

Habitat Shift of a Native Darter *Etheostoma olmstedi* (Teleostei: Percidae) in Sympatry with a Non-native Darter *Etheostoma zonale*

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ABSTRACT.—*Etheostoma zonale*, the banded darter, was introduced to the Susquehanna River basin of Pennsylvania through an interbasin transfer, or transplantation of native fishes outside their natural range. We examined the habitat use of a darter native to the Susquehanna River drainage *E. olmstedi*, the tessellated darter, in sympatry and allopatry with *E. zonale* to determine if its habitat use was different. In the presence of *E. zonale*, *E. olmstedi* occupied significantly ($P < 0.05$) shallower habitats (mean depth < 27 cm) with smaller substrates (mean substrate index < 32) and slower water velocities (mean water velocity < 0.13 m s⁻¹) than in sites without *E. zonale*. The habitat shift of *E. olmstedi* was accompanied by a compression of niche breadth. The results are consistent with the hypothesis that *E. zonale* excludes *E. olmstedi* from riffle and run habitats, restricting *E. olmstedi* to shallow pools and stream margins.

INTRODUCTION

The introduction of non-native fishes has become a global problem (Zaret and Paine, 1973; Courtenay and Stauffer, 1990; Lassuy, 1995; Rahel, 2000). In North America, at least 70 fishes of foreign origin (exotic) have become established in fresh and marine waters (Courtenay *et al.*, 1986; Courtenay, 1995; Courtenay and Moyle, 1996). Most non-native fishes in the United States (150 species), however, are the result of interbasin rather than intercontinental transfers (Courtenay *et al.*, 1986). Interbasin transfers include fishes that have been intentionally or unintentionally transplanted beyond their native range in North America (Moyle *et al.*, 1986; Ross, 1991; Courtenay and Moyle, 1996) and are homogenizing fish faunas in the United States (Rahel, 2000). Although interbasin transfers are much more common than the introduction of exotic species, they are studied less frequently (Ross, 1991). Ecological effects of non-native fishes on native species and communities include habitat alteration (vegetation removal, changes in water quality, Mitchell, 1986), introduction of parasites and diseases (Moyle *et al.*, 1986), trophic alterations (competition for food, predation, Meffe, 1985; Hindar *et al.*, 1988; Townsend and Crowl, 1991; Moyle *et al.*, 2003), hybridization (Hocutt and Hambrick, 1973; Raesly *et al.*, 1990; Leary *et al.*, 1995), spatial alterations (competition for space, Moore *et al.*, 1983; Gatz *et al.*, 1987; Peterson and Fausch, 2003) and extirpation of native species (Schoenherr, 1981; Taylor *et al.*, 1984; Lemly, 1985). Ross (1991) found that the majority of studies (77%) examining effects of non-native species documented a decline of native fishes following the introduction of exotic or transplanted species. In the few cases in which a fish introduction has thought to have no effect, small localized populations or habitats heavily influenced by stochastic events were involved (Moyle *et al.*, 1986; Courtenay and Moyle, 1996; Brown and Moyle, 1997).

Kneib (1972) first collected *Etheostoma zonale*, the banded darter, from the Susquehanna

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River drainage in Little Pine Creek, a tributary to Pine Creek, Lycoming County, Pennsylvania, in 1971. Its presence in the Atlantic slope was attributed to a bait-bucket introduction from an Allegheny River drainage population that probably occurred in the late 1960s. In 1972, *E. zonale* was collected more than 400 km downstream from Little Pine Creek (Denoncourt *et al.*, 1975), perhaps aided by the record flood of Hurricane Agnes in 1972. It is currently the most abundant darter in many localities throughout the Susquehanna River drainage (Raesly, 1991) and has hybridized with *E. olmstedii*, the tessellated darter (Raesly *et al.*, 1990).

