Habitat and food resource partitioning among four species of darters (Percidae: Etheostoma) in a southern Ontario stream

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Habitat and food resource partitioning among four species of darters (Percidae: *Etheostoma*) in a southern Ontario stream

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Resource partitioning among four species of darters (Percidae: *Etheostoma*) in an Ontario stream was investigated by determining diet and relative abundance in two habitats. The four species partitioned both food and habitat resources. *E. caeruleum* and *E. flabellare* dominated the riffles; the former took prey from rock surfaces, the latter took prey from between and beneath rocks. *Etheostoma microperca* and *E. nigrum* dominated the weed beds; the former feeding on prey on and around plants, the latter feeding on benthic prey. Diets were closely related to morphology, but habitat utilization was not. Determining the importance of habitat versus food partitioning is difficult, because microhabitat and foraging habitat may be nearly identical.

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L'étude de la diète alimentaire et de l'abondance relative de quatre espèces de dards (Percidae: *Etheostoma*) dans deux habitats d'un ruisseau de l'Ontario ont permis de déterminer la séparation des ressources. Il y a de fait séparation des ressources alimentaires et de l'habitat entre les quatre espèces. *Etheostoma caeruleum* et *E. flabellare* sont les espèces dominantes des eaux rapides où la première se nourrit à la surface des pierres et la seconde s'alimente entre les pierres ou en-dessous. *Etheostoma microperca* et *E. nigrum* vivent surtout dans la végétation; la première chasse des proies vivant sur les plantes ou tout près, alors que la seconde recherche des proies benthiques. La diète est fortement reliée à la morphologie, mais l'utilisation de l'habitat ne l'est pas. Il est difficile de déterminer l'importance relative de la séparation de l'habitat et de la séparation des ressources alimentaires, car l'habitat de recherche de nourriture et le microhabitat peuvent être à peu près identiques.

[Traduit par le journal]

Introduction

If Gause's (1934) competitive exclusion principle is valid, then resource partitioning among coexisting species is an expected consequence of past or present competition. Analyses of resource partitioning are an integral part of community structure studies (Cody and Diamond 1975, p. 7), although the philosophical basis for such analyses has been criticized (Peters 1976). Animals partition resources along three axes (listed in order of importance): habitat, food, and time (Schoener 1974). Fisheries investigators have observed partitioning along all three axes (see Helfman 1978 for a review), but habitat partitioning appears to be the most important (Gorman and Karr 1978).

Morphology is related to ecology (Hespenheide 1973), and morphological differences have often been related to resource utilization differences among coexisting species (Schoener 1974). Adaptations for resource utilization may be physiological and behav-

ioural, as well as morphological, but morphological features are a powerful indicator of community structure in stream fishes (Gatz 1979a, 1979b).

Speciation in darters (Etheostomatini) has been extensive, and coexistence of two or more species is common in Ontario waters (Scott and Crossman 1973). The ecology of darters in Ontario has received little attention, despite their importance in smaller waterways. This study investigates resource partitioning among four coexisting species of *Etheostoma*, *E. caeruleum*, *E. flabellare*, *E. microperca*, and *E. nigrum*, in Irvine Creek, Ontario. Partitioning of habitat and food resources was examined by analyzing diet and habitat utilization; partitioning of time was considered unimportant as darters are visual feeders, active during daylight only (Adamson and Wissing 1977; Cordes and Page 1980; Daugherty *et al.* 1976; Mathur 1973; Roberts and Winn 1962; Schenk and Whiteside 1977). Characteristics of the mouth and body of the four species were measured and related to diet and habitat utilization.

Materials and methods

Study site

Irvine Creek is located in Wellington County, Ontario, and is a tributary of the Grand River (Fig. 1). The creek is divided into two main habitat types, riffles and weed beds. Riffles are
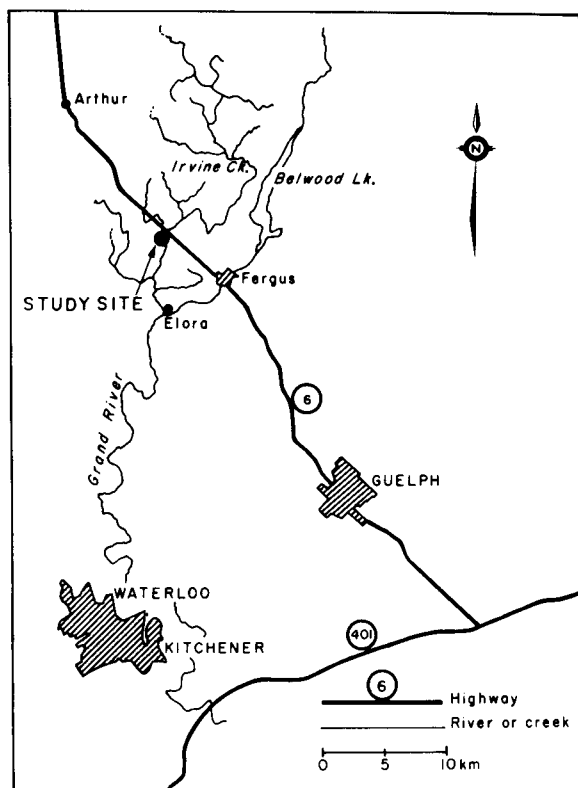
FIG. 1. Location of the study site.

