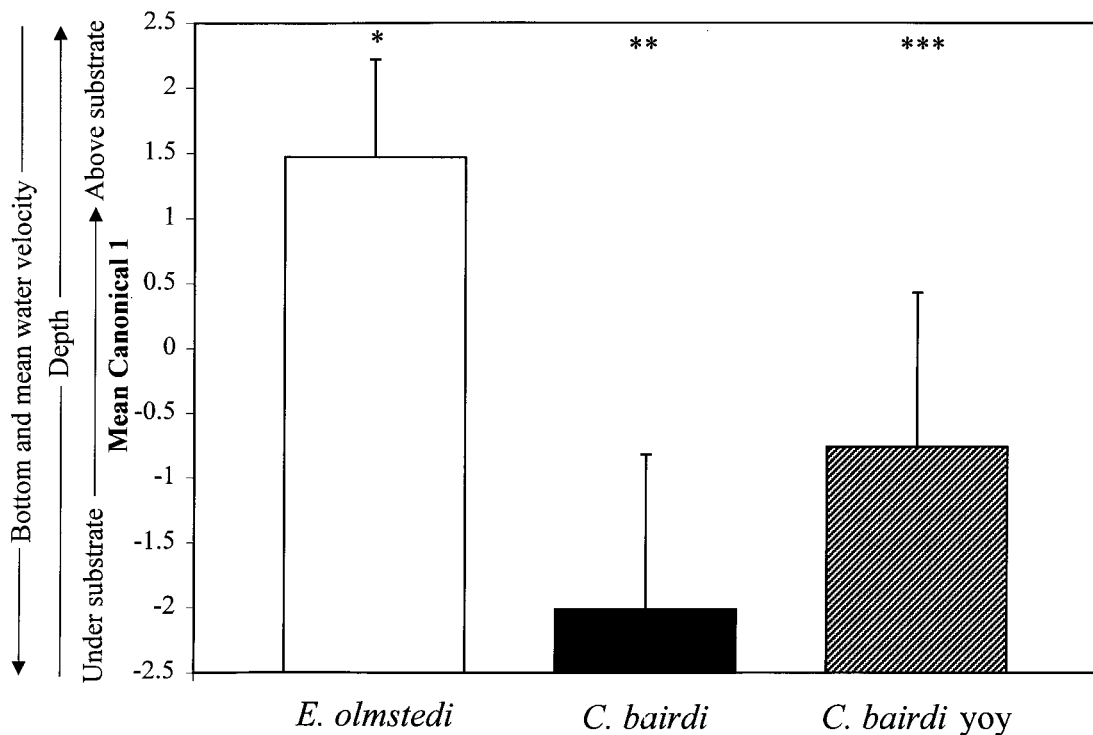| Site	Species	Population estimate (95% CI)
Nescopeck Creek	*E. olmstedi*	0.40 (0.30, 0.86)
	C. bairdi	0.77 (0.73, 0.89)
	C. bairdi yoy	0.33 (0.33, 0.36)
Jack's Creek	*E. olmstedi*	0.17 (0.16, 0.21)
	C. cognatus	0.20 (0.20, 0.32)

Figure 2. Mean canonical discriminant scores of the habitat use by *E. olmstedi* and adult and yoy *C. bairdi* plus one standard deviation in Nescopeck Creek. Asterisks indicate statistically significant differences between populations.

9 df; p = 0.3600). None of the *E. olmstedi* individuals observed occurred under substrate.

Canonical discriminant analysis of the six habitat variables revealed differences in habitat use among *E. olmstedi*, *C. bairdi*, and *C. bairdi* yoy in Nescopeck Creek (Figure 2). Depth, mean and bottom water velocity, and position were highly loaded on the first canonical axis, the only axis with an eigenvalue greater than one (Table 1). ANOVA and the Tukey-Kramer multiple comparison method indicated statistically significant differences among all three clusters on the first canonical axis (F = 92.20; 2, 80 df; p = 0.0001). *Etheostoma olmstedi* occupied deeper areas (mean depth = 27.9 cm) with slower water velocities (mean bottom and mean water velocity = 0.07, 0.12 m sec^{-1}) than adult and yoy *C. bairdi* (mean depth < 18.5 cm; mean bottom and mean water velocity > 0.24, 0.36 m sec^{-1}, Table 2). Adult *Cottus bairdi* were most often found under substrate, whereas *E. olmstedi* and *C. bairdi* yoy were most often found above substrate.

