Transactions of the American Fisheries Society 126:822–840, 1997

Food Resource Partitioning by Nine Sympatric Darter Species

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Abstract.—We compared the diets among members of the diverse darter community of French Creek, Pennsylvania, in relation to seasonal prey availability, feeding ontogeny, and sex. Prey taxa and size attributes were characterized for nine syntopic darter species; taxon, size, and availability of macroinvertebrate prey were also analyzed from Surber samples. In general, darters fed opportunistically on immature insects; few taxa were consumed in greater proportions than they were found in the environment. Some variation in diet composition was expressed, however, among different life stages and species. Juvenile darters consumed smaller prey and more chironomids than did adults. *Etheostoma blennioides* and *E. zonale* consumed the fewest taxa (2–3), whereas *E. maculatum, E. variatum,* and *Percina evides* had the most diverse diets (7–10 taxa). *Etheostoma maculatum, E. flabellare, E. variatum,* and *P. evides* consumed larger prey (1–13 mm in standard length), whereas *E. blennioides, E. caeruleum, E. camurum, E. tippecanoe,* and *E. zonale* rarely consumed prey longer than 6 mm. *Percina evides* fed on larger prey, fewer chironomids, and more fish eggs than *Etheostoma* species. Females consumed more prey than males and overlapped less in diet composition with males during the spawning season than afterwards. Fish diets did not seem related to habitat use. Greater trophic partitioning was observed in April, when prey resources were scarce, than in July, when prey were abundant. Darter species fed opportunistically when prey were dense, whereas they partitioned food resources mainly through the prey size dimension when prey were less abundant. The divergence of darter diets during a period of low food availability may be attributed to interspecific competition. Alternatively, the greater abundance of large prey in April may have facilitated better prey size selectivity, resulting in less overlap among darter species.

Trophic partitioning is expected to be better defined than habitat partitioning in aquatic habitats (Schoener 1974; Ross 1986). Trophic resource use among fishes has been extensively studied, and dietary differences in taxa consumed (Zaret and Rand 1971; Johnson and Dropkin 1995) and in prey size (Keast and Webb 1966; Miller 1983) have been observed among sympatric fish species. Trophic relationships may also be affected by predator morphology (Matthews et al. 1982), sex (Weddle 1992), ontogeny (Jones and Maughan 1989; Gutowski and Stauffer 1993; Knight and Ross 1994), and prey characteristics such as evasiveness (Brusven and Rose 1981; Hershey and Dodson 1985; Hershey 1987). Page (1983) hypothesized that differences in darter diets may be related to habitat segregation as observed in several other fish groups (Zaret and Rand 1971).

Ecologically similar species such as darters, which are primarily diurnal, visual predators of benthic insects (Roberts and Winn 1962; Daugherty et al. 1976; Adamson and Wissing 1977), may coexist through trophic segregation. Previous comparative studies of darter diets have focused on partitioning among relatively few darter species (Wynes and Wissing 1982; Hlohowskyj and White 1983; Todd and Stewart 1985; Weddle 1992). However, Greenberg (1991) compared the habitat use and feeding behavior among thirteen benthic stream fishes. The objectives of this study were to compare diets among members of a diverse darter community of the upper Allegheny River drainage, Pennsylvania, in relation to seasonal prey avail-

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ability, feeding ontogeny, and sex. We hypothesized that females would consume significantly more prey items than males during and preceding the spawning season and that the pattern of food resource use among darters would be similar to the pattern of habitat partitioning found by Stauffer et al. (1996), who examined habitat use of the French Creek, Pennsylvania, darters in a companion study. Scientific and common names of the nine darter species collected during our study are listed in Table 1.

Methods

Study area.—The Allegheny River drainage contains a diverse fish fauna composed of 68 species, including 15 darter species (Lachner et al. 1950; Cooper 1983). French Creek, a fourth-order tributary to the Allegheny River, drains approximately 3,000 km^2 of southwestern New York and northwestern Pennsylvania. Four sites on French Creek were selected for sampling based on their similarities in physical characteristics, fish, and macroinvertebrate faunas. Site names were Carlton, Cochranton, Meadville, and Venango, located in Crawford and Mercer counties, Pennsylvania. Each site consisted of a riffle, run, and pool sequence approximately 50 m long and 30–55 m wide with cobble and gravel substrates. All four sites were sampled once during 25–27 July 1988, and Cochranton, Meadville, and Venango were sampled once during 27–28 April 1988.

Field methods.—Fishes were collected with a seine (1.5 × 3 m, 0.32-cm mesh) in all available habitats and placed in quinaldine to prevent regurgitation before fixation in 10% formalin and storage in 50% isopropanol. Macroinvertebrates were collected in triplicate with a Surber sampler (500-μm mesh) at each site on each date in the habitats in which fishes were collected. Each sample was preserved in 50% isopropanol and 1% formalin.

Laboratory methods.—All darters were identified to species, sexed, and measured to the nearest 0.1 mm (standard length, SL). The entire digestive system was removed from each fish. Stomach content items and Surber sample contents were identified to the lowest practical taxon, measured to the nearest millimeter, and enumerated. For each collection site and date, the contents of the three Surber samples were pooled.

Data analysis.—Size and taxa frequency histograms were constructed for the Surber samples from each site and collection date and examined for the possibility of pooling across sites and months with similar distributions. Taxa composing less than 2% of the total number of individuals in the collections were considered incidental for the Surber samples and stomach contents. Macroinvertebrates were combined into 2-mm size-classes.

Variation in stomach contents among different fish length-classes and between sexes was examined. The range of standard lengths was divided into three equal-sized categories for each darter species. Based on length frequency distributions and the literature, length-class 1 consisted of primarily juvenile fishes (ages 0–2) and length-classes 2 and 3 were adults (ages 2–5). Taxa and size frequency histograms were examined for each fish species among length-groups that included at least four individuals with stomach contents. Fewer than 25% of all fish in each group had empty stomachs; these fishes were excluded from the analysis. Histogram comparisons indicated that the diets of juvenile males and females were similar; therefore, the data for these diets were pooled to increase the sample size. The diets of length-classes 2 and 3 were similar and, therefore, pooled; however, diets of adult males and females were analyzed separately.

Strauss's (1979) linear index of food selection (L), Hurlbert's (1978) standardized niche breadth, and Morisita's (1959) index of similarity were calculated for both prey taxa and prey size to quantify feeding relationships among darter species. Strauss's L indicates selection, avoidance, or opportunistic consumption of different taxa or size classes. The index ranges from -1 to $+1$ with values near 0 indicating opportunistic feeding (consumption of food in proportion to its abundance in the environment), negative values indicating avoidance, and positive values indicating selection. In this study, Strauss's L-values greater than 0.3 for a macroinvertebrate taxon or size class were considered to indicate selection, L-values less than -0.3 were considered to indicate avoidance, and L-values between 0.3 and -0.3 indicated opportunistic feeding. Hurlbert's (1978) standardized niche breadth indicates where a fish species falls on the continuum of generalist to specialist in resource use. The index ranges from 0 to 1 with low values indicating generalized feeding and high values indicating specialized feeding. Morisita's (1959) index of similarity quantifies the degree of resource use overlap for a given species pair and has the lowest bias and standard deviation of overlap indices (Ricklefs and Lau 1980). The index ranges from 0 to 1, and although no statistics have been developed to determine significance for in-

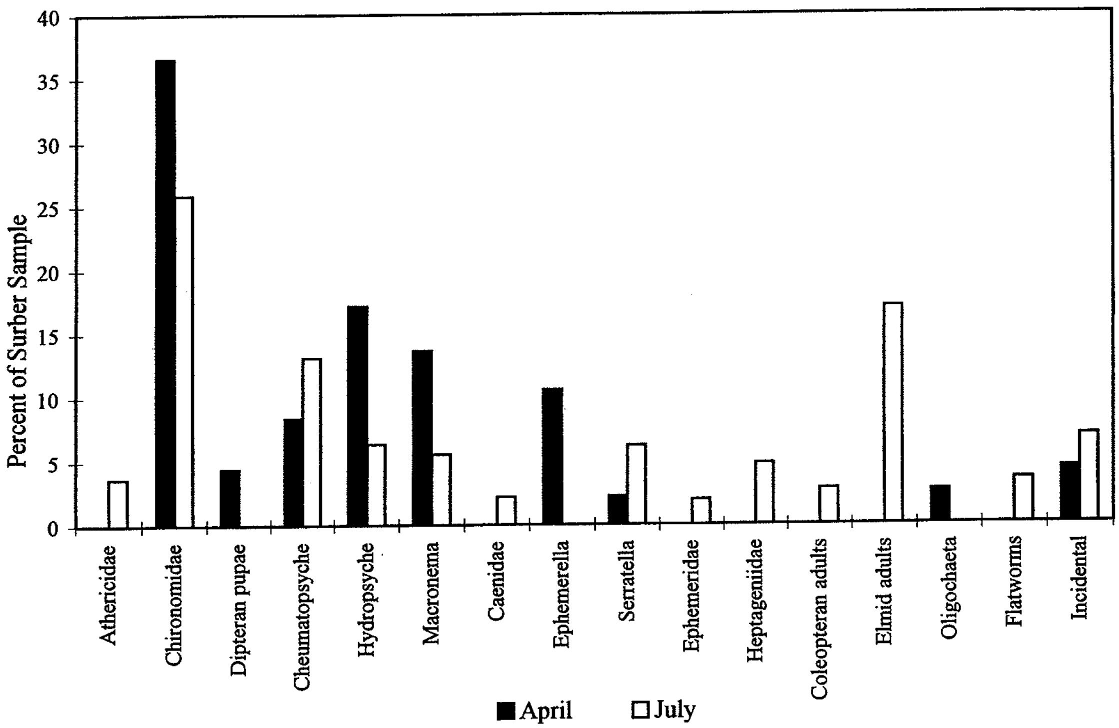

FIGURE 1.—Occurrence (%) of macroinvertebrate taxa in Surber samples collected from French Creek, Pennsylvania, in April and July 1988.

dices, overlap values greater than 0.6 are considered to be biologically significant or high (Zaret and Rand 1971). A cluster analysis was performed on the similarity values for prey taxa and size by using Euclidean distances and the single-linkage method.

