

Substrate Choice by Three Species of Darters (Teleostei: Percidae) in an Artificial Stream: Effects of a Nonnative Species

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Etheostoma zonale, the banded darter, was introduced to the Susquehanna River basin, Pennsylvania, through an interbasin transfer. We examined the effects of darter density and the presence of *E. zonale* on the substrate choice of two native darter species (*Etheostoma olmstedi*, the tessellated darter, and *Percina peltata*, the shield darter) in an artificial stream. In single species trials, *E. olmstedi*, *E. zonale*, and *P. peltata* exhibited nonrandom substrate selection and occupied patches of large substrate significantly ($P < 0.05$) more often than expected. No intraspecific density effects were observed. The presence of *E. zonale* did not affect the substrate choice of *P. peltata* but did induce a shift of *E. olmstedi* from large to small substrate in high-density trials ($P < 0.05$). *Etheostoma zonale* was most frequently the aggressor in behavioral interactions. Neither *E. olmstedi* nor *P. peltata* directed any agonistic behavior toward *E. zonale*; however 40% of aggressive acts initiated by *E. zonale* were directed toward *E. olmstedi* and *P. peltata*. Displacement of *E. olmstedi* by the aggressor *E. zonale* suggests potential deleterious effects on the native species.

THE introduction, establishment, and proliferation of nonnative fishes has become one of the primary factors contributing to the endangerment of native fishes, secondary only to habitat alteration (Taylor et al., 1984; Miller et al., 1989; Lassuy, 1995). In North America, 70 fish species of foreign origin (exotic) have become established (Courtenay et al., 1986; Courtenay, 1995; Courtenay and Moyle, 1996). Most nonnative fishes in the United States (150 species), however, are the result of interbasin rather than intercontinental transfers (Courtenay and Moyle, 1996). 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). Although many studies have focused on impacts of exotic fish on native fauna, comparatively few studies have examined effects of interbasin transfers on native fishes despite their numerical dominance (Ross, 1991). Nonnative fishes introduced by interbasin transfers have affected native fishes through hybridization (Hocutt and Hambrick, 1973), predation (Lemly, 1985), displacement from preferred habitats (Brown and Moyle, 1991; Douglas et al., 1994), and suppression of population size or biomass (Moore et al., 1983; Lemly, 1985; Nakano et al., 1998).

Etheostoma zonale, the banded darter, was most likely introduced to the Susquehanna River basin in the 1960s via a bait-bucket introduction from an Allegheny River drainage population (Kneib, 1972; Gray, 1998) and is currently the most abundant darter in many localities

throughout the Susquehanna River basin (Raesly, 1991). *Etheostoma zonale* has hybridized with a native darter species, *Etheostoma olmstedi*, the tessellated darter, in the Susquehanna River basin (Raesly et al., 1990). In a companion study, Gray (1998) compared the habitat use of *E. olmstedi* in sympatry and allopatry with the nonnative *E. zonale*. *Etheostoma olmstedi* exhibited a habitat shift when sympatric with *E. zonale*; *E. olmstedi* was found in shallower, slower velocity habitats with smaller substrates in sites sympatric with *E. zonale* compared to sites in which *E. zonale* was absent (Gray, 1998). Thus, it appeared that *E. zonale* excluded *E. olmstedi* from preferred riffle and run habitats in sympatry, restricting *E. olmstedi* to pool and stream margin habitats.

The purpose of this study was to examine the substrate choice of *E. zonale*, *E. olmstedi*, and *Percina peltata*, the shield darter, a second native species, in an artificial stream, thus allowing control of abiotic and biotic factors not possible in the field. We chose to examine substrate choice because previous studies have shown substrate size to be important in darter habitat selection (Kessler et al., 1995; Stauffer et al., 1996; Gray, 1998), and segregation by habitat is predicted to be important among fishes (Werner, 1977). Our objectives were to examine the relative effects of intraspecific and interspecific biotic interactions on the substrate selection of *E. olmstedi*, *E. zonale*, and *P. peltata*, determine whether *E. zonale* induced a habitat shift of *E. olmstedi* or *P. peltata*, and determine whether aggressive interactions occurred among the three species.