areas of fast current (0.75–1.15 m/s) and shallow depth (10–30 cm), with a rubble substrate. Weed beds are areas of slow flow (0–0.20 m/s) and moderate depth (25–100 cm), with a substrate of rubble, fine sand, and silt supporting beds of *Potomageton*. Depth and flow measurements given are early summer values and are greater during spring and fall spates. Some intermediate habitats, similar to the raceways of Winn (1958), or the channels of Smart and Gee (1979), were also present in the sample area, but were extremely variable in flow, depth, and extent of plant cover, and were not considered.

Collection of fish samples

Fish were collected at four riffle stations and three weed-bed stations on July 15, 16, August 15, 16, November 2, 3, 1977, and June 15, 1978. Darters were captured in the riffles with a kick-net as described by Karr (1963), and in the weed beds with a 5-m, 5-mm mesh two-man seine. At each riffle site, collecting was terminated after 10–15 min of kicking; at each weed bed site three 5–10 m passes with the seine net were made over different areas. All darters captured at each site were placed in a screened holding cage, then identified and counted after the site had been completely sampled. A maximum of 10–15 fish per species per site was preserved in 4% formaldehyde. The remaining fish were released. Preserved fish were transferred to 95% ethanol in the laboratory, and stored until needed for stomach analysis.

Stomach analysis

The standard lengths of all preserved fish were measured, and their stomach contents were examined. A modified points method (Hynes 1950, 1970) was used to determine diet composition by volume. For each fish, points were awarded on the basis of stomach fullness, then divided among the contributing items.

Chironomidae larvae were treated as a single item in determining volumetric diet composition. A separate analysis, using the numbers method (Hynes 1950), was carried out on the Chironomidae alone.

Interspecific diet overlaps were calculated using the percent similarity coefficient (P_s) described by Whittaker and Fairbanks (1958). This is the simplest of overlap measures, unencumbered by any assumptions (Hurlbert 1978). Hurlbert criticized P_s as an overlap index only because it ignores resource abundance levels; this criticism does not apply to this study as resource abundance levels were not measured. Overlaps were calculated using diet compositions with food categories at the lowest taxonomic (usually genus) level. Numerical contributions of individual Chironomidae genera were converted to volumetric contributions by dividing the volumetric contribution of all Chironomidae among the contributing genera according to their numerical contributions.

Morphological characteristics

Six morphological characteristics were examined, three related to body form (relative caudal peduncle length, relative pectoral fin length, flatness or lateral compression index) and three related to mouth structure (relative mouth height, mor position, snout protrusibility). The body form characterist. give an indication of the manoeuverability and swimming ability of the fish; mouth structure characteristics give an indication of the size and type of potential prey. Ten formalin-preserved fish of each species, collected from Irvine Creek in late August 1979, were examined. Measurements of body form characteristics were made to the nearest 0.1 mm using calipers; measurements of mouth height were made with an ocular micrometer to the nearest 0.2 mm.

Relative pectoral fin length and flatness index were measured as described in Gatz (1979a); these characteristic are presumably directly related to lateral and low-speed manoeu-verability (Alexander 1967; Kanep 1971; Nikolskii 1933). Caudal peduncle length was measured as described by Hubbs and Lagler (1958) and divided by standard length to give relative peduncle length. Caudal peduncle length is presumably directly related to swimming ability (Kanep 1971).

Relative mouth height was measured as described by Gatz (1979a) and is directly related to maximum and optimum prey size (Werner 1974). Mouth positions were defined as described by Gatz (1979a); protrusibility was scored as the presence or absence of protrusible premaxillae. These two characteristics determine the orientation of the mouth opening.

Interspecific morphological differences were analyzed using one-way analyses of variance (ANOVA's) (Kleinbaum and Kupper 1978). An ANOVA was carried out for each quantitative characteristic; each species was treated as a different level of the same factor. F-statistics were computed

r each ANOVA and pair-wise comparisons between species means were done using Tukey's test (Kleinbaum and Kupper 1978).

Results

Habitat

Etheostoma flabellare and *E. caeruleum* were numerically dominant in the riffles whereas *E. microperca* and *E. nigrum* were dominant in the weed beds (Fig. 2). The latter two species were extremely rare or absent in the riffles whereas a few *E. flabellare* and *E. caeruleum* were present in the weed beds during all sampling periods.