We compared the habitat use by *Etheostoma olmstedii* in sympatry and allopatry with the non-native *E. zonale* to determine if a habitat shift has occurred. We examined microhabitat (on scales of centimeters or smaller, Harding *et al.*, 1998) use because most darters are habitat specialists (White and Aspinwall, 1984; Stauffer *et al.*, 1996) that show few dietary differences (Martin, 1984; Schlosser and Toth, 1984; Gray *et al.*, 1997). Habitat shifts are among the most common immediate effects of introductions of fishes (Werner, 1984). Measuring overlap in spatial resources does not demonstrate the existence of interspecific competition (Colwell and Futuyma, 1971). Nevertheless, a niche shift, a change or reduction of the realized niche (Hutchinson, 1957) of one species when in sympatry with another (Schoener, 1974; Gatz *et al.*, 1987; Greenberg, 1988; Taylor, 1996), may identify the importance of intraspecific vs. interspecific interactions and provide insight into the effects of a non-native species on resource use of native species.

METHODS

Study sites.—Four sites within the Susquehanna River basin were selected for sampling based on darter distributions. Nescopeck Creek, a third order stream located in Luzerne County, Pennsylvania, and two sites on Jack's Creek (1 and 2), a fourth order stream located in Mifflin County, Pennsylvania, did not contain *Etheostoma zonale*. In Sugar Creek, a third order stream in Bradford County, Pennsylvania, both *E. olmstedii* and *E. zonale* occurred. In Jack's Creek (1 and 2) and Sugar Creek, *Percina peltata*, the shield darter, was also present but at very low densities. Jack's Creek 2 was sampled in July 1994. During June to September of 1994 and 1995, Nescopeck Creek was sampled seven times, Jack's Creek 1 was sampled six times and Sugar Creek was sampled five times.

Data collection.—Each site contained a 40-m long riffle, run and pool sequence that was snorkeled. Typically two investigators each spent 2 h snorkeling during each visit. We restricted our observations to times of good visibility. We began at the downstream end of the site and moved slowly upstream so that fishes were not disturbed. An observation was excluded if the fish was startled by the observer. Loose rocks were turned over as snorkeling proceeded so that observations were not biased against hidden fishes. Water temperature ranged from 15 C–26 C during the study period. The study streams were 15–20 m wide at each site.

Following a darter observation, a numbered flag was secured in the stream bed at the specific location of the fish and the following variables were recorded: flag number, species, age group (adult or young of the year, yoy, visually estimated), orientation to the current (1 = snout facing upstream, 2 = snout facing the right or left bank and 3 = snout facing downstream; subsequently referred to as direction), the type of vegetation present, if any, and orientation to the substrate (subsequently referred to as position). Each fish was classified into one of four categories for the position variable: under substrate, on the top surface of substrate (subsequently referred to as above), between substrate or 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 s^{-1}), water velocity at 0.6 depth or mean water velocity (m s^{-1} , Bovee, 1986) and substrate size. Water velocity was recorded 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 each of the 25 squares was examined for rocks that encompassed at least one half of the square's area. The rock size category (R) was quantified by determining how many squares each rock covered. The rock size category could range from one square to 25 squares, representing 5×5 cm rock to 25×25 cm rock. A substrate index (I) was determined by the sum of the number of rocks (n) observed in each size category multiplied by the category squared: $I = \sum nR^2$. The index ranges from 25–625 and increases as substrate size increases. For example, if there was one 25×25 cm rock under the grid, it would occupy 25 squares and the substrate index (I) would be $1 \times 25^2 = 625$ ($n = 1$, $R = 25$). If all the substrate under the grid was smaller than 5×5 cm, the substrate index (I) would be $25 \times 1^2 = 25$ ($n = 25$, $R = 1$).

Habitat availability.—Systematic transect sampling was conducted to quantify habitat availability at each site. Six equally spaced transects were made across the stream throughout each study site on each sampling date. Five equidistant points across each transect were sampled for the four abiotic variables: depth, bottom water velocity, mean water velocity and substrate size. The type of vegetation, if present, was also noted.