Mann–Whitney tests ($P < 0.10$) were used to evaluate the hypothesis that females consumed more prey items than males during the spawning season (April) compared with postspawning periods (July). In addition, Morisita's index of similarity was calculated separately for males and females of each species to test for differences in dietary overlap coinciding with the spawning season.

To test the hypothesis that stomach contents reflect habitat use (Page 1983), our data were compared with the results of Stauffer et al. (1996). In a companion study, Stauffer et al. (1996) documented habitat partitioning among the French Creek darters in July 1988; however, no significant differences in habitat use were found among *E. caeruleum, E. variatum,* and *E. zonale.* In our study, dietary overlap values were, therefore, expected to be greatest among *E. caeruleum, E. variatum,* and *E. zonale* sampled in July.

Results

Resource Availability

Few differences were observed in the taxa and size frequency histograms of Surber sample contents at each site along French Creek; therefore, all samples collected in the same month were pooled. The Surber samples collected in April were considerably less diverse and contained fewer total individuals than the Surber samples from July (Figure 1); therefore, data from April and July were analyzed separately. The Surber samples collected in July contained 686 individuals per site (2,458.8 individuals/m^2) and 12 taxa (excluding incidental taxa), whereas samples collected in April contained 8 taxa and 110 individuals per site (394.3 individuals/m^2). Abundant taxa in both months included Chironomidae (greater than 25%), and the hydropsychid genera *Cheumatopsyche, Hydropsyche,* and *Macronema.* In April, *Ephemerella* (12%) was also abundant, and in July, elmid adults composed greater than 15% of the collections. The April samples contained more large macroinvertebrates than the July samples (Figure 2). Although the most common insect size-class was 3–4 mm in both months, July samples

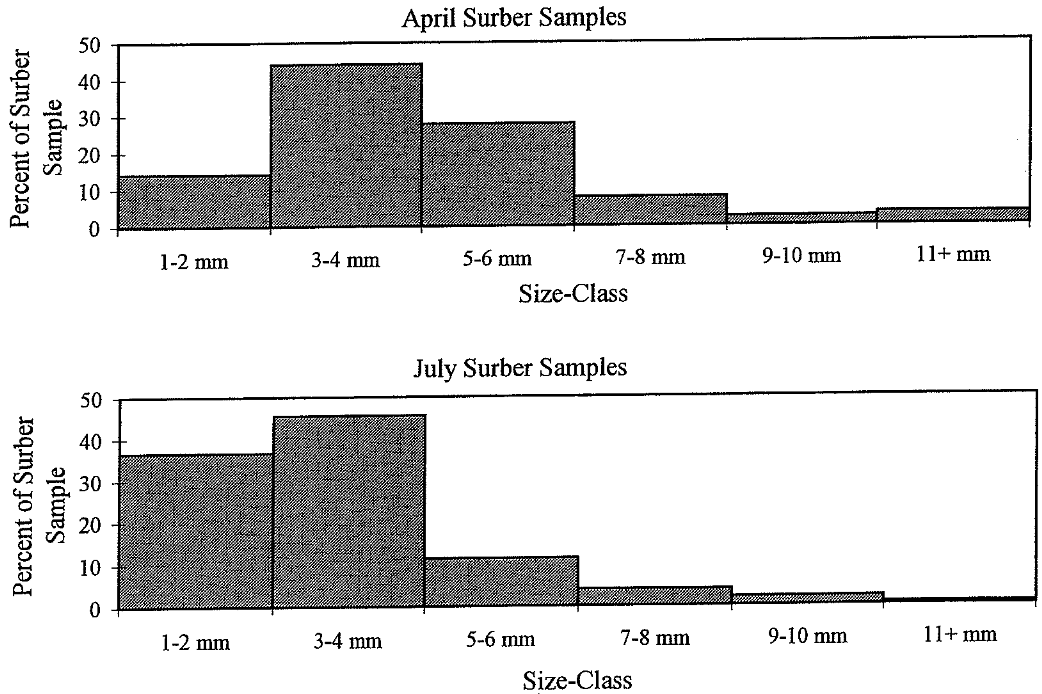

FIGURE 2.—Occurrence (%) of macroinvertebrate size-classes (mm) in Surber samples collected from French Creek, Pennsylvania, in April and July 1988.

contained a larger percentage of 1–2-mm macroinvertebrates (37%) than April samples (14%), and April samples had a larger percentage of 5–6-mm macroinvertebrates (27%) than July samples (11%).

Prey Taxa

Immature insects were the most important prey items for the nine darter species collected (Table 1; Appendix Tables A.1, A.2), although *P. evides* mainly consumed fish eggs. Common taxa consumed included Chironomidae, Simuliidae, hydropsychid genera (*Cheumatopsyche, Hydropsyche,* and *Macronema*), Ephemerellidae, Heptageniidae, elmid larvae, and *Hydracarina* species. Some taxa such as simuliids varied in their seasonal importance; simuliids were important in the diet of darters in April but not in July. *Percina evides* exhibited trophic separation from the *Etheostoma* species by consuming fish eggs and few chironomids. Juvenile darters generally consumed more chironomids than adults. *Etheostoma blennioides* and *E. zonale* had the narrowest diets and typically fed on 2–3 taxa (excluding incidental taxa), whereas *E. caeruleum, E. camurum, E. flabellare, E. maculatum, E. tippecanoe, E. variatum,* and *P. evides* usually fed on 4 or more taxa. *Etheostoma maculatum* (7–8 taxa), *E. variatum* (6–10 taxa), and *P. evides* (7 taxa) had the broadest diets.

Strauss's *L*-values indicated that darters fed opportunistically on most macroinvertebrate taxa in April and July (Appendix Tables A.1, A.2). The majority of taxa had *L*-values close to zero, indicating consumption of prey items in proportion to their availability in the environment (Figure 1). Some preferences were evident, however: chironomids were preferred by *E. blennioides, E. camurum, E. zonale,* and juvenile *E. caeruleum* in April, but were avoided by female *P. evides*; in July, chironomids were preferred by *E. blennioides, E. camurum, E. maculatum, E. zonale,* juvenile and female *E. flabellare,* and juvenile and male *E. caeruleum,* simuliids were preferred by adult *E. maculatum* and male *E. variatum* in April; *Serratella* was preferred by female *E. caeruleum* and juvenile *E. flabellare* in April; and female *P. evides* preferentially consumed fish eggs in April.

Prey Size

Darters tended to consume the most abundant prey sizes available in each month (Figure 2; Appendix Table A.3); in July, 1–2-mm prey was the most common size-class in Surber samples and fish stomachs except for adult *E. variatum,* which con-

TABLE 1.—Species, standard length ranges, and numbers of darters (*N*) collected in April and July 1988. Females and males are adult fish.

Species,[a] common name and group	Length range (mm)	*N* Apr	*N* Jul
E. blennioides			
greenside darter			
Juveniles	31.2–46.8	20	28
Females	46.9–78.1	28	19
Males	46.9–78.1	11	32
E. caeruleum			
rainbow darter			
Juveniles	23.1–31.4	20	16
Females	31.5–48.0	25	28
Males	31.5–48.0	13	17
E. camurum			
bluebreast darter			
Juveniles	36.1–41.0	12	5
Females	41.1–50.8	6	
Males	41.1–50.8		6
E. flabellare			
fantail darter			
Juveniles	21.2–34.4	5	32
Females	34.5–60.7	11	15
Males	34.5–60.7	13	12
E. maculatum			
spotted darter			
Juveniles	17.3–33.5		5
Females	33.6–66.0	7	
Males	33.6–66.0	4	
E. tippecanoe			
Tippecanoe darter			
Juveniles	25.2–28.3		7
Males	28.4–34.6		4
E. variatum			
variegate darter			
Juveniles	29.6–45.9	24	30
Females	46.0–78.5	9	23
Males	46.0–78.5	26	27
E. zonale			
banded darter			
Juveniles	25.1–35.1	13	18
Females	35.2–55.2	32	29
Males	35.2–55.2	15	33
P. evides			
gilt darter			
Females	51.7–57.8	6	

[a] *Etheostoma* (*E.*) and *Percina* (*P.*).

sumed more 3–4-mm prey than 1–2-mm prey. In April the most common prey size was 3–4 mm in Surber samples and fish stomachs, although juvenile *E. blennioides*, juvenile and male *E. caeruleum*, juvenile *E. camurum*, female *E. maculatum*, juvenile and female *E. zonale*, and female *P. evides* consumed more 1–2-mm prey than 3–4-mm prey. Juveniles fed upon smaller prey than adults. *Etheostoma flabellare*, *E. maculatum*, *E. variatum*, and *P. evides* were the only species that fed substantially on prey longer than 5–6 mm.