Hurlbert's niche breadth values indicated differences in the relative importance of the habitat variables for *E. olmstedi* and *C. bairdi* (Table 4). *Etheostoma olmstedi* had a low niche breadth value for depth, indicative of specialization (i.e. < 0.33), whereas adult and yoy *C. bairdi* had high niche breadth values for depth, indicative of habitat generalization (i.e. > 0.66) for this variable. *Etheostoma olmstedi* was generalistic in use of bottom and mean water velocity, whereas adult and yoy *C. bairdi* tended towards specialization for these variables. None of the three groups were specialistic with respect to substrate size.

Table 4. Hurlbert's standardized niche breadth values for the four microhabitat variables of species habitat use in Nescopeck and Jack's creeks.

Species	Depth	Bottom velocity	Mean velocity	Substrate index
Nescopeck creek				
E. olmstedi	0.140	0.741	0.810	0.843
C. bairdi	0.886	0.328	0.431	0.595
C. bairdi yoy	0.804	0.308	0.482	0.781
Jack's creek				
E. olmstedi	0.215	0.133	0.131	0.963
C. cognatus	0.907	0.001	0.002	0.702
C. cognatus yoy	0.843	0.000	0.001	0.857

Cottus cognatus and Etheostoma olmstedi
in Jack's Creek

Densities of fish were lower at Jack's Creek than Nescopeck Creek; population estimates were 0.17 fish m^{-2} for *E. olmstedi* and 0.20 fish m^{-2} for *C. cognatus*.

In Jack's Creek, the habitat use of *C. cognatus* (N = 25, including 7 yoy and both sampling months) and *E. olmstedi* (N = 39) was evaluated (Table 2). Comparison of the habitat availability data and species habitat use indicated that *E. olmstedi* and adult and yoy *C. cognatus* exhibited habitat selection and utilized significantly different habitats from those available for most variables. *Etheostoma olmstedi*, *C. cognatus*, and *C. cognatus* yoy occupied areas with significantly faster mean water velocities than those available (*E. olmstedi*: t = 2.29; 97 df; p = 0.0240; *C. cognatus*: t = 6.73; 76 df; p = 0.0000; *C. cognatus* yoy: t = 5.32; 65 df; p = 0.0000). *Etheostoma olmstedi* occupied significantly deeper waters than those available (t = 8.24; 97 df; p = 0.0000). Adult and yoy *C. cognatus* occupied significantly faster bottom water velocities than those available (adult: t = 6.83; 76 df; p = 0.0000; yoy: t = 5.77; 65 df; p = 0.0000). There was no significant difference between the area and volume of rocks adult and yoy *C. cognatus* used for cover (area: t = −0.24; 6 df; p = 0.8200; volume: t = 0.02; 7 df; p = 0.9900). Of the 39 *E. olmstedi* individuals observed, only 3 individuals occurred under substrate.