Statistical analysis.—Because habitat use of stream fishes changes with abiotic fluctuations such as depth and flow (Kessler *et al.*, 1995; Stauffer *et al.*, 1996), we used multivariate analysis of variance (MANOVA, SAS 6.12, Proc GLM) of the continuous habitat availability variables (depth, bottom water velocity, mean water velocity and substrate index) to determine whether collections had similar habitat availability and could be pooled. For all statistical tests we used Levene's test to determine if transformation of variables was necessary (SAS Institute Inc., 1996). Univariate analysis of variance (ANOVA, SAS 6.12, Proc GLM) and the Tukey-Kramer multiple comparison method (Day and Quinn, 1989) tested for differences among collections for each microhabitat variable. Collections with no significant differences in abiotic variables were pooled for subsequent analyses so that darter habitat use could be examined independent of the habitat parameters that we measured. Alpha values were less than or equal to 0.05 for all statistical tests.

MANOVA of the continuous dependent microhabitat variables (depth, bottom water velocity, mean water velocity and substrate index) was used to test whether *Etheostoma olmstedi* shifted its habitat use in the presence of *E. zonale*. Univariate analysis of variance (ANOVA, SAS 6.12, Proc GLM) and the Tukey-Kramer multiple comparison method (Day and Quinn, 1989) tested species differences for each microhabitat variable. The habitat use of *E. olmstedi* was examined across sites in sympatry and allopatry with *E. zonale* to test for habitat shifts. Chi-square tests of homogeneity were used to determine whether use of position and direction categories differed among species. Young-of-the-year and adult fish were treated separately due to potential ecological differences (Polis, 1984).

Niche breadth.—Levins' (1968) measure of niche breadth was calculated for each species. Niche breadth indicates where species fall on the continuum from generalist to specialist in resource use. The index is calculated by the following formula (Levins, 1968): $B = 1 / (\sum p_j^2)^{-1}$, where B = Levins' niche breadth measure and p_j = the proportion of individuals found in resource state j . The index is standardized to a scale of 0–1.0 by the following formula (Hurlbert, 1978): $B_A = (B - 1) [(n - 1)]^{-1}$, where B_A = Levins' standardized niche breadth, B = Levins' niche breadth measure and n = the number of possible resource states. Levins' standardized niche breadth (Hurlbert, 1978) values approaching one indicate habitat generalization and values approaching zero indicate habitat specialization. Although no

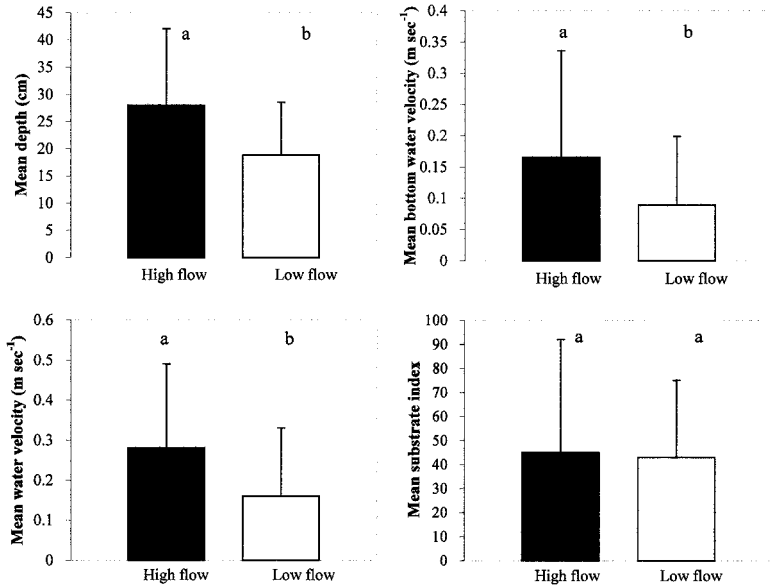


FIG. 1.—Mean depth, bottom and mean water velocity and substrate index plus one standard deviation of the habitat availability of the high and low flow data sets. Different letters indicate significant differences