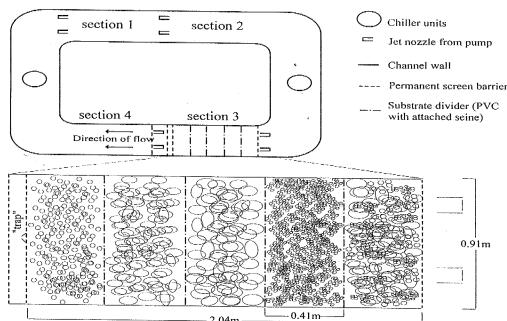


Fig. 1. Diagram of the artificial stream, viewed from above (not to scale).

MATERIALS AND METHODS

The experiments were conducted in an indoor, recirculating, acrylic artificial stream with four $0.91\text{ m} \times 2.04\text{ m}$ experimental sections separated by 0.7 mm mesh screens (Fig. 1). Growlights above the stream were on a LutronTM lighting system that allowed for a 14:10 L:D summer photoperiod including a 2 h sunrise and sunset period in which light intensity slowly changed. Two chiller units maintained water temperature at $20.6\text{ }^{\circ}\text{C} \pm 1\text{ C}$. Water depth was maintained at $25.0 \pm 0.8\text{ cm}$. Two water pumps discharging upstream of each section maintained water velocity at $0.20 \pm 0.04\text{ m/sec}$ on the inside of the stream and $0.14 \pm 0.03\text{ m/sec}$ on the outside of the stream. The pH was 7.6, and ammonia was below detectable amounts. A curtain enclosed the artificial stream to minimize external disturbances during experiments.

The entire bottom of each section was covered with 2.6 cm of sand. Within each of the four sections, five patches of differing substrate sizes (diameters) were installed: $2\text{--}4\text{ cm}$, $4\text{--}6\text{ cm}$, $6\text{--}10\text{ cm}$, $10\text{--}25\text{ cm}$, and a mixture of the four substrate sizes (Fig. 1). All substrate but the largest size class was obtained from a local quarry. Substrate $10\text{--}25\text{ cm}$ in diameter was collected from a local stream, cleaned, dried indoors for five months, and scrubbed a second time before use. The order of the substrates was randomly assigned, and substrate was placed on the sand in each patch. Substrate patches were separated by 4.45 cm PVC pipes that contained a rolled seine. All four seines within a section were tied to a bar on the outside of the stream, such that the seines could be lifted vertically in unison, thus simultaneously isolating the five substrate patches and preventing darter movement from patch to patch during data collection. We fed fish a combination of live California blackworms and ground trout pellets three times daily at 0800, 1200, and 1600 through

tubes that emptied at the stream bottom at the upstream end of each substrate patch in each of the four sections.

The native species were collected by seining in the Susquehanna River basin, Pennsylvania, including Conococheague Creek, Emma Creek, Little Juniata River, Marsh Creek, Sugar Creek, and Swatara Creek. *Etheostoma zonale* was collected from Little Pine Creek, Pennsylvania. Fish were kept in holding tanks by species, fed as during the experiments, and kept for a minimum of four weeks before use in experiments. Only adult darters were used in experiments, and the fish were not sexed. Size ranges of darters used were $4\text{--}9\text{ mm}$ for *E. olmstedi* (mean = 6.25 mm) and *P. peltata* (mean = 6.32 mm) and $4\text{--}6\text{ mm}$ for *E. zonale* (mean = 5.35 mm).

We designed substrate choice trials to examine the effect of interspecific versus intraspecific effects upon the three species' substrate choice. Densities in single species trials included 6, 12, and 24 fish, corresponding to 3, 6, and 12 fish/ m^2 , which did not exceed natural fish densities (Grady and Bart, 1987; Ross et al., 1990; Gray, 1998). Results of three trials were compared to determine whether *E. zonale* induced a habitat shift of each native species: (1) *E. olmstedi* or *P. peltata* held alone; (2) *E. olmstedi* + *P. peltata*; and (3) *E. olmstedi* + *P. peltata* + *E. zonale*. It was necessary to include two experimental designs to have unconfounded conclusions regarding interspecific interactions. We also included two density levels for each experimental design. The additive experimental design tested for the existence of interspecific biotic interactions upon substrate choice (Underwood, 1986; Fausch, 1988). In this design, the total density of fish in the three trials varies; however the number of conspecifics is fixed across trials. The low-density trials for the additive design were (1) 6o, (2) 6o + 6p, and (3) 6o + 6p + 6z (o = *E. olmstedi*, p = *P. peltata*, and z = *E. zonale*); and the high-density trials were (1) 12o, (2) 12o + 12p, and (3) 12o + 12p + 12z. The substitutive design tests the relative strength of interspecific relative to intraspecific biotic interactions for each species (Underwood, 1986; Fausch, 1988). In this design, the total fish density in the three experiments is fixed, and the number of conspecifics varies across trials. The low-density trials for the substitutive design were (1) 12o, (2) 6o + 6p, and (3) 4o + 4p + 4z, and the high-density trials were (1) 24o, (2) 12o + 12p, and (3) 8o + 8p + 8z.