Strauss's *L*-values for prey size indicated that darters preferred small prey (Appendix Table A.3). In April, most darters preferred prey 1–2 mm in size, except adult *E. blennioides*, female *E. camurum*, *E. flabellare*, *E. variatum*, and male *E. maculatum* and *E. zonale*. Juveniles had higher selection values for this prey size-class than adults. Juvenile *E. flabellare* selected prey 3–4 mm in size, whereas other darters consumed this class more in proportion to its abundance. Prey 5–6 mm in size were generally avoided by *Etheostoma* species but were eaten in proportion to their abundance by female *P. evides*. Prey size-classes larger than 5–6 mm were fed upon opportunistically. In July, most darters preferred prey 1–2 mm in length; however, male *E. blennioides* and *E. flabellare* and all *E. variatum* fed opportunistically on this size-class. Prey 3–4 mm long was avoided by all species except *E. variatum*, which fed opportunistically on this size-class. Prey size-classes 5–6 mm and greater were fed upon opportunistically.

Niche Breadth

Hurlbert's standardized niche breadth values for prey taxa were close to zero for all darters in both months, indicating extreme resource generalization (Table 2). Niche breadth values for prey size selection were low in April (0.04–0.24) but higher in July (0.06–0.52). Adult *E. caeruleum* specialized on prey size with niche breadth values around 0.50. A regression of species sample size and niche breadth value indicated no significant relationship.

Niche Overlap

Niche overlap values suggested ontogenetic trophic divergence among members of this benthic guild in April. Morisita's index of similarity values for taxa consumed by juvenile darter species were higher than overlap among males or females in April (Figure 3A–C). Nearly all overlap values were biologically significant among darter juveniles (0.58–0.97), whereas almost all overlap values between females and between males were less than 0.6 (28 and 15 comparisons, respectively) except female *E. blennioides* × *E. camurum*, female *E. blennioides* × *E. zonale*, female *E. camurum* × *E. zonale*, and male *E. blennioides* × *E. zonale*. Overlaps between female *P. evides* and other darter females were low (average = 0.06). Overlaps between juveniles and females in April were less than 0.6 (6 comparisons) except for *E. blennioides*, *E. camurum*, and *E. zonale* (Table 3). Between juveniles and males and between the sexes, only *E. blennioides* and *E. zonale* overlaps were biologically significant in April.

Darter diets were generally characterized by

TABLE 2.—Hurlbert's standardized niche breadth values (ranging 0–1) of prey taxa and size-class consumed by darters in April and July 1988. Low values indicate generalized feeding and higher values indicate specialized feeding. Females and males are adults.

Species[a] and group	Prey taxa		Prey size	
	Apr	Jul	Apr	Jul
E. blennioides				
Juveniles	0.1538	0.0027	0.0826	0.1934
Females	0.0064	0.0010	0.0735	0.2377
Males	0.0008	0.0016	0.0790	0.0964
E. caeruleum				
Juveniles	0.0006	0.0015	0.0930	0.3247
Females	0.0004	0.0029	0.0790	0.5232
Males	0.0002	0.0029	0.0787	0.4740
E. camurum				
Juveniles	0.0023	0.0019	0.0987	0.2153
Females	0.0003		0.0724	
Males		0.0016		0.1890
E. flabellare				
Juveniles	0.0015	0.0443	0.2428	0.3160
Females	0.0003	0.1318	0.1057	0.3294
Males	0.0016	0.0357	0.0654	0.2231
E. maculatum				
Juveniles		0.1065		0.2541
Females	0.0002		0.0413	
Males	0.0002		0.0913	
E. tippecanoe				
Juveniles		0.0144		0.1990
Males		0.0454		0.1590
E. variatum				
Juveniles	0.0033	0.0593	0.0737	0.1948
Females	0.0007	0.0156	0.0355	0.1213
Males	0.0005	0.0001	0.0570	0.0596
E. zonale				
Juveniles	0.0806	0.0779	0.0993	0.3172
Females	0.0073	0.0142	0.0829	0.2565
Males	0.0022	0.0298	0.0964	0.2243
P. evides				
Females	0		0.0475	

[a] *Etheostoma* (*E.*) and *Percina* (*P.*).

greater overlap among species and life stages in July than in April. In July, juveniles did not have higher overlaps than adults (Figure 3D–F). Most overlap values between juveniles, between females, and between juveniles and females were biologically significant. Overlap values were less than 0.6 among *E. tippecanoe* and *E. variatum* and other darter males, between juvenile and male *E. flabellare, E. tippecanoe,* and *E. variatum,* and between female *E. caeruleum* and *E. variatum.* Overlap was biologically significant between the sexes for all species except *E. variatum* (Table 3).

Prey size use was more similar between life stages and between sexes in July than in April. Morisita's index of similarity values for prey size were generally low whether among juveniles, males, females, or between the sexes in April (Figure 4A–C). However, juvenile–female and juvenile–male *E. flabellare* overlap values were significant that month (Table 4). In July, all overlap values for prey size were significant among juveniles (Figure 4D). Among females, most overlap values were biologically significant; however, *E. variatum* exhibited low overlap in prey size consumption with all species but *E. caeruleum* (Figure 4e). Among males, *E. variatum* also exhibited low overlaps (Figure 4f). Juvenile versus female *E. variatum* and juvenile versus male *E. blennioides* and *E. variatum* exhibited low prey size overlap in July (Table 4). However, significant overlaps occurred between the sexes that month for all species except *E. variatum.*

Number of Prey Items Consumed

Etheostoma blennioides (P = 0.0189), *E. caeruleum* (P = 0.0541), *E. maculatum* (P = 0.0782), *E. variatum* (P = 0.0053), and *E. zonale* (P = 0.0001) females consumed significantly more prey items than did males in April. Male *E. flabellare* consumed more prey items than did females. In July, no significant differences occurred in the number of prey items consumed by males and females.

Discussion

Resource availability data is critical to resource partitioning studies. For example, insect life history can affect the temporal and seasonal availability of prey resources and, thus, the pattern of trophic partitioning by fish. In this study, resource availability contributed insights into how niche partitioning was manifested; the marked increase of available prey resources from April to July was accompanied by a convergence of the darter diets. The low overlap of darter diets during a period of low food availability may be attributed to interspecific competition. Alternatively, the greater abundance of large prey in April might have facilitated better prey size selectivity, fortuitously resulting in less dietary overlap among the darter species. The diets of trophic competitors are expected to converge when prey is abundant and to diverge in times of low food availability, a pattern documented by Zaret and Rand (1971), Werner and Hall (1976), and Horn (1983). Fisher and Pearson (1987) observed a dietary shift to larger prey by *E. flabellare* in the presence of the redline darter *E. rufilineatum.* Although resource overlap does not equate with competition (Colwell and Futuyma 1971), it is a good estimate of shared resource use (Adams 1980).