Canonical discriminant analysis of the six habitat variables indicated habitat partitioning among *E. olmstedi*, *C. cognatus*, and *C. cognatus* yoy (Figure 3). The highest loadings on the first canonical axis, the only axis with an eigenvalue greater than one, were depth, position, bottom and mean water velocity (Table 1). ANOVA and the Tukey-Kramer multiple comparison method revealed statistically significant differences among all three clusters on the first canonical axis (F = 74.33; 2, 61 df; p = 0.0001). *Etheostoma olmstedi* occupied significantly deeper areas (mean depth = 30.2 cm) with slower water velocities (mean bottom and mean water velocity = 0.06, 0.16 m sec^{-1}) than adult and yoy *C. cognatus* (mean depth < 21.4 cm; mean bottom and mean water velocity > 0.18, 0.30 m sec^{-1}, Table 2). In addition, most *E. olmstedi* individuals occurred above substrate whereas most adult and yoy *C. cognatus* individuals occurred under substrate. *Cottus cognatus* yoy occupied significantly shallower habitats than adult *C. cognatus* and *E. olmstedi*.
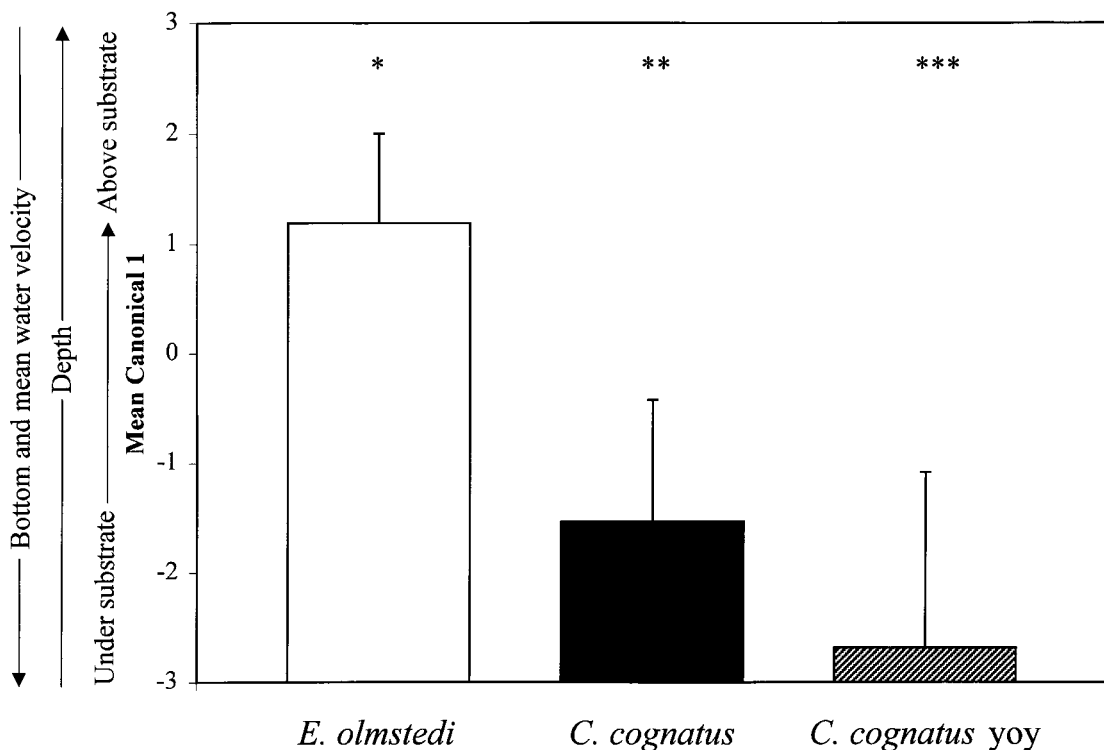
450

Figure 3. Mean canonical discriminant scores of the habitat use by *E. olmstedi* and adult and yoy *C. cognatus* plus one standard deviation in Jack's Creek. Asterisks indicate statistically significant differences between populations.

Etheostoma olmstedi was a habitat specialist for depth, whereas both age classes of *C. cognatus* exhibited generalistic patterns of habitat use for this variable (Table 4). *Cottus cognatus* age classes and *E. olmstedi* were habitat specialists for the water velocity measures. For substrate size, all three groups exhibited generalistic patterns of habitat use.

Discussion

The underwater observation technique of Stauffer et al. (1996) was effective in examining the habitat use of these stream fishes. We attempted to refine their method through the addition of three variables: position, direction, and vegetation. The direction variables (orientation of the fish with respect to the current) were not highly loaded in the analyses and vegetation was not observed at the study sites. However, position, or orientation of the fish with respect to the substrate, was an important addition to the technique. As previous investigators have highlighted (Finger 1982, Schlosser &

Toth 1984, Greenberg & Holtzman 1987, Greenberg 1988, Brown 1991), benthic fishes often use interstitial spaces between and under substrate for cover, and this behavior is species-specific. Although substrate size was not heavily loaded in the multivariate analyses, sculpins and *E. olmstedi* oriented to the substrate in different ways. *Etheostoma olmstedi* occurred most frequently on the top surface of the substrate whereas *C. bairdi* and *C. cognatus* occurred most frequently under substrate. Gorman (1988 a,b) discovered that communities of cyprinids in pools segregated almost exclusively by vertical position in the water column. Baltz et al. (1987) found that measuring habitat variables in addition to the three variables most commonly measured in instream flow habitat studies (depth, mean water velocity, and substrate size) increased the variance explained in discriminant analyses.