Diet

Hydropsychidae and Chironomidae larvae were the most important items in the diets of the riffle-dwelling *E. flabellare* and *E. caeruleum* during all sampling periods (Fig. 3). Hydropsychidae larvae were slightly more important for *E. flabellare* whereas *Antocha* and Hydroptilidae larvae were more important for *E. caeruleum*. Within the Chironomidae, Orthocladiinae and Tanytarsini were more important for *E. caeruleum* than for *E. flabellare*; Chironomini and Diamesinae were more important for *E. flabellare* (Fig. 4).

In the weedbeds, *E. microperca* and *E. nigrum* fed on Chironomidae larvae and, to a lesser extent, on Ephemeroptera nymphs and microcrustaceans (Fig. 3). *E. croperca* ate Baetidae nymphs whereas *E. nigrum* ate *aenis* nymphs. Interspecific differences in consumption of the three microcrustacean classes were evident only in November when *E. microperca* fed on Cladocera and Copepoda whereas *E. nigrum* fed on Ostracoda. Within the Chironomidae, Chironomini and *Cladotanytarsus* were more important for *E. nigrum* than for *E. microperca*; Orthocladiinae and Tanytarsini (except *Cladotanytarsus*) were more important for *E. microperca* (Fig. 4). Despite the seasonal diet changes evident from Figs. 3 and 4, diet overlaps between the dominant species in each habitat were relatively constant throughout the four sampling periods (Table 1). Diet overlaps in the riffles were consistently greater than overlaps in the weed beds.

Morphology

The sizes of the fish used in the diet analyses are presented in Table 2. The four species can be ranked in the following order of increasing size: *E. microperca*, *E. flabellare*, *E. nigrum*, *E. caeruleum*. The size ranges of the three largest species overlap considerably.

Morphological characteristics for the four species are also presented in Table 2. *Etheostoma microperca* is the most compressed fish, with the largest relative pectoral fin length and relative caudal peduncle length. *Etheostoma flabellare* scored low on all three of these charac-
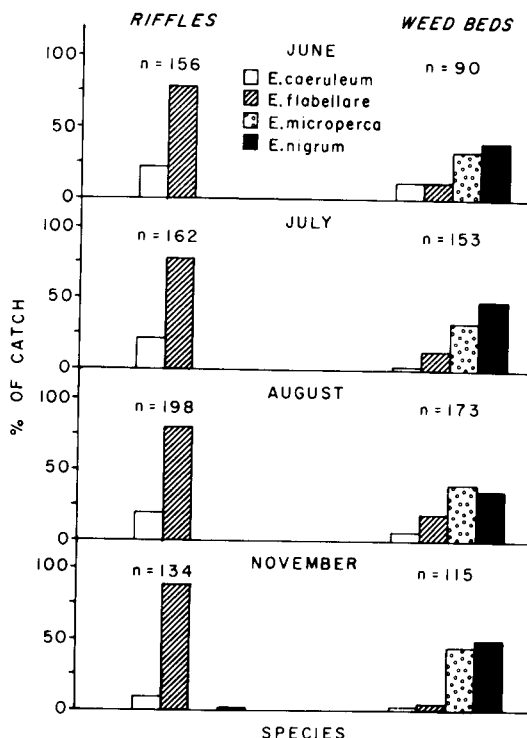

FIG. 2. The monthly relative abundances of the four *Etheostoma* species in riffles and weed beds; *n*, total number of darters captured per month in each habitat type.

teristics, having either the lowest value or a value not significantly different from the lowest value. *Etheostoma nigrum* and *E. caeruleum* are intermediate between the other two species in terms of body form, with *E. caeruleum* being more compressed, but with a smaller peduncle. Relative pectoral fin lengths did not differ significantly between the two species. The four species were ranked in the following order of increasing relative mouth height: *E. microperca*, *E. nigrum*, *E. caeruleum*, *E. flabellare*. Relative to *E. microperca* and *E. flabellare*, which have terminal mouths, *E. caeruleum* and *E. nigrum* have subterminal mouths. Only *E. nigrum* possesses protrusible premaxillae.