The major dietary component of juvenile darters

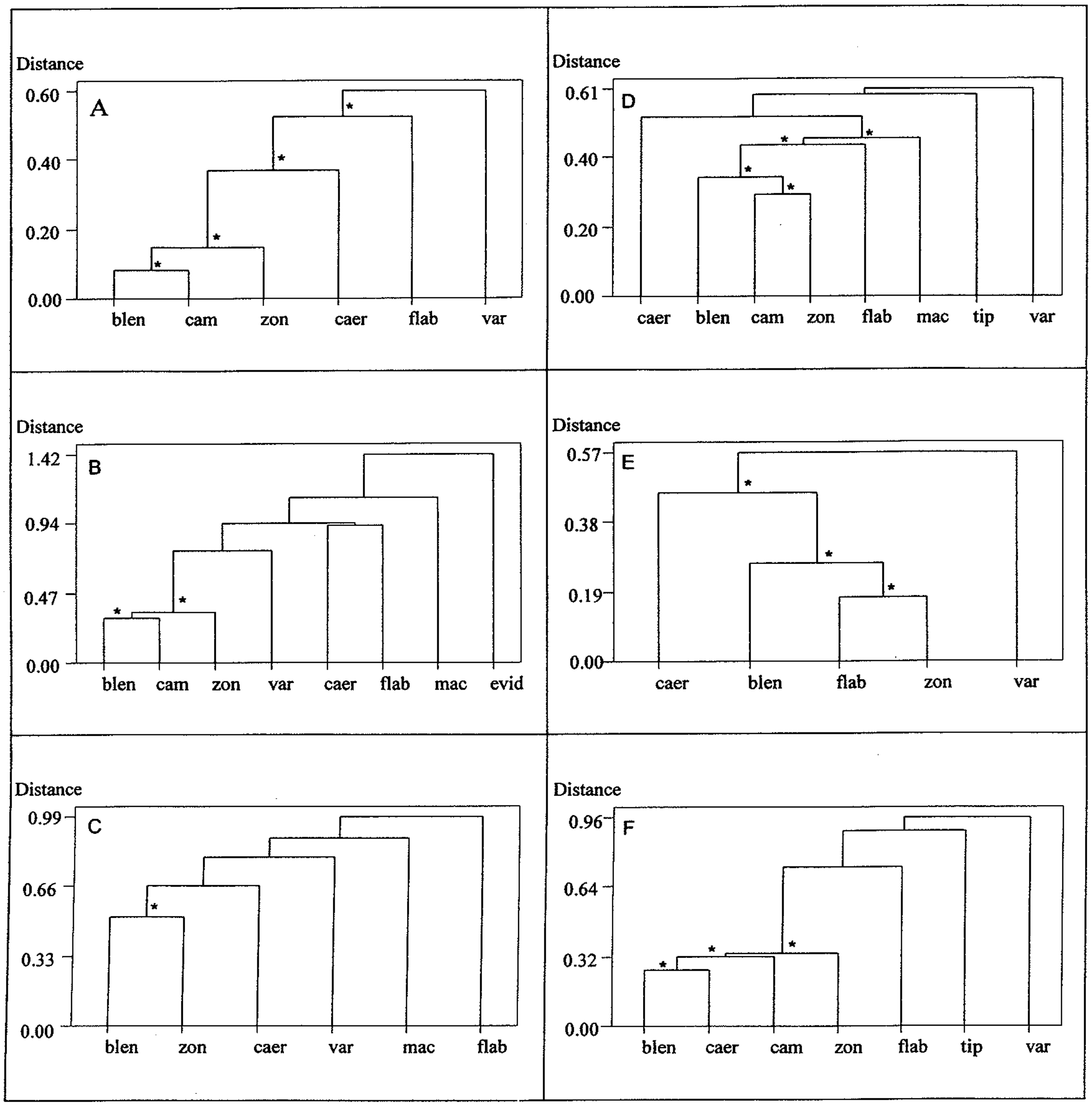

FIGURE 3.—Cluster analysis of Morisita's index of similarity values for taxa consumed in (A–C) April and (D–F) July by (A, D) juvenile, (B, E) female, and (C, F) male darters (*Etheostoma* and *Percina*). Asterisks indicate similarity values greater than 0.6; blen = *E. blennioides*, caer = *E. caeruleum*, cam = *E. camurum*, evid = *P. evides*, flab = *E. flabellare*, mac = *E. maculatum*, tip = *E. tippecanoe*, var = *E. variatum*, and zon = *E. zonale*.

was not microcrustaceans (Cordes and Page 1980; Page 1983) as has been found in several previous studies (Scalet 1972; Fisher 1990), although the smallest darters examined (21 mm, SL) might have been too large to pick up this early ontogenetic shift. Knight and Ross (1994) postulated that microcrustaceans may not be important prey items for all juvenile darters. Nevertheless, an ontogenetic shift in prey size and taxa occurred along with a divergence in interspecific dietary overlap from juvenile to adulthood. Juvenile fishes consumed smaller prey and more chironomids than did adults. Rakocinski (1991) recognized two feeding tactics of darters, number-maximizing and prey-size-selective feeding, and observed that most darters switch from the number-maximizing to the size-selective feeding tactic through ontogeny. Darters may follow a trend, exhibited by many fish species (Aadland 1993), in which interspecific diet overlap is greater among juveniles than among

TABLE 3.—Morisita's index of pairwise similarity (ranging 0–1) of taxa consumed by juvenile (J) and adult female (F) and male (M) darters in April and July 1988. Overlap values greater than 0.6 are considered to be biologically significant.

	Apr			Jul		
Species[a]	F–M	J–F	J–M	F–M	J–F	J–M
E. blennioides	0.6337	0.8320	0.6849	0.8681	0.8736	0.7178
E. caeruleum	0.3914	0.4223	0.5559	0.8685	0.6461	0.8110
E. camurum		0.9203				0.7675
E. flabellare	0.3447	0.5210	0.5435	0.5823	0.7654	0.5533
E. maculatum	0.3200					
E. tippecanoe						0.4235
E. variatum	0.4006	0.4616	0.4277	0.4079	0.5491	0.3494
E. zonale	0.7303	0.7784	0.8022	0.8224	0.8378	0.7617

[a] *Etheostoma (E.).*

adults. In our study, low food availability coincided with high juvenile densities (April), suggesting that recruitment in darter populations may be related more to juvenile dietary requirements and limitations than to adult resource use (Paine 1984).

Increased food consumption by adult females and lower overlaps between the sexes were observed during the darter spawning season compared with postspawning periods. Adult female Kentucky darters *E. rafinesquei* lose weight during the spawning season and exhibit a compensatory increase of food consumption during that time (Weddle 1992). During the spawning season, males and females often occupy different habitats, which could contain different prey taxa or abundances (Orth and Maughan 1983), thus leading to dietary differences between males and females. In several darter species including *E. blennioides, E. variatum,* and *E. zonale,* males defend spawning areas on riffles while the females occupy runs or pools before selecting mates (Winn 1958). Alternatively, females may increase feeding intensity before spawning.

The hypothesis that differences in darter diets are related to habitat use (Page 1983) was not supported by the data. *Etheostoma caeruleum, E. variatum,* and *E. zonale* did not have diets more similar than other French Creek darters, as was predicted based on their habitat use described by Stauffer et al. (1996) in a companion study. Other factors such as fish morphology or foraging microhabitat may have greater potential than habitat use in explaining variation among darter diets. Wood and Bain (1995) found morphology and habitat use to be closely correlated in darters and cyprinids. Matthews et al. (1982) found that gape size and jaw length were related to prey size taken by three darter species including *E. flabellare.* In our study, species with the largest body sizes, *E. maculatum, E. flabellare, E. variatum,* and *P. evides,* also consumed the largest prey with the exception of *E. blennioides.* Although *E. blennioides* is the largest species of *Etheostoma* (Page 1983), its small, blunt, subterminal mouth may restrict its prey size range to smaller items. Fisher and Pearson (1987) also found that *E. flabellare* consumed larger prey than *E. caeruleum.* Moreover, *E. fla-*

TABLE 4.—Morisita's index of pairwise similarity (ranging 0–1) of size-classes consumed by juvenile (J) and adult female (F) and male (M) darters in April and July 1988. Overlap values greater than 0.6 are considered to be biologically significant.

	Apr			Jul		
Species[a]	F–M	J–F	J–M	F–M	J–F	J–M
E. blennioides	0.4971	0.4757	0.4815	0.6370	0.7489	0.5609
E. caeruleum	0.4630	0.4796	0.5272	0.9401	0.7729	0.6819
E. camurum		0.4963				0.9414
E. flabellare	0.4855	0.6778	0.6137	0.7422	0.8270	0.7029
E. maculatum	0.5131					
E. tippecanoe						0.5942
E. variatum	0.4463	0.4384	0.4730	0.4424	0.5113	0.3907
E. zonale	0.4787	0.5296	0.4581	0.6628	0.7700	0.7168