statistics have been developed to determine significance for this index, we considered values greater than 0.66 to indicate habitat generalization and values less than 0.33 to indicate habitat specialization. We hypothesized that if interspecific interactions between *Etheostoma zonale* and *E. olmstedii* are stronger than intraspecific interactions among *E. olmstedii*, a compression of its niche width will be observed in the presence of *E. zonale*. We calculated percent change in niche width by the following formula: percent change = $[(\text{mean niche width of sympatric sites}) - (\text{mean niche width of allopatric sites}) \times (\text{mean niche width of allopatric sites})^{-1}] \times 100$.

RESULTS

Habitat availability.—Habitat availability differed among collections ($F = 2.98$; 68, 2070 df; $P = 0.0001$). Univariate ANOVAs showed that collections differed in depth ($F = 4.82$; 17, 522 df; $P = 0.0001$), bottom water velocity ($F = 3.28$; 17, 522 df; $P = 0.0001$) and mean water velocity ($F = 4.84$; 17, 522 df; $P = 0.0001$) distributions, but did not differ in substrate size ($F = 1.64$; 17, 522 df; $P = 0.0507$). Collections with no significant differences in habitat availability were pooled, resulting in two data sets. The first data set included two Nescopeck Creek collections and two Sugar Creek collections, whereas the second data set included four Nescopeck Creek collections, four Jack's Creek collections and three Sugar Creek collections. Average depths, bottom and mean water velocities were greater in the first data set (mean depth = 28.0 cm, mean bottom and mean water velocity = 0.17, 0.28 m s⁻¹) than the second (mean depth = 18.8 cm, mean bottom and mean water velocity = 0.09, 0.16 m s⁻¹). Therefore, the two data sets are subsequently referred to as high flow and low flow, respectively (Fig. 1). The darter habitat use data were pooled for each stream within a data set and analyzed separately to remove effects of habitat availability.

TABLE 1.—Mean and standard deviation (in parentheses) of depth, bottom and mean water velocity and substrate size used by *Etheostoma olmstedi* in sympatry and allopatry with *E. zonale* for each data set. For position, direction and vegetation, modes and percent of individuals at the mode is given. For direction, the categories are: 1 = snout facing upstream, 2 = snout facing the right or left bank, and 3 = snout facing downstream. Sample sizes of each group are given underneath the species name

| Site Data set | Species | Position | Direction | Vegetation | Depth cm | Bottom velocity m s ⁻¹ | Mean velocity m s ⁻¹ | Substrate index |
|--|------------------------|----------|-----------|---------------|-------------|---|---------------------------------------|--------------------|
| Sympatry/Allopatry with <i>E. zonale</i> | | | | | | | | |
| High flow | | | | | | | | |
| Allopatry | <i>E. olmstedi</i> | above | 1 | no vegetation | 38.3 | 0.09 | 0.22 | 38.30 |
| | 56 | 82% | 55% | 100% | (10.2) | (0.09) | (0.17) | (16.5) |
| Sympatry | <i>E. olmstedi</i> | above | 1 | no vegetation | 26.4 | 0.06 | 0.10 | 31.70 |
| | 46 | 59% | 59% | 76% | (6.0) | (0.08) | (0.11) | (25.8) |
| Low flow | | | | | | | | |
| Allopatry | <i>E. olmstedi</i> | above | 1 | no vegetation | 30.0 | 0.07 | 0.18 | 55.70 |
| | 181 | 76% | 43% | 100% | (7.5) | (0.08) | (0.14) | (65.8) |
| | <i>E. olmstedi</i> yoy | above | 1 | no vegetation | 22.8 | 0.02 | 0.05 | 49.40 |
| | 39 | 87% | 44% | 100% | (7.6) | (0.03) | (0.06) | (29.5) |
| Sympatry | <i>E. olmstedi</i> | above | 1 | no vegetation | 22.8 | 0.06 | 0.12 | 30.50 |
| | 59 | 81% | 54% | 80% | (6.5) | (0.10) | (0.15) | (12.5) |
| | <i>E. olmstedi</i> yoy | above | 1 | no vegetation | 22.6 | 0.08 | 0.15 | 33.30 |
| | 20 | 100% | 70% | 100% | (4.3) | (0.07) | (0.11) | (11.5) |

