

Microhabitat partitioning in a diverse assemblage of darters in the Allegheny River system

Jay R. Stauffer, Jr.,¹ Jeff M. Boltz,² Karen A. Kellogg¹ & Ellen S. van Snik¹

¹ School of Forest Resources, The Pennsylvania State University, University Park, PA 16802, U.S.A.

² EA Engineering, Science & Technology, 11019 McCormick Road, Hunt Valley, MD 21031, U.S.A.

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Synopsis

Habitat partitioning among eleven species of darters (Percidae: Etheostomatini) from the Allegheny River system was studied through underwater observation. *Percina caprodes* and *Percina copelandi* showed consistent segregation from *Etheostoma* by occupying deeper habitats. Substrate size, depth, and water velocity were important variables by which *Etheostoma* species segregated. Analysis of niche breadth values indicated that species differed widely in their degree of specialization in habitat use; based on the variables measured, *Etheostoma zonale* was a habitat generalist whereas *Etheostoma camurum*, *Etheostoma tippecanoe*, and *Percina caprodes* tended towards habitat specialization. Habitat segregation appears to be an important mechanism allowing the coexistence of these closely related and ecologically similar species. Microhabitat quantification on a fine scale was important in discovering habitat differences in this diverse system.

Introduction

Darters (Percidae: Etheostomatini) are a speciose group, encompassing over 130 species (Kuehne & Barbour 1983) and represent a major vertebrate component of riffle communities. Resource partitioning may be a mechanism by which ecologically similar species coexist (Schoener 1974). Given that darters are members of a benthic invertebrate-feeding guild, competition among darters is expected to be high, and habitat segregation is predicted to be important. The majority of studies examining habitat partitioning among darters have found high degrees of overlap among species, although qualitative (e.g. riffle, run, or pool) or univariate measurement techniques were employed (Englert & Seghers 1983; Hlohowskyj & Wissing 1986, Matthews et al. 1982, Smart & Gee 1979). In addition,

most studies have focused on partitioning in streams with relatively few (2–3) darter species (Hlohowskyj & Wissing 1986, Kessler & Thorp 1993, Schlosser & Toth 1984, Smart & Gee 1979). Quantification of the microhabitat exploited by each species using direct observation is necessary for revealing small-scale habitat differences among many species of darters (Chipps et al. 1994, Greenberg 1991, Leidy 1992). The purpose of this study was to develop a method for accurately quantifying microhabitat use by darters, and to examine microhabitat partitioning by a diverse assemblage of darters, where habitat partitioning is expected to be well-defined. The Allegheny drainage contains a diverse ichthyofauna, composed of sixty-eight species, including fifteen darter species (Lachner et al. 1950, Cooper 1983).

Methods

Four study sites were selected for sampling in the upper Allegheny River system, which was formed through the interplay of four glacial advances and retreats (Flint 1947, Netting 1956). The Allegheny runs for approximately 523 km and drains 29 785 km² of north-central Pennsylvania, southern New York and western Pennsylvania (Schwartz 1965). The first study site (Turtle Point) was located in the headwaters of the Allegheny River in McKean County, Pennsylvania, while the remaining three (Meadville, Venango, and Cochranon) were all located in Crawford County, Pennsylvania, on French Creek, a tributary of the Allegheny River. All of the sites were approximately 10–12 m wide. The length of stream snorkeled varied from 25 m at Turtlepoint, 35–45 m at Venango, and 20–30 m at Meadville and Cochranon. Underwater visibility (clear) and habitat types were similar at all of the sites.

Data were collected over several months in 1988. The sampling dates for each site were as follows: Turtle Point – 25 July 1988; Meadville – 22 June 1988, 25 July 1988; Venango – 11 June 1988, 21 June 1988, 30 September 1988; and Cochranon – 20 June 1988.

Darter observations were made while snorkeling at depths of 0–1 m in defined areas encompassing the three major habitat types: riffle, run, and pool. Roughly 75% of the collection period was spent in the riffles, 20% in runs, and 5% in pools. The investigators began at the bottom of a riffle and made their way slowly upstream, minimizing disturbances. An observation was excluded if the fish was startled by the observer.