[a] *Etheostoma (E.).*

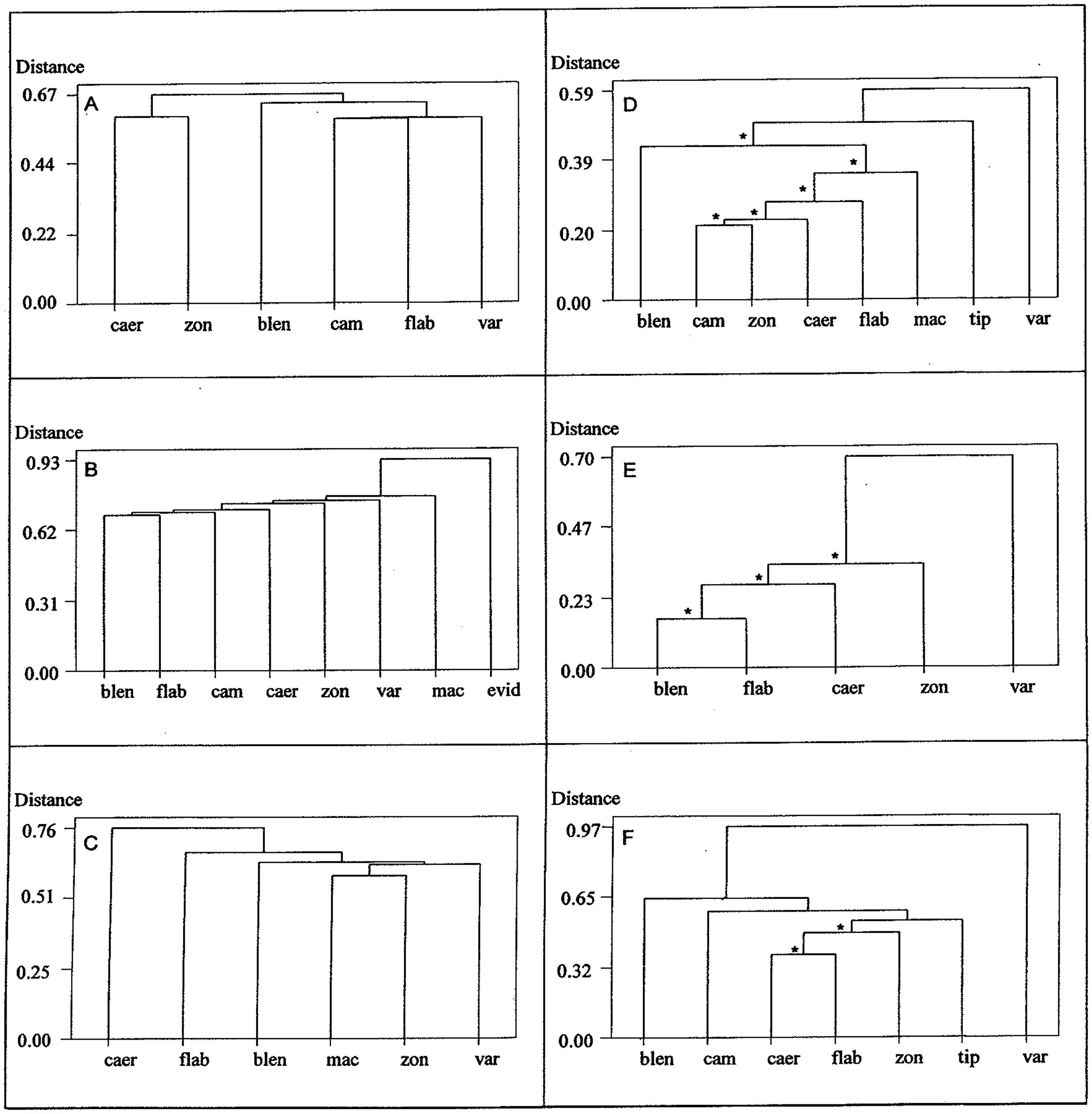

FIGURE 4.—Cluster analysis of Morisita's index of similarity values for prey size consumed in **(A–C)** April and **(D–F)** July by (A, D) juvenile, (B, E) female, and (C, F) male darters (*Etheostoma* and *Percina*). Asterisks indicate similarity values greater than 0.6. Abbreviations are defined in Figure 3 caption.

bellare is known to feed among the interstices of rocks, whereas other darter species, such as *E. caeruleum* take prey from the rock surface (Paine et al. 1982; Schlosser and Toth 1984).

Although darters as a group are specialized benthic insectivores, several previous investigators have maintained that the large resource base of aquatic macroinvertebrates results in opportunistic feeding and a lack of partitioning of food resources by darter species (Martin 1984; Schlosser and Toth 1984). Although few studies have discovered differences in prey taxa consumed within *Etheostoma* (Adamson and Wissing 1977; Fisher and Pearson 1987), differences have been observed between the diets of *Percina* and *Etheostoma* species and within *Etheostoma* through prey size in this study and others (Smart and Gee 1979; Wynes and Wissing 1982; Todd and Stewart 1985; Fisher and Pearson 1987). *Percina evides* fed on larger prey, fewer chironomids, and more fish eggs than *Etheostoma* species and had low overlaps with all sympatric darter species. Previous studies have also shown ecological differences between *Etheostoma* and *Percina* in both habitat and foraging behavior (Smart and Gee 1979; Greenberg 1991).

The results of this study support the assertion that darters are generalist benthic insectivores, although dietary overlap may increase to a greater degree during competitive bottlenecks. Only *E. caeruleum* exhibited specialist feeding based on prey size. Most darters foraged opportunistically, however some species exhibited preferences for chironomids, simuliids, *Serratella,* and fish eggs. Females consumed more prey items and overlapped less with males during the spawning season than afterwards. Interspecific dietary overlap was mediated by the abundance of prey resources.

Acknowledgments

We thank S. Boltz, M. J. Gutowski, and R. L. Raesly for field assistance. F. M. Williams provided valuable input, and R. F. Carline and M. J. Gray critically reviewed the manuscript. This study was supported by Pennsylvania's Wild Resource Conservation Fund.

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Received May 20, 1996
Accepted March 4, 1997

Appendix: Strauss's Electivity Indices and Percent of Prey by Taxa and Size-Class in the Diets of Darters.

TABLE A.1.—Percent of prey by taxa in the diets of eight darter species (*Etheostoma* and *Percina*) and Strauss's electivity index (*L*; in parentheses) for taxa consumed in April 1988. For Strauss's *L*, range is −1 to +1; positive values indicate selection of prey, negative values indicate avoidance, and values near zero indicate opportunistic feeding by darters. Females and males are adults.

	E. blennioides			*E. caeruleum*			*E. camurum*
Prey taxa	Juveniles	Females	Males	Juveniles	Females	Males	Juveniles
Diptera							
Athericidae	0.00	<2.00 (0.0024)	0.00	2.62 (0.0262)	<2.00 (0.0099)	2.22 (0.0222)	0.00
Chironomidae	94.64 (0.5807)	81.43 (0.4486)	67.20 (0.3063)	71.73 (0.3516)	38.21 (0.0165)	53.33 (0.1677)	92.26 (0.5569)
Simuliidae	4.02 (0.0270)	14.76 (0.1344)	25.16 (0.2416)	8.90 (0.0758)	11.17 (0.0984)	2.22 (0.0090)	<2.00 (0.0061)
Tipulidae	<2.00 (−0.0132)	<2.00 (−0.0124)	<2.00 (−0.0132)	<2.00 (−0.0132)	<2.00 (−0.0132)	<2.00 (−0.0132)	<2.00 (−0.0132)
Trichoptera							
Eunionidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Hydropsychidae							
Cheumatopsyche	<2.00 (−0.0783)	<2.00 (−0.0821)	<2.00 (−0.0741)	<2.00 (−0.680)	2.98 (−0.0539)	2.22 (−0.0615)	<2.00 (−0.0772)
Hydropsyche	<2.00 (−0.1718)	<2.00 (−0.1710)	<2.00 (−0.1686)	<2.00 (−0.1613)	<2.00 (−0.1619)	2.96 (−0.1422)	<2.00 (−0.1718)
Ephemeroptera							
Baetidae	0.00	0.00	<2.00 (0.0096)	0.00	<2.00 (0.0124)	0.00	0.00
Ephemerellidae							
Ephemerella	<2.00 (−0.1030)	<2.00 (−0.1057)	<2.00 (−0.1025)	<2.00 (−0.0953)	<2.00 (−0.0859)	<2.00 (−0.0835)	<2.00 (−0.0928)
Serratella	<2.00 (−0.0220)	<2.00 (−0.0141)	<2.00 (−0.0029)	3.66 (0.0146)	32.01 (0.2981)	12.59 (0.1039)	<2.00 (−0.0156)
Heptageniidae							
Stenonema	0.00	0.00	0.00	<2.00 (0.0105)	<2.00 (0.0099)	<2.00 (0.0148)	<2.00 (0.0065)
Oligoneuriidae	0.00	0.00	0.00	0.00	<2.00 (0.0025)	0.00	<2.00 (0.0065)
Plectoptera							
Perlidae	0.00	0.00	0.00	<2.00 (0.0052)	<2.00 (0.0199)	0.00	0.00
Other							
Fish eggs	0.00	0.00	<2.00 (0.0096)	<2.00 (0.0052)	<2.00 (0.0199)	14.81 (0.1481)	0.00
Hydracarina	0.00	0.00	0.00	4.71 (0.0471)	<2.00 (0.0174)	4.44 (0.0444)	<2.00 (0.0194)
Incidental	1.34	3.81	7.64	8.38	15.63	5.19	7.74

TABLE A.1—Extended.