The order of experiments as well as which section was used for each experiment was determined randomly. All first replicate experiments were completed before beginning the

second replicates. Fish were selected randomly from holding tanks, measured to the nearest 0.5 cm standard length (SL), and placed in the stream. Each experiment included 72 h of acclimation in the artificial stream, and observations were made on days 3, 5, and 7. Observations were conducted at three different times: 0900, 1300, and 1500 (hereafter referred to as morning, afternoon, and evening, respectively), one hour after feeding, and the order of these observation times was determined randomly. First, the fish in each section were observed for a period of 15 min, and behavioral data were collected. Each visible fish was observed for 1 min and aggressive interactions were recorded. Aggressive behaviors were classified into categories used by Hartman (1965): nips, chases, and displays (only lateral displays were observed). In addition, the position of the fish with respect to the substrate was recorded at first sighting: in the water column, under, or above (on the top surface of) substrate. Following the behavioral data, the seines were lifted simultaneously, and the water pumps were turned off. The number and species of fish in each substrate patch were recorded. A day of reacclimation was allowed between observations because disturbance of substrate was necessary to count all the fish in each section. All five substrate patches were disturbed during data collection.

We used individual fish in more than one experiment because of facility restraints. In selecting fish for the experiments, all fish of a given species were used before using any of the fish a second time (Tyler and Clapp, 1995). On average, each individual *E. olmstedi* was used in three experiments, each *E. zonale* was used twice, and each *P. peltata* was used in four experiments.

We used a two-factor analysis of variance to determine the effect of time of day and average SL on substrate selection by the three darter species. *P*-values were considered significant if less than or equal to 0.05 for all statistical tests. Neither time of day nor average SL influenced darter substrate selection ($F = 1.35$, $df = 149$, $P = 0.26$). Therefore, data from the three time periods were pooled for subsequent analyses. Examination of histograms indicated that darters did not discriminate among all five substrate patches. Instead, darters discriminated among patches that allowed use of interstitial spaces for cover. Therefore, the data from patches with substrate 2–4 cm and 4–6 cm were pooled and referred to as "small substrate," and the data from patches with substrate 6–10 cm, 10–25 cm, and a mixture of all substrate sizes were pooled and referred to as "large substrate."

To examine the substrate preference of each species, a χ^2 test was used. For each species and each density (6, 12, and 24 individuals), we compared the frequency of use of small and large substrate patches with the expected frequency of use based on an equal distribution of fish across the two substrate size classes. If no substrate selection occurred, we expected 40% of individuals to be in small substrate patches and 60% of individuals to be in large substrate patches because there were two small substrate patches and three large substrate patches. For the experiments testing a density of six fish, Fisher's exact test was used because the expected frequency of at least 20% of the cells was less than five (Glantz, 1992). Fisher's exact test was also used to determine whether intraspecific effects on substrate choice occurred. Each species' substrate choice was compared across the three densities to determine whether substrate selection changed with density of conspecifics.

We used χ^2 tests of homogeneity to test for habitat shifts resulting from interspecific effects. Again, Fisher's exact test was used in experiments with small sample sizes. The results of three trials were compared to determine whether *E. zonale* induced a habitat shift of either of the native species as outlined previously: (1) *E. olmstedi* or *P. peltata*; (2) *E. olmstedi* + *P. peltata*; and (3) *E. olmstedi* + *P. peltata* + *E. zonale*. When significance was found, further χ^2 tests were used to determine which experiments differed. Reduced alpha levels (α/n , where n is the number of pairwise comparisons) were used to correct for experimentwise error. In addition, the substrate choice of *E. zonale* in single species trials was compared to the substrate choice of *E. zonale* when held with the two native species to determine whether the substrate choice of *E. zonale* was affected by the native species.