Following a darter observation, a numbered flag was secured in the substrate and the fish was identified. Subsequently, water depth (cm) was measured at each darter location and the water velocity (m sec⁻¹) at the substrate level was recorded using a Marsh-McBirney analog flow meter (bulb sensor). Although it is difficult to obtain an accurate reading of the currents affecting darter habitat selection in the interstitial substrate space, water velocity measurements at the substrate plane adequately quantify the flows influencing the majority of the individuals observed in this study. Although most individu-

als were found on the substrate, a significant proportion of the individuals (mainly *Percina* species) were in the water column. Therefore, a second measure of current, average water velocity, was made at 0.6 of the depth (Bovee 1986). Finally, the specific locality of each individual and the immediately surrounding area was assessed for substrate size and heterogeneity. A clear acrylic sheet was marked with a grid of 25.5 cm × 5 cm squares. The center of the grid was aligned with the flag location and each of the 25 squares were examined for the rock size that encompassed at least one-half of the square's area. The rock size was quantified by examining how many of the twenty-five grid squares the rock covered. A total of four size classes were considered: (1) 25 cm² or less; (2) > 25 and ≤ 100 cm²; (3) > 100 and ≤ 225 cm²; and (4) anything > 225 cm². If the grid was positioned such that a rock of a larger size class overlapped only a portion of the grid, it was relocated to allow for the measurement of that rock and was then returned to its original position. The mean substrate size class was calculated and used as a substrate index.

To establish habitat preferences of each species, we collected random samples of habitat availability. The section of stream snorkeled was divided into numbered 2 × 2 m cells. Approximately 20% of the cells were selected randomly, and the four abiotic variables (depth, bottom velocity, average velocity (0.6 of depth), substrate size) were gauged in the center of each plot.

Univariate tests were not expected to give a clear indication of habitat partitioning in a drainage harboring many darter species; therefore, a multivariate approach was deemed necessary to evaluate the snorkeling and habitat availability data. Principal Components Analysis (PCA) (MINITAB 10 for Windows) was used to evaluate the habitat availability data. PCA is the appropriate technique given that a priori grouping by month or site is impossible due to environmental fluctuations. MANOVA and Duncan's Multiple Range Test (SAS 6.07, Proc ANOVA) of the first and second principal component scores were used to evaluate the significance ($p < 0.05$) of clustering by either site or season so that the possibility of pooling data could be objectively examined.

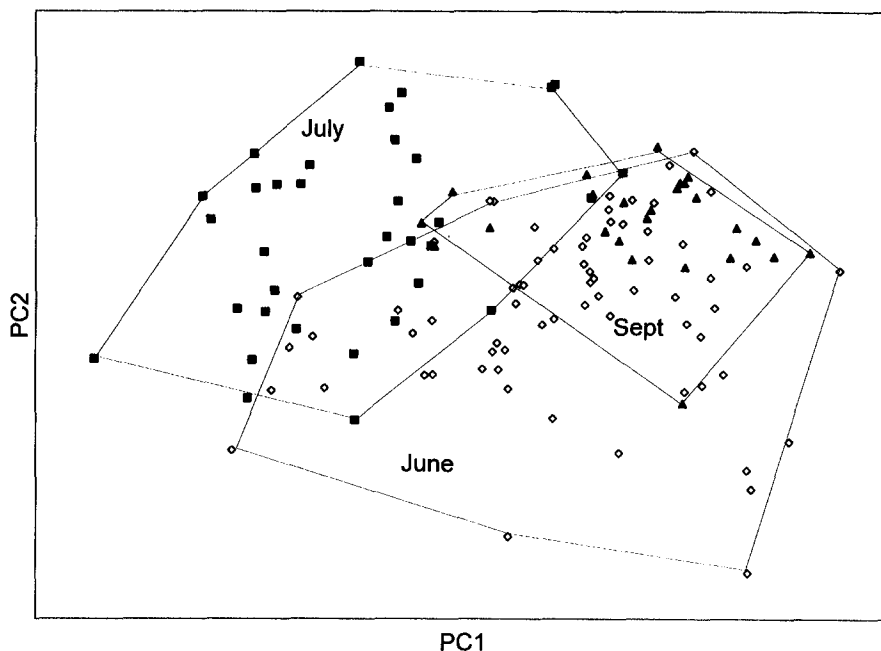


Fig. 1. Principal components plot (PC1 against PC2) of habitat availability by month.