Sympatry and allopatry with Etheostoma zonale.—*Etheostoma olmstedi* shifted its habitat in the presence of *E. zonale*. In the high flow data set, *E. olmstedi* populations in sympatry and allopatry with *E. zonale* differed in depth ($F = 42.48$; 1, 100 df; $P = 0.0001$) and mean water velocity distribution ($F = 12.46$; 1, 100 df; $P = 0.0006$; Table 1; Fig. 2). When *E. zonale* was absent, *E. olmstedi* occurred in significantly deeper faster microhabitats than in the presence of *E. zonale* ($P < 0.05$, Fig. 2, Table 1). Allopatric and sympatric *E. olmstedi* differed in distribution among position ($P < 0.05$), but not direction ($P > 0.05$) categories (Table 1). In the presence of *E. zonale*, *E. olmstedi* occurred significantly less frequently between substrate and more frequently under substrate than without *E. zonale* (Table 1). Comparisons of use of vegetation could not be made because vegetation was observed only in Sugar Creek.

In the low flow data set, adult and yoy *Etheostoma olmstedi* sympatric and allopatric with *E. zonale* differed in distribution of all four continuous habitat variables (depth – $F = 24.33$; 3, 295 df; $P = 0.0001$; bottom water velocity – $F = 5.30$; 3, 295 df; $P = 0.0014$; mean water velocity – $F = 4.51$; 3, 295 df; $P = 0.0041$; substrate size – $F = 3.94$; 3, 295 df; $P = 0.0088$; Fig. 2; Table 1). In the absence of *E. zonale*, adult *E. olmstedi* were associated with significantly deeper, fast-moving habitats with larger substrates than in the presence of *E. zonale* ($P < 0.05$, Fig. 2). *Etheostoma olmstedi* yoy populations were associated with shallow slow-moving waters. However, *E. olmstedi* yoy with *E. zonale* occurred in significantly faster bottom and mean water velocities than when without *E. zonale* ($P < 0.05$, Table 1; mean bottom water velocity = 0.08, 0.02 m s⁻¹; mean water velocity = 0.05, 0.15 m s⁻¹, respectively). There were no significant differences among *E. olmstedi* populations in position with respect to the substrate or direction with respect to the current ($P > 0.05$, Table 1).

Niche breadth.—*Etheostoma olmstedi* had a compressed niche in the presence of *E. zonale* (Table 2). Adult and yoy *E. olmstedi* were habitat specialists for all variables in Sugar Creek. In