Differences in habitat use were observed between *E. olmstedi* and *C. bairdi*, *C. cognatus*, and *Cottus* yoy. Species differed in microhabitat use along the position, water velocity, and depth gradients. Daniels (1987),

Finger (1982), and Matheson & Brooks (1983) found water velocity to be the most important variable in distinguishing among the habitat use of sculpins. In this study, adult sculpins occupied shallower habitats with significantly higher water velocities than *E. olmstedi*, and were found much more frequently under substrate than *E. olmstedi*. Less than one percent of *E. olmstedi* individuals were observed under substrate, whereas 61% of adult *C. cognatus* and 76% of adult *C. bairdi* were under substrate. Significant differences were also observed between the habitat use of young-of-the-year and adult sculpins. In contrast, Daniels (1987) found no significant differences between the habitat use of adult and yoy *Cottus asperrimus* Rutter (rough sculpin). *Cottus cognatus* yoy occupied the shallowest habitats available, similar to the findings of Brandt (1986) and Johnson et al. (1992), who reported that smaller *C. cognatus* inhabited shallower areas than larger sculpin. *Cottus bairdi* yoy occupied similar depths as adults but occurred above substrate more frequently.

Several phenomena have been postulated to affect the habitat use of stream fishes, including predation (Anderson 1985, Gilliam & Fraser 1987, Schlosser 1987, Brown & Moyle 1991), physiological constraints (Facey & Grossman 1990), preference for abiotic factors such as temperature (Baltz et al. 1982, Baltz et al. 1987), stochastic environmental events (Greenberg 1988, Grossman & de Sostoa 1994), and competition for resources, such as space (Gorman 1988 a,b, Freeman & Stouder 1989) and optimal foraging positions (Fausch & White 1981). Predation could play a significant role in the distribution of the three species. Both *C. bairdi* and *C. cognatus* feed on fishes, including their own species (Koster 1937, Johnson et al. 1983, Brown 1991) and darters (Koster 1937, Rohde & Arndt 1981), although the bulk of their diets consist of insect larvae (Novak & Estes 1974, Johnson et al. 1983, Brown et al. 1995). The presence of adult sculpins in riffles could discourage young-of-the-year sculpins and *E. olmstedi* from occupying them due to predation risk (Downhower & Brown 1979). Freeman & Stouder (1989) determined that small *C. bairdi* occurred in shallower habitats than larger *C. bairdi* in field enclosures. However, all sizes of *C. bairdi* preferred the same depths when tested singly (12–32 cm). Thus the occurrence of *Cottus* yoy in shallower waters than adults may be due to intraspecific interactions rather than size-specific depth preferences (Freeman & Stouder 1989). The disjunct distribution

of tessellated darters and sculpins at the study sites supports this hypothesis. Darters occupied runs, pools, and the upstream portion of riffles, whereas sculpins occupied the middle and downstream end of riffles (personal observation).

Competition for space or foraging positions is also a likely factor explaining the distribution of the three species. In Oregon streams, *Cottus perplexus* Gilbert & Evermann, the reticulate sculpin, occurred in a wider variety of habitat types when existing alone as compared to its habitat use in the presence of congeners (Finger 1982). Petty & Grossman (1996) demonstrated that *C. bairdi* occupied patches with higher prey densities than available patches. These results suggest that sculpins are able to assess the habitat quality of patches in terms of prey availability and select the most profitable areas. Several investigators in different systems found that the highest densities of macroinvertebrates were in riffles as opposed to runs or pools (Schlosser 1987, Vogt & Coon 1990). *Cottus bairdi* and *C. cognatus* may exclude *E. olmstedi* from riffle areas with higher prey densities through competition or predation.