A second statistical technique, Canonical Discriminant Analysis (SAS 6.07, Proc CANDISC), was used to evaluate the clustering of species based on the four microhabitat variables. Again, MANOVA and Duncan's Multiple Range Test (SAS 6.07) of the first and second canonical scores were used to assess the significance ($p < 0.05$) of the clustering. Finally, Hurlbert's standardized niche breadth (1978), which scales resource use according to availability, was calculated for the four abiotic variables so that species could be evaluated on the continuum from generalist to specialist. High niche breadth values are indicative of habitat generalization whereas low niche breadth values are indicative of habitat specialization.

Results

Habitat availability

Evaluation of the plot of the first and second principal components of the habitat availability data indicates that habitat availability during the July sampling periods was significantly different from the

habitat availability during June and September periods ($p < 0.05$, Fig. 1). Unusual amounts of rainfall in late June and early July caused high water conditions in July (a mean difference of 10 cm in depth), which resulted in increased standard deviations in most habitat variables (Table 1). Therefore, in July there was an increase in habitat area and habitat heterogeneity. Although habitat availability in June and September was not significantly different ($p > 0.05$), the data from each month were analyzed separately due to seasonal shifts in darter habitat use, which may be associated with reproductive behavior (Winn 1958, Wynes & Wissing 1982). No significant differences were found among sampling dates within a month or among sites within a month. Therefore all data for a given month were pooled.

Species studied

Habitat use data were collected for a total of eleven darter species: *Etheostoma blennioides* (greenside darter), *Etheostoma caeruleum* (rainbow darter), *Etheostoma camurum* (bluebreast darter), *Etheostoma flabellare* (fantail darter), *Etheostoma macu-*

Table 1. Summary statistics for the four microhabitat variables listed by month. Sample sizes are shown for pooled random (habitat availability) and species data. Variable means are listed on the first line under each category and standard deviations are enclosed in parentheses on the second line.

| | Sample size | Depth (cm) | Bottom velocity (cm sec ⁻¹) | Mean velocity (cm sec ⁻¹) | Mean substrate size class |
|-------------------------------|-------------|------------------|---|---------------------------------------|---------------------------|
| June: | | | | | |
| Random-habitat availability | 68 | 20.49 (5.54) | 26.71 (15.8) | 49.32 (21.41) | 2.25 (1.17) |
| <i>Etheostoma blennioides</i> | 23 | 22.52 (4.21) | 14.87 (11.8) | 40.04 (21.03) | 2.07 (0.55) |
| <i>Etheostoma caeruleum</i> | 41 | 19.46 (3.60) | 12.32 (8.23) | 26.56 (11.50) | 2.08 (0.53) |
| <i>Etheostoma camurum</i> | 7 | 21.42 (3.90) | 21.42 (14.05) | 59.08 (34.19) | 2.02 (0.53) |
| <i>Etheostoma flabellare</i> | 8 | 17.75 (5.01) | 25.25 (17.01) | 40.38 (13.08) | 2.25 (0.21) |
| <i>Etheostoma maculatum</i> | 18 | 20.06 (3.75) | 14.11 (8.87) | 38.00 (17.77) | 2.39 (0.46) |
| <i>Etheostoma tippecanoe</i> | 7 | 20.14 (5.73) | 12.43 (8.85) | 35.14 (14.40) | 2.03 (0.66) |
| <i>Etheostoma variatum</i> | 41 | 20.10 (4.27) | 23.51 (20.37) | 49.20 (27.78) | 2.09 (0.49) |
| <i>Etheostoma zonale</i> | 66 | 20.83 (4.49) | 23.50 (13.16) | 47.95 (23.09) | 1.84 (0.48) |
| <i>Percina caprodes</i> | 14 | 21.33 (1.53) | 36.67 (47.83) | 72.33 (43.84) | 2.17 (0.60) |
| July: | | | | | |
| Random-habitat availability | 35 | 30.71 (9.22) | 35.60 (18.91) | 78.20 (21.55) | 1.39 (0.28) |
| <i>Etheostoma blennioides</i> | 18 | 35.11 (7.46) | 31.17 (17.90) | 62.89 (34.84) | 1.97 (0.60) |
| <i>Etheostoma caeruleum</i> | 15 | 27.07 (4.73) | 29.13 (16.51) | 62.27 (17.53) | 2.07 (0.56) |
| <i>Etheostoma variatum</i> | 13 | 28.50 (9.44) | 40.29 (11.84) | 75.21 (21.67) | 1.61 (0.55) |
| <i>Etheostoma zonale</i> | 17 | 26.30 (10.33) | 36.93 (19.02) | 65.93 (22.61) | 1.56 (0.48) |
| <i>Percina caprodes</i> | 6 | 47.00 (0.00) | 0.00 (0.00) | 4.00 (0.00) | 1.48 (0.00) |
| <i>Percina copelandi</i> | 14 | 41.14 (6.19) | 5.70 (7.58) | 10.79 (10.26) | 1.59 (1.03) |
| September: | | | | | |
| Random-habitat availability | 25 | 20.76 (6.34) | 8.00 (7.37) | 42.36 (22.68) | 1.55 (0.38) |
| <i>Etheostoma blennioides</i> | 19 | 22.63 (4.89) | 5.42 (6.04) | 34.00 (14.96) | 1.65 (0.36) |
| <i>Etheostoma caeruleum</i> | 8 | 21.25 (5.20) | 6.75 (6.30) | 31.00 (8.02) | 1.63 (0.41) |
| <i>Etheostoma flabellare</i> | 7 | 17.71 (7.06) | 7.29 (9.32) | 43.14 (28.87) | 1.35 (0.27) |
| <i>Etheostoma variatum</i> | 18 | 21.78 (4.56) | 9.00 (5.86) | 36.50 (17.24) | 1.80 (0.42) |
| <i>Etheostoma zonale</i> | 19 | 19.21 (3.49) | 6.58 (4.90) | 30.58 (9.11) | 1.72 (0.39) |