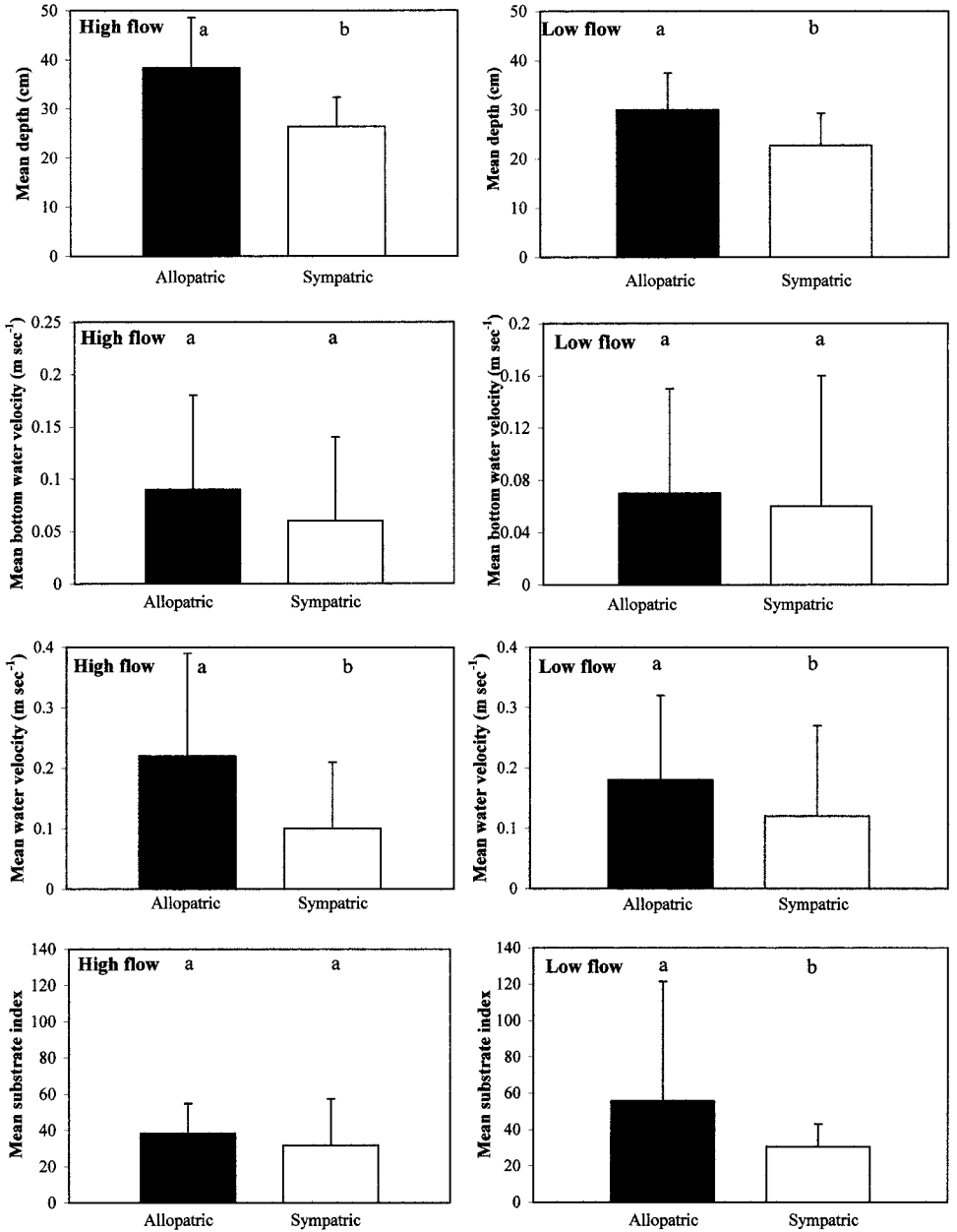


FIG. 2.—Mean depth, bottom and mean water velocity and—substrate index plus one standard deviation of *Etheostoma olmstedi* populations in sympatry and allopatry with the non-native *E. zonale*, illustrating the shift of *E. olmstedi* from preferred riffle habitats to pools in the presence of *E. zonale*. Different letters indicate significant differences