RESULTS

In single species trials at all three densities, *E. olmstedi*, *E. zonale*, and *P. peltata* exhibited non-random substrate selection and selected large substrate significantly more often than expected ($P < 0.05$; Table 1). None of the three species showed intraspecific effects on substrate choice ($P > 0.05$; Table 1).

Mixed species trials examined interspecific effects on the three species' substrate use. At low densities, there were no significant differences in substrate choice of *E. olmstedi* in the additive ($6o/6o + 6p/6o + 6p + 6z$) and substitutive ($12o/6o + 6p/4o + 4p + 4z$) analyses ($P > 0.05$; Table 1). At high densities, however, the substrate use by *E. olmstedi* was significantly dif-

TABLE 1. AVERAGE SIZE (mm SL) AND PERCENT OF INDIVIDUALS PER SPECIES OCCURRING IN SMALL AND LARGE SUBSTRATE PATCHES IN EXPERIMENTAL TRIALS. Abbreviations include o = *Etheostoma olmstedi*, p = *Percina peltata*, and z = *Etheostoma zonale*.

Trial	Time of day	<i>E. olmstedi</i>		<i>P. peltata</i>			<i>E. zonale</i>			
		Average size (mm)	Small substrate	Large substrate	Average size (mm)	Small substrate	Large substrate	Average size (mm)	Small substrate	Large substrate
6	morning	6.2	0.0%	100.0%	5.6	16.7%	83.3%	5.2	0.0%	100.0%
	afternoon	33.3%	66.7%		16.7%	83.3%		0.0%	100.0%	
	evening	16.7%	83.3%		0.0%	100.0%		0.0%	100.0%	
	morning	6.3	16.7%	83.3%	6.7	0.0%	100.0%	5.5	0.0%	100.0%
	afternoon	0.0%	100.0%		0.0%	100.0%		0.0%	100.0%	
	evening	0.0%	100.0%		16.7%	83.3%		16.7%	83.3%	
12	morning	6.3	20.0%	80.0%	6.1	0.0%	100.0%	5.0	0.0%	100.0%
	afternoon	0.0%	100.0%		18.2%	81.8%		0.0%	100.0%	
	evening	0.0%	100.0%		0.0%	100.0%		0.0%	100.0%	
	morning	6.3	0.0%	100.0%	6.5	25.0%	75.0%	5.7	16.7%	83.3%
	afternoon	0.0%	100.0%		8.3%	91.7%		16.7%	83.3%	
	evening	0.0%	100.0%		16.7%	83.3%		8.3%	91.7%	
24	morning	6.3	25.0%	75.0%	6.5	16.7%	83.3%	5.0	12.5%	87.5%
	afternoon	8.3%	91.7%		8.3%	91.7%		8.3%	91.7%	
	evening	16.7%	83.3%		8.3%	91.7%		12.5%	87.5%	
	morning	6.1	8.3%	91.7%	6.6	4.2%	95.8%	5.3	12.5%	87.5%
	afternoon	8.3%	91.7%		12.5%	87.5%		4.2%	95.8%	
	evening	4.2%	95.8%		16.7%	83.3%		8.3%	91.7%	
6o+6p	morning	6.3	0.0%	100.0%	5.7	33.3%	66.7%	—	—	—
	afternoon	0.0%	100.0%		33.3%	66.7%		—	—	—
	evening	16.7%	83.3%		33.3%	66.7%		—	—	—
	morning	6.3	16.7%	83.3%	5.9	16.7%	83.3%	—	—	—
	afternoon	16.7%	83.3%		33.3%	66.7%		—	—	—
	evening	0.0%	100.0%		0.0%	100.0%		—	—	—
12o+12p	morning	5.7	10.0%	90.0%	5.9	0.0%	100.0%	—	—	—
	afternoon	10.0%	90.0%		0.0%	100.0%		—	—	—
	evening	0.0%	100.0%		0.0%	100.0%		—	—	—
	morning	6.6	25.0%	75.0%	6.8	16.7%	83.3%	—	—	—
	afternoon	33.3%	66.7%		8.3%	91.7%		—	—	—
	evening	0.0%	100.0%		8.3%	91.7%		—	—	—
4o+4p+4z	morning	5.6	25.0%	75.0%	6.5	0.0%	100.0%	5.4	0.0%	100.0%
	afternoon	0.0%	100.0%		25.0%	75.0%		0.0%	100.0%	
	evening	0.0%	100.0%		25.0%	75.0%		0.0%	100.0%	
	morning	7.5	0.0%	100.0%	7.1	0.0%	100.0%	5.9	0.0%	100.0%
	afternoon	0.0%	100.0%		0.0%	100.0%		0.0%	100.0%	
	evening	25.0%	75.0%		50.0%	50.0%		0.0%	100.0%	
6o+6p+6z	morning	6.5	16.7%	83.3%	5.8	0.0%	100.0%	4.8	16.7%	83.3%
	afternoon	50.0%	50.0%		16.7%	83.3%		16.7%	83.3%	
	evening	0.0%	100.0%		0.0%	100.0%		0.0%	100.0%	
	morning	5.9	50.0%	50.0%	6.6	16.7%	83.3%	5.2	0.0%	100.0%
	afternoon	16.7%	83.3%		0.0%	100.0%		16.7%	83.3%	
	evening	16.7%	83.3%		16.7%	83.3%		16.7%	83.3%	
8o+8p+8z	morning	6.6	0.0%	100.0%	6.7	12.5%	87.5%	5.6	0.0%	100.0%
	afternoon	50.0%	50.0%		0.0%	100.0%		12.5%	87.5%	
	evening	37.5%	62.5%		25.0%	75.0%		12.5%	87.5%	
	morning	6.1	50.0%	50.0%	6.3	12.5%	87.5%	5.9	0.0%	100.0%
	afternoon	12.5%	87.5%		0.0%	100.0%		0.0%	100.0%	
	evening	75.0%	25.0%		0.0%	100.0%		0.0%	100.0%	
12o+12p+12z	morning	5.5	41.7%	58.3%	6.0	41.7%	58.3%	5.1	0.0%	100.0%
	afternoon	75.0%	25.0%		25.0%	75.0%		25.0%	75.0%	
	evening	18.2%	81.8%		0.0%	100.0%		0.0%	100.0%	
	morning	6.4	33.3%	66.7%	6.6	25.0%	75.0%	5.5	8.3%	91.7%
	afternoon	66.7%	33.3%		25.0%	75.0%		8.3%	91.7%	
	evening	41.7%	58.3%		8.3%	91.7%		0.0%	100.0%	