latum (spotted darter), *Etheostoma nigrum* (johnny darter), *Etheostoma tippecanoe* (tippecanoe darter), *Etheostoma variatum* (variegated darter), *Etheostoma zonale* (banded darter), *Percina caprodes* (logperch), and *Percina copelandi* (channel darter). Other species found in the Allegheny River system, *Percina evides* (gilt darter), *Percina macrocephala* (longhead darter), *Percina maculata* (blackside darter), and *Etheostoma pellucidum* (eastern sand darter), were not observed while snorkeling.

Young-of-the-year were observed for several species, however small sample sizes prevented analyses, with the exception of *E. zonale*. Young of the year *E. zonale* occupied shallower habitats with higher water velocities than adults. Because there was a significant difference between habitat use of adults and young-of-the-year *E. zonale*, all subsequent analyses included only adults ($p < 0.05$). In addition, adult sample sizes of one or two were excluded from the analysis.

Habitat use

In June, July, and September, the four habitat variables had very similar loading patterns. For both canonical axes, substrate size had the heaviest loading. Depth, bottom water velocity, and velocity at 0.6 depth (in order of importance) were also heavily weighted.

Patterns of habitat partitioning emerged that were consistent across months; although more segregation was observed in July when the habitat was more heterogeneous. The two species of *Percina*, *P. copelandi* and *P. caprodes*, occupied significantly deeper habitats than all *Etheostoma* species in July (Table 2). In June, *P. caprodes* used a microhabitat that was significantly different from that of all but two *Etheostoma* species: *E. camurum* and *E. zonale*. Because the *Percina* species were found to be distinct from the *Etheostoma* species, canonical discriminant analysis was also conducted on the *Etheostoma* species alone. The following results refer to this analysis (Table 2).

Etheostoma blennioides, *E. variatum*, and *E. zonale* had similar patterns of habitat use in June and September, however in July their habitat use was

distinct (Table 2). In July, *Etheostoma zonale* occupied habitats with smaller substrates than *E. blennioides* and slower water velocities than *E. variatum*. *Etheostoma blennioides* used a microhabitat with deeper water than *E. variatum* and *E. zonale*. In June, *Etheostoma caeruleum* occupied microhabitats that were indistinguishable from *E. blennioides*, but with significantly slower water velocities than areas inhabited by *E. variatum* and *E. zonale*. In July, the habitat use of *E. caeruleum* was significantly different from *E. blennioides*, *E. variatum* and *E. zonale*, whereas in September its habitat use was similar to the other three species.