TABLE 2.—Levins' standardized niche breadth measures of depth, bottom and mean water velocity and substrate index for *Etheostoma olmstedi* in sympatry and allopatry with *E. zonale*. The percent decrease in niche width from populations in sympatry to populations in allopatry with *E. zonale* are given

| Data set Species | Sugar Creek – sympatry | | | | Jack's Creek – allopatry | | | | Nescopeck Creek – allopatry | | | |
|------------------------|------------------------|--------------------|------------------|-----------------|--------------------------|--------------------|------------------|-----------------|-----------------------------|--------------------|------------------|-----------------|
| | Depth | Bottom velocity | Mean velocity | Subst. index | Depth | Bottom velocity | Mean velocity | Subst. index | Depth | Bottom velocity | Mean velocity | Subst. index |
| High flow | | | | | | | | | | | | |
| <i>E. olmstedi</i> | 0.342 | 0.115 | 0.192 | 0.023 | | | | | 0.633 | 0.198 | 0.553 | 0.081 |
| Percent decrease | -46% | -42% | -65% | -72% | | | | | | | | |
| Low flow | | | | | | | | | | | | |
| <i>E. olmstedi</i> yoy | 0.245 | 0.026 | 0.118 | 0.026 | 0.269 | 0.000 | 0.000 | 0.348 | 0.114 | 0.000 | 0.000 | 0.000 |
| <i>E. olmstedi</i> | 0.373 | 0.081 | 0.092 | 0.018 | 0.363 | 0.079 | 0.177 | 0.404 | 0.410 | 0.132 | 0.213 | 0.058 |
| Percent decrease | -3% | -23% | -53% | -92% | | | | | | | | |

sites allopatric with *E. zonale*, however, adult *E. olmstedi* were more generalized in resource use (Table 2). A reduction of the realized niche of *E. olmstedi* when in sympatry with *E. zonale* was observed. A substantial compression of niche width for all variables was observed from *E. olmstedi* populations in Nescopeck and Jack's creeks compared to Sugar Creek populations in high and low flows. The percent reduction in niche width varied from 42–72% in high flow and 3–92% in low flow conditions (Table 2). The greatest differences were seen in substrate size and mean water velocity distribution (Table 2). No niche width changes were observed for *E. olmstedi* yoy in the sympatry and allopatry with *E. zonale*.

DISCUSSION

Herbold and Moyle (1986) and Moyle and Light (1996) observed that many successful introductions have occurred in disturbed habitats and that introduced fishes usually displace native species. Habitat shifts of native species are one of the most likely immediate effects of introduction events (Werner, 1984). We demonstrated a habitat shift of *Etheostoma olmstedi* in sympatry with the non-native *E. zonale*. In the presence of *E. zonale*, *E. olmstedi* occupied shallower habitats with slower water velocities and smaller substrates compared to sites without *E. zonale*. *Etheostoma olmstedi* were, therefore, restricted to shallow pool and stream margins in sympatric sites, whereas in allopatry, *E. olmstedi* occupied more diverse habitats including riffles and runs. This shift in habitat use from allopatry to sympatry was accompanied by a compression of the realized niche.

This study was based on data from a limited number of sites. Studies of habitat shifts and resource use by fishes are often hampered by the ability to find a large number of sites characterized by particular combinations of species for comparisons. Previous studies of darter, trout, cyprinid and cisco habitat shifts were based upon a total of 3–6 sites, with 1–3 of the sites having the species of interest sympatric (Gatz *et al.*, 1987; Greenberg, 1988; Hindar *et al.*, 1988; Douglas *et al.*, 1994). We demonstrated a habitat shift between two darter species with a total of four sites, with one of the sites including the both species. There are problems with a lack of replication in sympatric sites. Nevertheless, Gray and Stauffer (2001) examined substrate choice and behavioral interactions among three species in an artificial stream and observed the same habitat shift. The presence of *Etheostoma zonale* induced a shift of *E. olmstedi* from preferred large substrate to small substrate. In addition, *E. zonale*

was most frequently the aggressor in behavioral interactions. *Etheostoma olmstedi* did not direct any agonistic behavior toward *E. zonale*, however 20% of aggressive acts initiated by *E. zonale* were directed towards *E. olmstedi* (Gray and Stauffer, 2001). Interference competition for space is therefore suggested as the mechanism of the habitat shift, although controlled experiments are required to test this hypothesis. Differences in fish habitat use can not be explained by differences in stream characteristics because no significant differences in measured abiotic conditions were found within each data set.