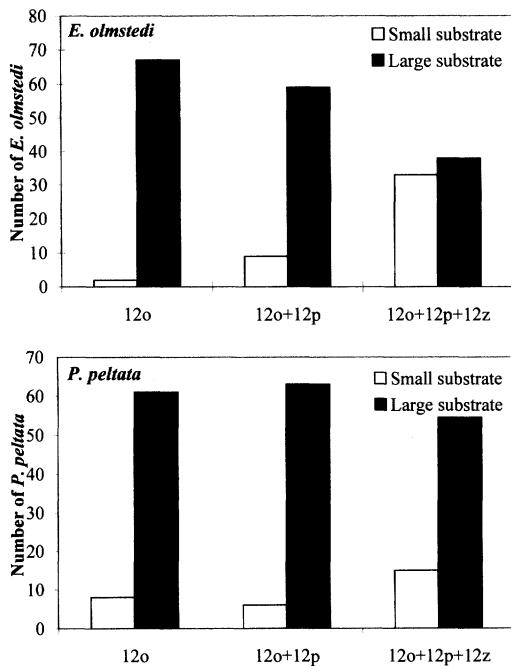


Fig. 2. Number of *Etheostoma olmstedi* and *Percina peltata* observed in small and large substrate patches in single and mixed species trials (including both replicates), illustrating the shift of *E. olmstedi* to small substrates in the presence of the nonnative *Etheostoma zonale*. *Percina peltata* did not exhibit a habitat shift. Abbreviations include o = *E. olmstedi*, p = *P. peltata*, and z = *E. zonale*.

ferent when *E. zonale* was present than when *E. olmstedi* occurred alone or with *P. peltata* ($P < 0.05$; Table 1; Fig. 2). This habitat shift from large to small substrate (Fig. 2) was evident in both the substitutive ($24o/12o + 12p/8o + 8p + 8z$) and additive ($12o/12o + 12p/12o + 12p + 12z$) analyses ($P < 0.05$; Table 1, Fig. 2).