Prey taxa	*E. camurum*	*E. flabellare*			*E. maculatum*	
	Females	Juveniles	Females	Males	Females	Males
Diptera						
Athericidae	0.00	0.00	<2.00 (0.0119)	0.00	<2.00 (0.0172)	0.00
Chironomidae	87.21 (0.5065)	44.44 (0.0788)	30.95 (−0.0561)	28.38 (−0.0819)	15.52 (−0.2105)	21.21 (−0.1535)
Simuliidae	5.81 (0.0449)	<2.00 (−0.0132)	9.52 (0.0820)	14.86 (0.1354)	35.34 (0.3402)	33.33 (0.3201)
Tipulidae	<2.00 (−0.0132)	11.11 (0.0979)	<2.00 (−0.0132	<2.00 (−0.0132)	<2.00 (−0.0132)	<2.00 (−0.0132)
Trichoptera						
Eunionidae	0.00	0.00	0.00	0.00	0.00	3.03 (0.0303)
Hydropsychidae						
Cheumatopsyche	<2.00 (−0.0779)	<2.00 (−0.0837)	17.86 (0.0949)	12.84 (0.0447)	15.52 (0.0715)	15.15 (0.0678)
Hydropsyche	<2.00 (−0.1660)	<2.00 (−0.1718)	2.38 (−0.1480)	4.05 (−0.1313)	4.31 (−0.1287)	6.06 (−0.1112)
Ephemeroptera						
Baetidae	0.00	0.00	0.00	2.70 (0.0270)	0.00	0.00
Ephemerellidae						
Ephemerella	<2.00 (−0.0999)	<2.00 (−0.1057)	<2.00 (−0.1057)	2.70 (−0.0787)	2.59 (−0.0712)	<2.00 (−0.1057)
Serratella	<2.00 (−0.0220)	33.33 (0.3113)	28.57 (0.2637)	30.41 (0.2820)	11.21 (0.0900)	12.12 (0.0992)
Heptageniidae						
Stenonema	0.00	11.11 (0.1111)	4.76 (0.0476)	<2.00 (0.0203)	<2.00 (0.0172)	3.03 (0.0303)
Oligoneuriidae	<2.00 (0.0058)	0.00	2.38 (0.0238)	<2.00 (0.0068)	<2.00 (0.0086)	0.00
Plectoptera						
Perlidae	0.00	0.00	<2.00 (0.0119)	0.00	<2.00 (0.0086)	0.00
Other						
Fish eggs	0.00	0.00	0.00	0.00	0.00	0.00
Hydracarina	3.49 (0.0349)	0.00	0.00	0.00	6.90 (0.0690)	6.06 (0.0606)
Incidental	3.49	0.00	3.57	4.05	8.62	0.00

TABLE A.1—Extended.

Prey taxa	*E. variatum*			*E. zonale*			*P. evides*
	Juveniles	Females	Males	Juveniles	Females	Males	Females
Diptera							
Athericidae	<2.00 (0.0039)	<2.00 (0.0035)	0.00	0.00	<2.00 (0.0027)	<2.00 (0.0047)	0.00
Chironomidae	57.53 (0.2097)	51.59 (0.1502)	31.39 (−0.0518)	88.42 (0.5186)	79.75 (0.4318)	70.62 (0.3405)	4.84 (−0.3173)
Simuliidae	19.69 (0.1837)	25.15 (0.2383)	45.26 (0.4393)	7.37 (0.0605)	14.08 (0.1285)	18.96 (0.1858)	<2.00 (−0.0132)
Tipulidae	<2.00 (−0.0094)	<2.00 (−0.0132)	<2.00 (−0.0132)	<2.00 (−0.0132)	<2.00 (−0.0123)	<2.00 (−0.0085)	<2.00 (−0.0132)
Trichoptera							
Eunionidae	0.00	0.00	<2.00 (0.0073)	0.00	0.00	0.00	0.00
Hydropsychidae							
Cheumatopsyche	5.02 (−0.0335)	6.35 (−0.0202)	2.19 (−0.0618)	<2.00 −(0.0784)	<2.00 (−0.0810)	<2.00 (−0.0837)	8.06 −(0.0031)
Hydropsyche	2.70 (−0.1448)	5.05 (−0.1213)	7.30 (−0.0988)	<2.00 (−0.1718)	<2.00 (−0.1718)	2.84 (−0.1434)	3.23 (−0.1395)
Ephemeroptera							
Baetidae	0.00	<2.00 (0.0035)	0.00	0.00	0.00	<2.00 (0.0142)	0.00
Ephemerellidae							
Ephemerella	2.70 (−0.0787)	2.00 (−0.0858)	2.19 (−0.0838)	<2.00 (−0.1057)	<2.00 (−0.1057)	<2.00 (−0.1010)	6.45 (−0.0412)
Serratella	7.34 (0.0513)	4.58 (0.0250)	2.92 (0.0072)	2.63 (0.0043)	3.63 (0.0143)	2.37 (0.0017)	<2.00 (−0.0059)
Heptageniidae							
Stenonema	<2.00 (0.0116)	<2.00 (0.0071)	2.19 (0.0219)	0.00	0.00	0.00	11.29 (0.1129)
Oligoneuriidae	<2.00 (0.0039)	0.00	0.00	0.00	0.00	0.00	6.45 (0.0645)
Plectoptera							
Perlidae	<2.00 (0.0116)	<2.00 (0.0129)	2.92 (0.0292)	0.00 (0.0000)	0.00 (0.0000)	<2.00 (0.0047)	0.00
Other							
Fish eggs	0.00	0.00	0.00	0.00	0.00	0.00	56.45 (0.5645)
Hydracarina	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Incidental	5.02	5.29	3.65	1.58	2.54	5.21	3.23

TABLE A.2.—Percent of prey by taxa in the diets of eight darter (*Etheostoma*) species and Strauss's electivity index (L; in parentheses) for taxa consumed in July 1988. The range for Strauss's L is -1 to $+1$; positive values indicate selection of prey, negative values indicate avoidance, and values near zero indicate opportunistic feeding by darters. Females and males are adults.

	E. blennioides			*E. caeruleum*			*E. camurum*
Prey taxa	Juveniles	Females	Males	Juveniles	Females	Males	Juveniles
Diptera							
Athericidae	<2.00 (−0.0202)	<2.00 (−0.0321)	<2.00 (−0.0188)	<2.00 (−0.0253)	<2.00 (−0.0364)	<2.00 (−0.0364)	<2.00 (−0.0364)
Chironomidae	76.42 (0.5057)	82.25 (0.5640)	63.08 (0.3722)	60.00 (0.3414)	53.85 (0.2799)	63.83 (0.3797)	81.48 (0.5563)
Simuliidae	<2.00 (−0.0067)	<2.00 (−0.0067)	1.98 (0.0131)	<2.00 (−0.0067)	<2.00 (−0.0067)	<2.00 (−0.0067)	<2.00 (−0.0067)
Trichoptera							
Hydropsychidae							
Cheumatopsyche	7.32 (−0.0583)	<2.00 (−0.1142)	12.75 (−0.0040)	8.89 (−0.0426)	3.08 (−0.1007)	4.26 (−0.0889)	11.11 (−0.0204)
Hydropsyche	4.34 (−0.0202)	<2.00 (−0.0462)	10.77 (0.0442)	4.44 (−0.0191)	3.08 (−0.0328)	2.13 (−0.0423)	<2.00 (−0.0635)
Macronema	<2.00 (−0.0393)	<2.00 (−0.0469)	2.64 (−0.0292)	2.22 (−0.0333)	<2.00 (−0.0401)	<2.00 (−0.0555)	<2.00 (−0.0555)
Hydroptilidae	<2.00 (−0.0058)	<2.00 (−0.0058)	<2.00 (−0.0058)	<2.00 (−0.0058)	<2.00 (−0.0058)	<2.00 (−0.0058)	<2.00 (−0.0058)
Leptoceridae	<2.00 (−0.0004)	<2.00 (0.0012)	<2.00 (−0.0031)	<2.00 (−0.0031)	<2.00 (0.0123)	<2.00 (−0.0031)	<2.00 (−0.0031)
Philopotamidae	<2.00 (−0.0022)	<2.00 (−0.0022)	0.00	<2.00 (−0.0022)	<2.00 (−0.0022)	<2.00 (−0.0022)	<2.00 (−0.0022)
Trichopteran pupae	<2.00 (−0.0009)	<2.00 (−0.0009)	<2.00 (−0.0009)	<2.00 (−0.0009)	<2.00 (−0.0009)	4.26 (−0.0009)	<2.00 (−0.0009)
Ephemeroptera							
Caenidae	<2.00 (−0.0218)	<2.00 (−0.0174)	<2.00 (−0.0196)	<2.00 (−0.0218)	<2.00 (−0.0064)	<2.00 (−0.0218)	<2.00 (−0.0218)
Ephemerellidae							
Serratella	<2.00 (−0.0595)	<2.00 (−0.0622)	<2.00 (−0.0622)	<2.00 (−0.0622)	<2.00 (−0.0622)	<2.00 (−0.0622)	<2.00 (−0.0622)
Ephemeridae	<2.00 (−0.0195)	<2.00 (−0.0195)	<2.00 (−0.0152)	<2.00 (−0.0195)	<2.00 (−0.0195)	<2.00 (−0.0195)	<2.00 (−0.0195)
Oligoneuriidae	<2.00 (−0.0080)	<2.00 (−0.0107)	<2.00 (−0.0107)	<2.00 (−0.0107)	<2.00 (−0.0107)	2.13 (0.0106)	<2.00 (−0.0107)
Heptageniidae							
Stenonema	<2.00 (−0.0480)	<2.00 (−0.0393)	<2.00 (−0.0458)	<2.00 (−0.0369)	3.08 (−0.0172)	2.13 (−0.0267)	<2.00 (−0.0480)
Coleoptera							
Elmid larvae	<2.00 (−0.1652)	<2.00 (−0.1706)	<2.00 (−0.1684)	<2.00 (−0.1595)	6.15 (−0.1091)	<2.00 (−0.1706)	<2.00 (−0.1706)
Psephenidae	<2.00 (−0.0036)	<2.00 (−0.0036)	<2.00 (−0.0036)	<2.00 (−0.0036)	3.08 (0.0272)	<2.00 (−0.0036)	<2.00 (−0.0036)
Lepidoptera	2.71 (0.0271)	6.49 (0.0649)	<2.00 (0.0110)	0.00	0.00	0.00	0.00
Other							
Gammarus	0.00	0.00	<2.00 (0.0022)	0.00	0.00	0.00	3.70 (0.0370)
Hydracarina	<2.00 (−0.0004)	<2.00 (−0.0004)	<2.00 (−0.0004)	21.11 (0.2107)	18.46 (0.1842)	12.77 (0.1272)	3.70 (0.0366)
Leech	2.17 (0.0217)	<2.00 (0.0043)	<2.00 (0.0044)	0.00	0.00	0.00	0.00
Limpet	<2.00 (0.0081)	3.46 (0.0346)	<2.00 (0.0176)	0.00	4.62 (0.0462)	8.51 (0.0851)	0.00
Oligochaeta	<2.00 (−0.0102)	<2.00 (−0.0129)	<2.00 (−0.0129)	<2.00 (−0.0129)	<2.00 (−0.0129)	<2.00 (−0.0129)	<2.00 (−0.0129)
Incidental	7.05	7.79	8.79	3.33	4.62	0.00	0.00