This study did not address nocturnal habitat use by these species. Greenberg (1991) found that *C. bairdi* exhibits some nocturnal activity in the Tennessee River and Greenberg & Holtzman (1987) demonstrated nocturnal feeding and activity of *Cottus carolinae* Gill in the Little River. Considerable evidence exists that in northern lakes, *C. bairdi* is most active nocturnally when foraging using the lateral line system (Hoekstra & Janssen 1985, Janssen et al. 1990). Nevertheless, Freeman & Stouder (1989) observed intraspecific interactions among *C. bairdi* individuals during daytime observations and enclosure experiments in an Appalachian stream. Petty & Grossman (1996) provided evidence that sculpins remain in the same habitat patch during day and night. A lower proportion of sculpins may have been observed under substrate during nocturnal observations. However, analysis of the data for both creeks excluding the position variable yielded concordant results. Adult *Cottus* occupied significantly shallower habitats with faster water velocities than *E. olmstedi* (Nescopeck Creek: F = 43.27; 2, 80 df; p = 0.0001; Jack's Creek: F = 57.82; 2, 61 df; p = 0.0001).

Density of adult sculpins (0.20–0.77 fish m^{-2}) in the present study were similar to that reported by Greenberg & Holtzman (1987) and Brown et al. (1995), but significantly lower than that reported by Daniels

(1987, 1.8–3.3 fish m^{-2}). Nescopeck Creek supported higher densities of these benthic fishes than Jack's Creek. *Etheostoma olmstedi* was twice as abundant in Nescopeck Creek (0.40 fish m^{-2}) as Jack's Creek (0.17 fish m^{-2}), with non-overlapping confidence intervals. Habitat availability may be related to this trend; Nescopeck Creek had a higher mean and larger range of available water velocities than Jack's Creek.

Niche breadth analyses indicated that the three benthic species were habitat specialists for different variables. *Etheostoma olmstedi* was a habitat specialist for deeper waters, whereas *Cottus* adults were specialistic with respect to water velocity measures. Differences in habitat specialization was observed among *E. olmstedi* populations. The range of water velocities preferred by *E. olmstedi* were available in lower proportions in Jack's Creek than Nescopeck Creek. As a result, in Jack's Creek, *E. olmstedi* exhibited specialistic patterns of resource use for depth and water velocity measures, whereas in Nescopeck Creek, specialization was only observed for depth.

Differential habitat use by these benthic fishes is consistent with the hypothesis that resource partitioning facilitates species coexistence. While comparative studies are useful in identifying the relative importance of intraspecific vs. interspecific processes, experimental studies are needed to identify mechanistic processes. Further experimental studies which address whether the observed disjunct distribution of darters and sculpins result from microhabitat preferences, predator avoidance, interspecific competition, or other factors are warranted.

Acknowledgements

References cited

Anderson, C.S. 1985. The structure of sculpin populations along a stream size gradient. Env. Biol. Fish. 13: 93–102.

Baltz, D.M., P.B. Moyle & N.J. Knight. 1982. Competitive interactions between benthic stream fishes, riffle sculpin, *Cottus gulosus*, and speckled dace, *Rhinichthys osculus*. Can. J. Fish. Aquat. Sci. 39: 1502–1511.

Baltz, D.M., B. Vondracek, L.R. Brown & P.B. Moyle. 1987. Influence of temperature on microhabitat choice by fishes in a California stream. Trans. Amer. Fish. Soc. 116: 12–20.

Bovee, K.D. 1986. Development and evaluation of habitat suitability criteria for use in the instream flow incremental methodology. Instream flow information paper no. 21, Biological Report 86: 1–28.

Brandt, S.B. 1986. Ontogenetic shifts in habitat, diet, and diel-feeding periodicity of slimy sculpin in Lake Ontario. Trans. Amer. Fish. Soc. 115: 711–715.

Brown, L.R. 1991. Differences in habitat choice and behavior among three species of sculpin (*Cottus*) in artificial stream channels. Copeia 1991: 810–819.