Etheostoma flabellare, which was only observed in June and September, prefers shallower habitats than the other species and is significantly different

Table 2. Species comparisons by month with an 'x' indicating a significant difference between a pair ($p < 0.05$). The upper right portion of each graph displays relationships between pairs when *Percina* species are included in the analyses. The lower left portion represents comparisons when *Percina* species are excluded from the analysis. The shaded diagonal divides the two sets of analyses.

| June | <i>E. blennioides</i> | <i>E. caeruleum</i> | <i>E. camurum</i> | <i>E. flabellare</i> | <i>E. maculatum</i> | <i>E. tippecanoe</i> | <i>E. variatum</i> | <i>E. zonale</i> | <i>P. caprodes</i> |
|-----------------------|-----------------------|---------------------|-------------------|----------------------|---------------------|----------------------|--------------------|------------------|--------------------|
| <i>E. blennioides</i> | | | | | | | | | X |
| <i>E. caeruleum</i> | | | X | | | | | X | X |
| <i>E. camurum</i> | | X | | | X | X | | | |
| <i>E. flabellare</i> | | | | | | | | | X |
| <i>E. maculatum</i> | | X | X | | | | | | X |
| <i>E. tippecanoe</i> | | | X | | | | | | X |
| <i>E. variatum</i> | | X | | | | | | | X |
| <i>E. zonale</i> | | X | | | X | X | | | |

| July | <i>E. blennioides</i> | <i>E. caeruleum</i> | <i>E. variatum</i> | <i>E. zonale</i> | <i>P. caprodes</i> | <i>P. copelandi</i> |
|-----------------------|-----------------------|---------------------|--------------------|------------------|--------------------|---------------------|
| <i>E. blennioides</i> | | X | X | X | X | X |
| <i>E. caeruleum</i> | X | | | | X | X |
| <i>E. variatum</i> | X | X | | | X | X |
| <i>E. zonale</i> | X | X | | | X | X |

| September | <i>E. blennioides</i> | <i>E. caeruleum</i> | <i>E. flabellare</i> | <i>E. variatum</i> | <i>E. zonale</i> |
|-----------------------|-----------------------|---------------------|----------------------|--------------------|------------------|
| <i>E. blennioides</i> | | | X | | |
| <i>E. caeruleum</i> | | | X | | |
| <i>E. flabellare</i> | X | X | | X | X |
| <i>E. variatum</i> | | | X | | |
| <i>E. zonale</i> | | | X | | |

from all other species in September. In June, its habitat use was indistinguishable from the other *Etheostoma* species.

Etheostoma camurum, *E. maculatum* and *E. tippecanoe* were only observed in June. *Etheostoma camurum* occupied a microhabitat with significantly faster water velocities than *E. caeruleum*, *E. maculatum*, and *E. tippecanoe*. *Etheostoma maculatum* used a microhabitat with significantly larger substrate than *E. caeruleum*, *E. camurum* and *E. zonale*. The habitat used by *E. tippecanoe* had significantly slower water velocities than *E. camurum* and *E. zonale*.

Niche breadth

Percina caprodes and *P. copelandi* tended to have low niche breadth values (Table 3) for all variables except substrate size, indicating that they are specific to particular microhabitats. Some of the species such as *E. zonale* appear to be habitat generalists,

having high niche breadth values for most variables. *Etheostoma camurum* and *E. tippecanoe* tend towards specialization, having low niche breadth values for most variables.