TABLE A.2.—Extended.

	E. camurum	*E. flabellare*			*E. maculatum*	*E. tippecanoe*	
Prey taxa	Males	Juveniles	Females	Males	Juveniles	Juveniles	Males
Diptera							
Athericidae	2.17 (−0.0147)	<2.00 (−0.0199)	4.17 (0.0052)	<2.00 (−0.0364)	<2.00 (−0.0364)	<2.00 (−0.0206)	<2.00 (−0.0364)
Chironomidae	76.09 (0.5023)	58.68 (0.3282)	72.92 (0.4706)	47.06 (0.2120)	71.43 (0.4557)	53.97 (0.2811)	39.29 (0.1343)
Simuliidae	2.17 (0.0151)	<2.00 (0.0016)	<2.00 (−0.0067)	<2.00 (−0.0067)	<2.00 (−0.0067)	<2.00 (−0.0067)	<2.00 (−0.0067)
Trichoptera							
Hydropsychidae							
Cheumatopsyche	8.70 (−0.0445)	17.36 (0.0421)	6.25 (−0.0690)	32.35 (0.1920)	21.43 (0.0828)	23.81 (0.1066)	14.29 (0.0114)
Hydropsyche	<2.00 (−0.0635)	<2.00 (−0.0553)	<2.00 (−0.0635)	5.88 (−0.0047)	<2.00 (−0.0635)	11.11 (0.0476)	32.14 (0.2579)
Macronema	<2.00 (−0.0555)	3.31 (−0.0225)	4.17 (−0.0139)	5.88 (0.0033)	<2.00 (−0.0555)	<2.00 (−0.0397)	10.71 (0.0516)
Hydroptilidae	<2.00 (−0.0058)	<2.00 (−0.0058)	<2.00 (−0.0058)	<2.00 (−0.0058)	<2.00 (−0.0058)	<2.00 (−0.0058)	<2.00 (−0.0058)
Leptocericae	<2.00 (−0.0031)	<2.00 (−0.0031)	2.08 (0.0177)	<2.00 (−0.0031)	<2.00 (−0.0031)	<2.00 (0.0128)	<2.00 (−0.0031)
Philopotamidae	<2.00 (−0.0022)	<2.00 (−0.0022)	<2.00 (−0.0022)	5.88 (0.0566)	<2.00 (−0.0022)	<2.00 (−0.0022)	<2.00 (−0.0022)
Trichopteran pupae	<2.00 (−0.0009)	<2.00 (−0.0009)	<2.00 (−0.0009)	<2.00 (−0.0009)	<2.00 (−0.0009)	<2.00 (−0.0009)	<2.00 (−0.0009)
Ephemeroptera							
Caneidae	2.17 (0.0000)	<2.00 (−0.0135)	2.08 (−0.0009)	<2.00 (−0.0218)	<2.00 (−0.0218)	<2.00 −0.0218)	3.57 (0.0139)
Ephemerellidae							
Serratella	2.17 (−0.0405)	2.48 (−0.0374)	<2.00 (−0.0622)	2.94 (−0.0328)	7.14 (0.0092)	<2.00 (−0.0463)	<2.00 (−0.0622)
Ephemeridae	<2.00 (−0.0195)	<2.00 (−0.0195)	<2.00 (−0.0195)	<2.00 (−0.0195)	<2.00 (−0.0195)	<2.00 (−0.0195)	<2.00 (−0.0195)
Oligoneuriidae	<2.00 (−0.0107)	<2.00 (−0.0107)	<2.00 (−0.0107)	<2.00 (−0.0107)	<2.00 (−0.0107)	<2.00 (−0.0107)	<2.00 (−0.0107)
Heptageniidae							
Stenonema	<2.00 (−0.0480)	7.44 (0.0264)	4.17 (−0.0063)	<2.00 (−0.0480)	<2.00 (−0.0480)	3.17 (−0.0162)	<2.00 (−0.0480)
Coleoptera							
Elmid larvae	<2.00 (−0.1706)	<2.00 (−0.1706)	4.17 (−0.1289)	<2.00 (−0.1706)	<2.00 (−0.1706)	<2.00 (−0.1706)	<2.00 (−0.1706)
Psephenidae	<2.00 (−0.0036)	<2.00 (−0.0036)	<2.00 (−0.0036)	<2.00 (−0.0036)	<2.00 (−0.0036)	<2.00 (−0.0036)	<2.00 (−0.0036)
Lepidoptera	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Other							
Gammarus	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Hydracarina	6.52 (0.0648)	<2.00 (−0.0004)	<2.00 (−0.0004)	<2.00 (−0.0004)	<2.00 (−0.0004)	<2.00 (0.0154)	<2.00 (−0.0004)
Leech	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Limpet	0.00	<2.00 (0.0165)	0.00	0.00	0.00	0.00	0.00
Oligochaeta	<2.00 (−0.0129)	3.31 (0.0202)	<2.00 (−0.0129)	<2.00 (−0.0129)	<2.00 (−0.0129)	<2.00 (−0.0129)	<2.00 (−0.0129)
Incidental	0.00	7.44	0.00	0.00	0.00	7.94	0.00

TABLE A.2.—Extended.

Prey taxa	*E. variatum* Juveniles	*E. variatum* Females	*E. variatum* Males	*E. zonale* Juveniles	*E. zonale* Females	*E. zonale* Males
Diptera						
Athericidae	<2.00 (−0.0324)	<2.00 (−0.0254)	<2.00 (−0.0204)	<2.00 (−0.0319)	<2.00 (−0.0273)	<2.00 (−0.0337)
Chironomidae	52.44 (0.2658)	41.76 (0.1590)	19.79 (−0.0607)	82.06 (0.5621)	87.84 (0.6199)	78.10 (0.5224)
Simuliidae	<2.00 (−0.0026)	4.40 (0.0373)	3.21 (0.0254)	2.24 (0.0158)	4.59 (0.0392)	11.29 (0.1063)
Trichoptera						
Hydropsychidae						
Cheumatopsyche	18.29 (0.0514)	7.69 (−0.0546)	14.44 (0.0129)	8.52 (−0.0463)	<2.00 (−0.1269)	3.31 (−0.0984)
Hydropsyche	15.04 (0.0869)	20.88 (0.1453)	28.34 (0.2199)	4.04 (−0.0232)	2.29 (−0.0406)	3.17 (−0.0318)
Macronema	4.88 (−0.0068)	2.20 (−0.0336)	6.95 (0.0140)	<2.00 (−0.0510)	<2.00 (−0.0532)	<2.00 (−0.0445)
Hydroptilidae	<2.00 (0.0105)	5.49 (0.0492)	3.74 (0.0317)	<2.00 (−0.0058)	<2.00 (−0.0012)	<2.00 (0.0052)
Leptoceridae	<2.00 (0.0010)	<2.00 (−0.0031)	<2.00 (0.0022)	<2.00 (−0.0031)	<2.00 (−0.0031)	<2.00 (−0.0031)
Philopotamidae	<2.00 (−0.0022)	<2.00 (−0.0022)	<2.00 (−0.0022)	<2.00 (−0.0022)	<2.00 (−0.0022)	<2.00 (−0.0022)
Trichopteran pupae	<2.00 (−0.0009)	<2.00 (−0.0009)	<2.00 (−0.0009)	<2.00 (−0.0009)	<2.00 (−0.0009)	<2.00 (0.0005)
Ephemeroptera						
Caenidae	<2.00 (−0.0177)	<2.00 (−0.0218)	<2.00 (−0.0164)	<2.00 (−0.0083)	<2.00 (−0.0218)	<2.00 (−0.0218)
Ephemerellidae						
Serratella	4.47 (−0.0175)	4.40 (−0.0182)	5.88 (−0.0034)	<2.00 (−0.0577)	<2.00 (−0.0553)	<2.00 (−0.0581)
Ephemeridae	<2.00 (−0.0155)	<2.00 (−0.0086)	2.67 (0.0072)	<2.00 (−0.0195)	<2.00 (−0.0195)	<2.00 (−0.0195)
Oligoneuriidae	<2.00 (−0.0025)	<2.00 (0.0003)	2.67 (0.0161)	<2.00 (−0.0107)	<2.00 (−0.0107)	<2.00 (−0.0093)
Heptageniidae						
Stenonema	<2.00 (−0.0398)	<2.00 (−0.0040)	5.35 (0.0055)	<2.00 (−0.0435)	<2.00 (−0.0457)	<2.00 (−0.0480)
Coleoptera						
Elmid larvae	<2.00 (−0.1665)	6.59 (−0.1486)	<2.00 (−0.1706)	<2.00 (−0.1706)	<2.00 (−0.1706)	<2.00 (−0.1692)
Psephenidae	<2.00 (−0.0036)	<2.00 (−0.0036)	<2.00 (−0.0036)	<2.00 (−0.0036)	<2.00 (−0.0036)	<2.00 (−0.0036)
Lepidoptera	0.00	0.00	<2.00 (0.0107)	0.00	0.00	<2.00 (0.0014)
Other						
Gammarus	0.00	0.00	0.00	0.00	0.00	0.00
Hydracarina	<2.00 (0.0036)	<2.00 (0.0215)	<2.00 (0.0049)	<2.00 (−0.0004)	<2.00 (−0.0004)	<2.00 (−0.0004)
Leech	0.00	0.00	0.00	0.00	0.00	0.00
Limpet	0.00	0.00	<2.00 (0.0053)	0.00	<2.00 (0.0092)	0.00
Oligochaeta	<2.00 (−0.0129)	<2.00 (−0.0129)	<2.00 (−0.0129)	<2.00 (−0.0129)	<2.00 (−0.0129)	<2.00 (−0.0129)
Incidental	4.88	4.40	6.95	3.14	5.28	4.13