Brown, L. & J.L. Downhower. 1982. Summer movements of mottled sculpins, *Cottus bairdi* (Pisces: Cottidae). Copeia 1982: 450–453.

Brown, L.R. & P.B. Moyle. 1991. Changes in habitat and microhabitat partitioning within an assemblage of stream fish in response to predation by Sacramento squawfish (*Ptychocheilus grandis*). Can. J. Fish. Aquat. Sci. 48: 849–856.

Brown, L.R., S.A. Matern & P.B. Moyle. 1995. Comparative ecology of prickly sculpin, *Cottus asper*, and coastrange sculpin, *C. aleuticus*, in the Eel River, California. Env. Biol. Fish. 42: 329–343.

Cliff, N. 1988. The eigenvalues-greater-than-one rule and the reliability of components. Psychological Bulletin 103: 276–279.

Colwell, R.K. & D.J. Futuyma. 1971. On the measurement of niche breadth and overlap. Ecology 52: 567–576.

Cunjak, R.A. 1988. Behaviour and the microhabitat of young Atlantic salmon (*Salmo salar*) during winter. Can. J. Fish. Aquat. Sci. 45: 2156–2160.

Daniels, R.A. 1987. Comparative life histories and microhabitat use in three sympatric sculpins (Cottidae: *Cottus*) in northeastern California. Env. Biol. Fish. 19: 93–110.

Day, R.W. & G.P. Quinn. 1989. Comparison of treatments after an analysis of variance in ecology. Ecol. Mon. 59: 433–463.

Diamond, J.M. 1986. Overview: laboratory experiments, field experiments, and natural experiments. pp. 3–22. *In*: J. Diamond & T.J. Case (ed.) Community Ecology, Harper and Row Publishers, New York.

Digby, P.G.N. & R.A. Kempton. 1987. Multivariate analysis of ecological communities. Chapman and Hall, London. 206 pp.

Downhower, J.F. & L. Brown. 1979. Seasonal changes in the social structure of a mottled sculpin (*Cottus bairdi*) population. Anim. Behav. 27: 451–458.

Englert, J. & B.H. Seghers. 1983. Habitat segregation by stream darters (Pisces: Percidae) in the Thames River Watershed of Southwestern Ohio. Can. Field-Natur. 97: 177–180.

Facey, D.E. & G.D. Grossman. 1990. The metabolic cost of maintaining position for four North American stream fishes: effects of season and velocity. Physiological Zoology 63: 757–776.

Fausch, K.D. & R.J. White. 1981. Competition between brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) for positions in a Michigan stream. Can. J. Fish. Aquat. Sci. 38: 1220–1227.

Finger, T.R. 1982. Interactive segregation among three species of sculpins (*Cottus*). Copeia 1982: 680–694.

Freeman, M. C. 1995. Movements by two small fishes in a large stream. Copeia 1995: 361–367.

Freeman, M.C. & D.J. Stouder. 1989. Intraspecific interactions influence size specific depth distribution in *Cottus bairdi*. Env. Biol. Fish. 24: 231–236.

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

Gorman, O.T. 1988a. The dynamics of habitat use in a guild of Ozark minnows. Ecol. Mon. 58: 1–18.

Gorman, O.T. 1988b. An experimental study of habitat use in an assemblage of Ozark minnows. Ecology 69: 1239–1250.

Greenberg, L.A. 1988. Interactive segregation between the stream fishes *Etheostoma simoterum* and *E. rufilineatum*. Oikos 51: 193–202.

Greenberg, L.A. 1991. Habitat use and feeding behavior of thirteen species of benthic stream fishes. Env. Biol. Fish. 31: 389–401.

Greenberg, L.A. & D.A. Holtzman. 1987. Microhabitat utilization, feeding periodicity, home range and population size of the banded sculpin, *Cottus carolinae*. Copeia 1987: 19–25.

Grossman, G.D. & A. de Sostoa. 1994. Microhabitat use by fish in the lower Rio Matarrana, Spain, 1984–1987. Ecology of Freshwater Fish 1994: 123–136.