There were no significant differences among the substrate choice of *P. peltata* multispecies trials at low or high densities in the additive or substitutive analyses ($P > 0.05$; Fig. 2; Table 1). *Percina peltata* occupied large substrate habitats regardless of the presence of other species. In addition, the presence of *E. olmstedi* and *P. peltata* did not affect the substrate choice of *E. zonale*. There were no significant differences in the substrate use by *E. zonale* at low or high densities in the additive or substitutive analyses ($P > 0.05$; Table 1).

In 657 min of behavioral observations, *E. zonale* was most frequently the aggressor in agonistic interactions, and chases were the most common aggressive behavior observed (Fig. 3). Of 229 *E. olmstedi* observed, one nip and one display were directed conspecifically; *E. olmstedi* did

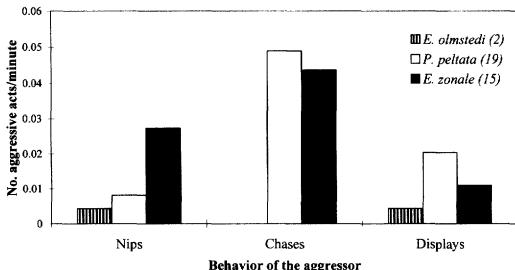


Fig. 3. Number and type of aggressive behaviors per minute initiated by *Etheostoma olmstedi*, *Percina peltata*, and *Etheostoma zonale*. Numbers in parentheses of legend indicate total number of aggressive acts initiated per species.

not direct any agonistic behavior toward *P. peltata* or *E. zonale* (Figs. 3–4). Of 245 *P. peltata* observed, two nips, 12 chases, and five displays were observed (Fig. 3). Eighty-four percent (16 acts) of the agonistic acts initiated by *P. peltata* were directed at conspecifics, and 16% (3 acts) were directed at *E. olmstedi*; neither *E. olmstedi* nor *P. peltata* directed any agonistic behavior toward *E. zonale* (Fig. 4). Fifteen agonistic acts were observed in which *E. zonale* was the aggressor, including five nips, two displays, and eight chases (183 *E. zonale* were observed; Fig. 3). *Etheostoma zonale* directed nine agonistic acts intraspecifically (60%) and three acts (20% each) each toward *E. olmstedi* and *P. peltata* (Fig. 4). The number of agonistic acts performed per minute was therefore 0.009, 0.078, and 0.082, for *E. olmstedi*, *P. peltata*, and *E. zonale*, respectively. Sixty-four percent of the aggressive acts by the three species occurred during mixed species experiments, including 44% in trials including all three species.

The three species differed in their position with respect to the substrate. *Percina peltata* exhibited vertical segregation from *E. olmstedi* and

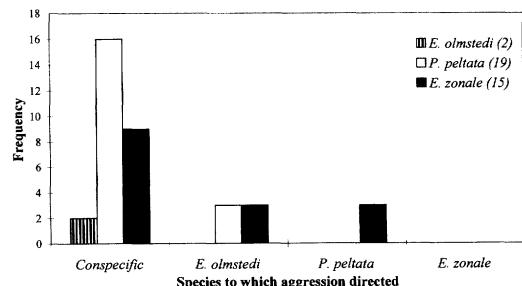


Fig. 4. Frequency of aggressive behavior directed toward conspecifics and heterospecifics by *Etheostoma olmstedi*, *Percina peltata*, and *Etheostoma zonale*. Numbers in parentheses of legend indicate total number of aggressive acts initiated per species.

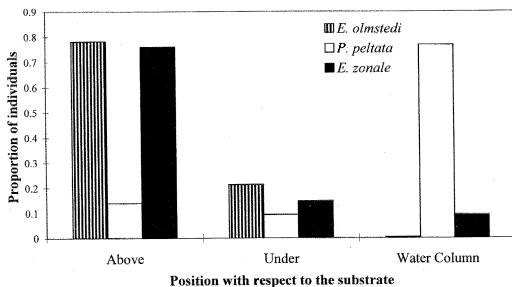


Fig. 5. Proportion of *Etheostoma olmstedi*, *Percina peltata*, and *Etheostoma zonale* individuals observed above substrate, under substrate, and in the water column.

E. zonale by occurring in the water column in >75% of the observations (Fig. 5). Both *E. olmstedi* and *E. zonale* occurred on top of the substrate in >75% of the observations; however *E. olmstedi* was found under rocks (21.4% of the observations) more frequently than *E. zonale* (14.8% of the observations, Fig. 5).