TABLE A.3.—Percent of prey by size-class and Strauss's electivity index (*L*; in parentheses) of prey size consumed by darters (*Etheostoma* and *Percina*) in April and July 1988. The range for Strauss's *L* is −1 to +1; positive values indicate selection of size-class, negative values indicate avoidance, and values near zero indicate opportunistic feeding by darters. Females and males are adults.

Darter species and group	1–2 mm		3–4 mm		5–6 mm	
	Apr	Jul	Apr	Jul	Apr	Jul
E. blennioides						
Juveniles	51.74	73.17	46.11	23.58	2.14	2.71
	(0.3754)	(0.3661)	(0.0200)	(−0.2200)	(−0.2565)	(−0.0871)
Females	37.38	74.89	58.65	17.75	3.73	6.06
	(0.2318)	(0.3833)	(0.1454)	(−0.2783)	(−0.2406)	(−0.0536)
Males	41.08	53.63	56.37	34.95	2.23	7.25
	(0.2688)	(0.1706)	(0.1226)	(−0.1063)	(−0.2557)	(−0.0416)
E. caeruleum						
Juveniles	64.40	81.11	31.94	16.67	3.66	2.22
	(0.5020)	(0.4455)	(−0.1217)	(−0.2891)	(−0.2413)	(−0.0919)
Females	43.42	58.46	50.87	33.85	4.96	6.15
	(0.2922)	(0.2190)	(−0.0676)	(−0.1173)	(−0.2283)	(−0.0526)
Males	59.26	74.47	34.81	14.89	4.44	6.38
	(0.4506)	(0.3791)	(−0.0929)	(−0.3069)	(−0.2335)	(−0.0503)
E. camurum						
Juveniles	50.32	77.78	45.81	14.81	3.23	7.41
	(0.3612)	(0.4122)	(0.0170)	(−0.3076)	(−0.2457)	(−0.0401)
Females	40.70		55.81		2.91	
	(0.2650)		(0.1171)		(−0.2489)	
Males		67.39		28.26		4.35
		(0.3083)		(−0.1732)		(−0.0707)
E. flabellare						
Juveniles	33.33	72.73	53.99	19.83	9.39	7.44
	(0.0802)	(0.3617)	(0.2256)	(−0.2575)	(−0.2779)	(−0.0398)
Females	34.52	79.17	58.33	16.67	4.76	2.08
	(0.2032)	(0.4261)	(0.1422)	(−0.2891)	(−0.2303)	(−0.0933)
Males	31.08	52.94	50.68	20.59	12.84	14.71
	(0.1688)	(0.1638)	(0.0657)	(−0.2499)	(−0.1496)	(0.0329)
E. maculatum						
Juveniles		75.00		21.43		3.57
		(0.3844)		(−0.2415)		(−0.0785)
Females	43.97		41.38		9.48	
	(0.2977)		(−0.0273)		(−0.1831)	
Males	30.30		54.55		3.03	
	(0.1610)		(0.1044)		(−0.2476)	
E. tippecanoe						
Juveniles		66.67		30.16		3.17
		(0.3011)		(−0.1542)		(−0.0824)
Males		60.71		28.57		7.14
		(0.2415)		(−0.1701)		(−0.0427)
E. variatum						
Juveniles	41.31	58.13	49.42	32.52	6.56	8.13
	(0.2711)	(0.2157)	(0.0531)	(−0.1306)	(−0.2123)	(−0.0329)
Females	29.38	36.26	56.29	43.96	10.11	12.09
	(0.1518)	(−0.0030)	(0.1218)	(−0.0162)	(−0.1769)	(0.0067)
Males	37.96	24.57	45.99	36.57	7.30	20.57
	(0.2376)	(−0.1199)	(0.0188)	(−0.0901)	(−0.2050)	(0.0915)
E. zonale						
Juveniles	67.89	84.75	32.11	15.25	0.00	0.00
	(0.5370)	(0.4819)	(−0.1200)	(−0.3033)		
Females	54.50	79.82	44.23	19.95	1.27	0.23
	(0.4030)	(0.4325)	(0.0012)	(−0.2563)	(−0.2652)	(−0.1119)
Males	34.12	71.35	62.56	27.27	3.32	1.38
	(0.1992)	(0.3479)	(0.1845)	(−0.1831)	(−0.2448)	(−0.1004)
P. evides						
Females	58.06		11.29		24.19	
	(0.4387)		(−0.3282)		(−0.0360)	

TABLE A.3.—Extended.

Darter species and group	7–8 mm		9–10 mm		11–13 mm	
	Apr	Jul	Apr	Jul	Apr	Jul
E. blennioides						
Juveniles	0.00	0.54 (−0.0337)	0.00	0.00	0.00	0.00
Females	0.24 (−0.0762)	0.87 (−0.0304)	0.00	0.00	0.00	0.00
Males	0.32 (−0.0754)	2.42 (−0.0149)	0.00	1.54 (−0.0046)	0.00	0.00
E. caeruleum						
Juveniles	0.00	0.00	0.00	0.00	0.00	0.00
Females	0.74 (−0.0711)	1.54 (−0.0237)	0.00	0.00	0.00	0.00
Males	1.48 (−0.0637)	2.13 (−0.0178)	0.00	2.13 (0.0013)	0.00	0.00
E. camurum						
Juveniles	0.65 (−0.0721)	0.00	0.00	0.00	0.00	0.00
Females	0.58 (−0.0727)		0.00		0.00	
Males		0.00		0.00		0.00
E. flabellare						
Juveniles	3.29 (0.0326)	0.00	0.00	0.00	0.00	0.00
Females	2.38 (−0.0547)	2.08 (−0.0183)	0.00	0.00	0.00	0.00
Males	5.41 (−0.0245)	5.88 (0.0197)	0.00	5.88 (0.0388)	0.00	0.00
E. maculatum						
Juveniles		0.00		0.00		0.00
Females	2.59 (−0.0527)		1.72 (−0.0069)		0.86 (−0.0276)	
Males	6.06 (−0.0179)		6.06 (0.0364)		0.00	
E. tippecanoe						
Juveniles		0.00		0.00		0.00
Males		3.57 (−0.0034)		0.00		0.00
E. variatum						
Juveniles	2.32 (−0.0554)	1.22 (−0.0269)	0.39 (−0.0203)	0.00	0.00	0.00
Females	4.00 (−0.0386)	5.49 (0.0159)	0.24 (−0.0218)	1.10 (−0.0090)	0.00	1.10 (0.0057)
Males	6.57 (−0.0129)	13.14 (0.0923)	0.73 (−0.0169)	4.00 (0.0200)	1.46 (−0.0217)	1.14 (0.0061)
E. zonale						
Juveniles	0.00	0.00	0.00	0.00	0.00	0.00
Females	0.00	0.00	0.00	0.00	0.00	0.00
Males	0.00	0.00	0.00	0.00	0.00	0.00
P. evides						
Females	4.84 (−0.0302)		1.61 (−0.0080)		0.98 (−0.0363)	