Guilday, J.E. 1985. The physiographic provinces of Pennsylvania. pp. 19–29. *In:* H.H. Genoways & F.J. Brenner (ed.) Species of Special Concern in Pennsylvania, Special Publication Number 11 of the Carnegie Museum of Natural History, Pittsburgh.

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

Hoekstra, D. & J. Janssen. 1985. Non-visual feeding behavior of the mottled sculpin, *Cottus bairdi*, in Lake Michigan. Env. Biol. Fish. 12: 111–117.

Hurlbert, S.H. 1978. The measurement of niche overlap and some relatives. Ecology 59: 67–77.

Janssen, J., S. Coombs & S. Pride. 1990. Feeding and orientation of mottled sculpin, *Cottus bairdi*, to water jets. Env. Biol. Fish. 29: 43–50.

Johnson, D.W., D.A. Cannamela & K.W. Gasser. 1983. Food habits of the shorthead sculpin (*Cottus confusus*) in the Big Lost River, Idaho. Northw. Sci. 57: 229–239.

Johnson, J.H., D.S. Dropkin & P.G. Shaffer. 1992. Habitat use by a headwater stream fish community in north-central Pennsylvania. Rivers 3: 69–79.

Kessler, R.K. & J.H. Thorp. 1993. Microhabitat segregation of the threatened spotted darter (*Etheostoma maculatum*) and closely related orangefin darter (*E. bellum*). Can. J. Fish. Aquat. Sci. 50: 1084–1091.

Koster, W.J. 1937. The food of sculpins (Cottidae) in central New York. Trans. Amer. Fish. Soc. 1: 374–381.

Matheson, R.E., Jr. & G.R. Brooks, Jr. 1983. Habitat segregation between *Cottus bairdi* and *Cottus girardi*: an example of complex inter- and intraspecific resource partitioning. Amer. Midl. Nat. 110: 165–176.

Novak, J.K. & R.D. Estes. 1974. Summer food habits of the black sculpin, *Cottus baileyi*, in the upper South Fork Holston River drainage. Trans. Amer. Fish. Soc. 2: 270–276.

Petty, J.T. & G.D. Grossman. 1996. Patch selection by mottled sculpin (Pisces: Cottidae) in a southern Appalachian stream. Freshwater Biology 35: 261–276.

Resetarits, W.J., Jr. 1995. Limiting similarity and the intensity of competitive effects on the mottled sculpin, *Cottus bairdi*, in experimental stream communities. Oecologia 104: 31–38.

Rimmer, D.M., U. Paim & R.L. Sanders. 1984. Changes in the selection of microhabitat by juvenile Atlantic salmon (*Salmo salar*) at the summer autumn transition in a small river. Can. J. Fish. Aquat. Sci. 41: 469–475.

Rohde, F.C. & R.G. Arndt . 1981. Life history of a coastal plain population of the mottled sculpin, *Cottus bairdi* (Osteichthys: Cottidae), in Delaware. Brimleyana 7: 69–94.

Schlosser, I.J. 1987. The role of predation in age- and size-related habitat use by stream fishes. Ecology 68: 651–659.

Schlosser, I.J. & L.A. Toth. 1984. Niche relationships and population ecology of rainbow (*Etheostoma caeruluem*) and fantail (*E. flabellare*) darters in a temporally variable environment. Oikos 42: 229–238.

Stauffer, J.R., Jr., J.M. Boltz, K.A. Kellogg & E.S. van Snik. 1996. Microhabitat partitioning in a diverse assemblage of darters in the Allegheny River system. Env. Biol. Fish. 46: 37–44.

Taylor, C.M. 1996. Abundance and distribution within a guild of benthic stream fishes: local processes and regional patterns. Freshwater Biology 36: 385–396.

Vogt, G.F., Jr. & T.G. Coon. 1990. A comparison of the foraging behavior of two darter (*Etheostoma*) species. Copeia 1990: 41–49.

Zippin, C. 1956. An evaluation of the removal method of estimating animal populations. Biometrics 12: 163–169.

Zippin, C. 1958. The removal method of population estimation. J. Widl. Manage. 22: 82–90.