Discussion

Through analysis of darter microhabitats, differences are revealed in habitat use among species, in contrast to other studies that used qualitative (e.g. riffle, run or pool) or univariate techniques, and found high overlap in the habitat use of darter species (Englert & Seghers 1983, Hlohowskyj & Wissing 1986, Matthews et al. 1982, Smart & Gee 1979). Quantifying habitat characteristics at the level perceived by the organism is necessary to study the factors that affect niche partitioning. Microhabitat segregation was found to be critically important in darter niche divergence, based on the four quantitative habitat variables measured in this study. Although all four variables were important in the observed

Table 3. Hulbert's standardized niche breadth for the four microhabitat variables by month.

| | Depth (cm) size class | Bottom velocity (cm sec ⁻¹) | Mean velocity (cm sec ⁻¹) | Mean substrate |
|-------------------------------|--------------------------|--|--|----------------|
| June | | | | |
| <i>Etheostoma blennioides</i> | 0.6280 | 0.4084 | 0.6367 | 0.5895 |
| <i>Etheostoma caeruleum</i> | 0.8564 | 0.3012 | 0.3689 | 0.4041 |
| <i>Etheostoma camurum</i> | 0.5467 | 0.2914 | 0.4667 | 0.3441 |
| <i>Etheostoma flabellare</i> | 0.6760 | 0.5952 | 0.7010 | 0.4609 |
| <i>Etheostoma maculatum</i> | 0.8115 | 0.3626 | 0.5486 | 0.2283 |
| <i>Etheostoma tippecanoe</i> | 0.7091 | 0.1986 | 0.4633 | 0.3669 |
| <i>Etheostoma variatum</i> | 0.9169 | 0.6380 | 0.6852 | 0.5239 |
| <i>Etheostoma zonale</i> | 0.8655 | 0.8149 | 0.7531 | 0.6475 |
| <i>Percina caprodes</i> | 0.3175 | 0.0925 | 0.1486 | 0.2079 |
| July | | | | |
| <i>Etheostoma blennioides</i> | 0.7335 | 0.8033 | 0.2893 | 0.1283 |
| <i>Etheostoma caeruleum</i> | 0.4468 | 0.6361 | 0.2494 | 0.0736 |
| <i>Etheostoma variatum</i> | 0.3367 | 0.4464 | 0.3634 | 0.4012 |
| <i>Etheostoma zonale</i> | 0.6933 | 0.8575 | 0.3013 | 0.2567 |
| <i>Percina caprodes</i> | 0.1177 | 0.0882 | 0.0000 | 0.7879 |
| <i>Percina copelandi</i> | 0.2413 | 0.1778 | 0.0000 | 0.7707 |
| September | | | | |
| <i>Etheostoma blennioides</i> | 0.8228 | 0.9367 | 0.8049 | 0.8743 |
| <i>Etheostoma caeruleum</i> | 0.6402 | 0.7485 | 0.6402 | 0.8913 |
| <i>Etheostoma flabellare</i> | 0.7304 | 0.7180 | 0.2393 | 0.8000 |
| <i>Etheostoma variatum</i> | 0.7121 | 0.9869 | 0.5926 | 0.6558 |
| <i>Etheostoma zonale</i> | 0.6776 | 0.9367 | 0.6826 | 0.7908 |

segregation, each species differed in their degree of specialization with respect to each variable. For example, *Percina caprodes*, which was frequently found in the water column, was a specialist for all of the habitat variables except substrate size, indicating that substrate is not an important component of its microhabitat.

Seasonal trends in habitat usage were observed that were consistent with environmental fluctuations. In July, when the habitat heterogeneity was high due to increased water levels, greater habitat separation was observed among the species. Hurlbert's (1978) standardized niche breadth values supported this relationship; a trend toward niche breadth compression indicative of increased specialization was realized in July when habitat availability increased. Seasonal habitat shifts may also be associated with reproduction (Winn 1958).

The microhabitat quantification method using direct observation was successful in observing habitat segregation in this diverse assemblage of fishes. Possible refinements of this technique for further studies include incorporating additional variables such as the presence of macrophytes, the orientation of the fish to the substrate (i.e. over, under, or between rocks), and the vertical distance from the fish to the substrate. In addition, increased sampling in run and pool habitats would inevitably result in greater separation among the species. Analysis of trophic axes as well as further microhabitat quantification may reveal additional differences among the species.

Microhabitat quantification at a level meaningful to the organism is the first step in understanding the coexistence of closely-related taxa, especially in diverse communities where habitat partitioning is critical. Refinement of this technique will allow for an in-depth look at the mechanisms allowing the coexistence of so many ecologically similar species in a diverse system such as found in the Allegheny River drainage.

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