The habitat shift by *Etheostoma olmstedi* may result in population decline or local extirpation of populations in the presence of *E. zonale*. Restriction of *E. olmstedi* to shallow pools and stream margins may result in a reduced food base (Schlosser, 1987; Vogt and Coon, 1990) or increased susceptibility to predation (Greenberg, 1994; Brown and Brasher, 1995; Greenberg *et al.*, 1997). In addition, observations of *E. olmstedi* nest sites have shown that in the presence of *E. zonale*, nests occur in deeper slower habitats than in allopatric populations (Gray, pers. obs.). It is unknown whether reproductive success of *E. olmstedi* is reduced in low velocity habitats. Nevertheless, niche shifts may not lead to extirpation; several trophic studies have shown species to modify their feeding regime in response to an introduced competitor (Crowder, 1984; Crowder and Crawford, 1984; Magnan and Fitzgerald, 1984).

Characteristics often associated with successfully invading species include abundance in its natural range, polyphagy, high reproductive rate, short generation time, long-range dispersal ability, phenotypic plasticity, genetic variability and ability to function in a wide range of physical conditions (Ehrlich, 1984; Taylor *et al.*, 1984; Townsend, 1991). *Etheostoma zonale* has most of these characteristics including abundance in its natural range, polyphagy, short generation time and generalization in habitat use as compared to other darter species (Stauffer *et al.*, 1996). In addition, *E. zonale* was more fecund than seven of eight *Etheostoma* species in tributaries of the Allegheny River, Pennsylvania (Kellogg *et al.*, 1997). It is unknown whether *E. zonale* is genetically more variable or is more phenotypically plastic than other darter species. Pimm (1987) stated that the greatest effect of introduced species are observed when the invading species is a generalist, and the greatest negative effect should be observed on resident species that are specialists. Our results agree with this assertion; *E. zonale* is a habitat generalist for most variables, whereas *E. olmstedi* is a habitat specialist. In addition, the Susquehanna River basin is species poor as compared to the Allegheny River drainage, and several investigators have observed that depauperate drainages may be more vulnerable to invasion by non-native species (Hocutt and Hambrick, 1973; Moyle, 1984; Courtenay, 1995).

Despite the abundance of studies that have demonstrated competition, predation or hybridization among native and introduced fish species (Meffe *et al.*, 1983; Lemly, 1985; Leary *et al.*, 1993), a theory of invasion ecology has yet to be developed and our ability to predict effects of introduced species is weak (Fausch, 1988; Townsend, 1991). Pimm (1987) and Li and Moyle (1981) have suggested approaches to predict community changes with regard to food webs. However, refinement of these models and additional work in this area is required for other potentially limiting resources, such as habitat. Although it is difficult to determine the cause of many introductions, at least seven species have been successfully introduced through bait-bucket introductions in California alone (Moyle, 1976) and Courtenay (1995) reported that approximately 75% of interbasin transfers in North America are related to recreational fishing. Potential policy changes to minimize interbasin transfers include education of anglers to either destroy unused baitfish or to use species that are native to the drainage. These measures may be worth the cost of implementation because it is impossible to predict the ecological effects of fish introductions and once

a species becomes established, it is essentially impossible to control or eradicate (Hubbs and Brodrick, 1963; Moore *et al.*, 1983; Simberloff and Stiling, 1996).

Acknowledgments.—We thank M. Arnegard, P. Danley, M. Gutowski, P. Koltz, D. LaMarie, D. Parise, H. Posner, I. Posner, R. Ruffing, C. Snyder, B. Stauffer, D. Stauffer, K. Walter and Z. Whisel for field assistance. This project was funded by the National Biological Survey RWO42.

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SUBMITTED 16 MARCH 2004

ACCEPTED 2 AUGUST 2004