DISCUSSION

Habitat shifts of native species are one of the most likely immediate effects of introduction events (Werner, 1984). In this study, substrate choice by *E. olmstedi* was influenced by the presence of a nonnative species. *Etheostoma olmstedi* exhibited a habitat shift from preferred large substrate to small substrates when *E. zonale* was present at high densities in both the additive and substitutive experimental designs. Shifts were not observed at low densities. However as space became limiting at higher densities, *E. zonale* displaced *E. olmstedi* from preferred larger substrates through aggressive interactions. The greatest effect on the substrate choice of *E. olmstedi* was not the density of conspecifics but the presence of *E. zonale*. The interaction was asymmetric, with neither native species affecting the habitat use of *E. zonale*. The shift observed in this study supports the results of the field study by Gray (1998), in which *E. olmstedi* occurred in shallower, slower velocity habitats with smaller substrates in sites sympatric with *E. zonale* compared to allopatric sites. Further studies on the effect of *E. zonale* on the growth, survival, and reproduction of *E. olmstedi* are required to determine the implications of the habitat shift for populations of *E. olmstedi* in the Susquehanna River basin. However, restriction of *E. olmstedi* to shallow pool and marginal habitats with smaller substrates may result in a reduced food base (Schlosser, 1987; Vogt and Coon, 1990), increased susceptibility to predation (Greenberg,

1994; Brown and Brasher, 1995; Greenberg et al., 1997), or exclusion from primary spawning habitat causing lowered reproductive success resulting from suboptimal oxygenation of eggs (Gray, 1998).

The habitat shift exhibited by *E. olmstedi* can be attributed to agonistic acts by *E. zonale*. Although 36 aggressive interactions were observed, the probability of observing agonistic acts in three 15-min periods per week is low (Diamond, 1978). More agonistic acts per minute were initiated by *E. zonale* (0.082) than by *P. peltata* (0.078) or *E. olmstedi* (0.009). In addition, the percentage of aggressive interactions directed at heterospecifics varies by species: 0%, 16%, and 40%, respectively, for *E. olmstedi*, *P. peltata*, and *E. zonale*. Although neither *E. olmstedi* nor *P. peltata* directed aggressive behavior toward *E. zonale*, 40% of aggressive acts initiated by *E. zonale* were directed toward the two native species, supporting interference competition for space as the mechanism in the habitat shift exhibited by *E. olmstedi*. This scenario is similar to that found by Hindar et al. (1988): cutthroat trout (*Salmo clarki*) excluded dolly varden (*Salvelinus malma*) from littoral and near-surface habitats in sympatry through aggressive dominance. *Etheostoma zonale* may also influence the habitat use of other darters in its native range (White and Aspinwall, 1984). White and Aspinwall (1984) found that the habitat use of *Etheostoma blennioides*, the greenside darter, and *Etheostoma tetrazonum*, the Missouri saddled darter, differed in sympatry and allopatry with *E. zonale*. *Etheostoma zonale* occurred frequently in submergent vegetation (*Potamogeton*), and *E. blennioides* and *E. tetrazonum* exhibited a marked increase in their use of *Potamogeton* where *E. zonale* was absent (White and Aspinwall, 1984).

Percina peltata occupied large substrates regardless of intraspecific or interspecific darter densities. Many ecological studies have highlighted ecological differences between the genera *Etheostoma* and *Percina* (Greenberg, 1991; Gray, 1998; Welsh and Perry, 1998). *Percina peltata* exhibits vertical segregation from *E. olmstedi* and *E. zonale*, in addition to occupying water velocities in between *E. zonale* (fastest water velocities) and *E. olmstedi* (slowest water velocities, Gray, 1998). Because *P. peltata* uses substrate for cover less frequently than the *Etheostoma* species, it is not surprising that neither *E. olmstedi* nor *E. zonale* affects its substrate selection.

There is a need for more studies of interbasin transfers. As Ross (1991) pointed out, although there are at least double the number of interbasin transfers than exotic species introductions in North America, exotic species are studied dis-

proportionally. Understanding the mechanisms of species interactions among unnaturally sympatric fish species may give us insight into community organization (Diamond, 1978; Fausch, 1988) as well as remind us of the importance of using conservatism when introducing new fish species beyond their natural range.

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