Discussion

The four darter species in Irvine Creek can be divided into two habitat groups, riffle species (*E. caeruleum*, *E. flabellare*) and weed bed species (*E. microperca*, *E. nigrum*). Within each habitat, food resources were partitioned as consistent diet differences were evident. The following discussion considers how diets are related to morphology, why habitat utilization is not closely related to morphology, and why food partitioning appears as important as habitat partitioning among the four species of darters.
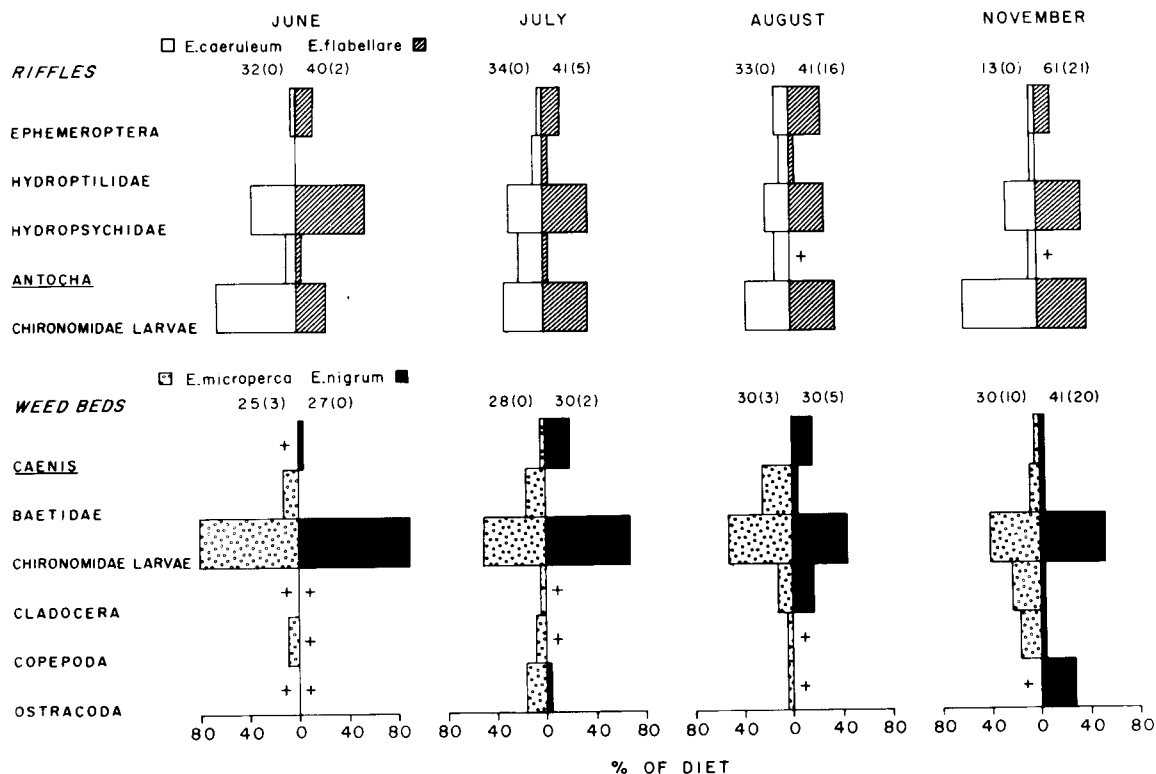
FIG. 3. The monthly volumetric contributions of some important prey items of *E. caeruleum* and *E. flabellare* from riffles ar *E. microperca* and *E. nigrum* from weed beds; n, numbers of each species examined (numbers of fish with empty stomachs); ̚ _ contribution of prey item less than 2%.

TABLE 1. Diet overlaps (P_s) between the dominant species in each habitat during the four sampling periods. Greater P_s values indicate greater overlap

Habitat	Dominant species	June	July	August	November
Riffles	E. caeruleum E. flabellare	64	64	56	54
Weed beds	E. microperca E. nigrum	40	35	30	26

The consistency of diet overlaps in both habitats suggests that well-defined differences in feeding styles were operative throughout the study period, despite seasonal diet changes. Differences in feeding styles can be related to morphology. In the weed beds, *E. microperca* is adapted for feeding on prey active on and around plants, whereas *E. nigrum* is adapted for feeding on sedentary benthic prey. *Etheostoma microperca* has a terminal mouth orienting the mouth opening towards prey anterior to the fish. With its long peduncle, long pectoral fins, and laterally compressed body, *E. microperca* is fast and manoeuverable enough to capture active prey. Climbers, clingers, and swimmers such as Baetidae nymphs, Tanytarsini (e.g., *Tanytarsus*) and Orthocladiinae (e.g., *Corynoneura, Cricotopus*) (Mer-

ritt and Cummins 1978) were the preferred prey of *E. microperca*. Most of the prey items eaten by *E. microperca* were small, as this species has the smallest mouth and body of the four species studied. Forbes (1880), Burr and Page (1979), and Cordes and Page (1980) also found that small items such as microcrustaceans and Chironomidae are important in the diet of *E. microperca*.

Etheostoma nigrum has a subterminal mouth, with protrusible premaxillae, and can therefore extend the upper jaw well beyond the lower, orienting the mouth opening towards prey below the fish. *Etheostoma nigrum* has a more rounded body than *E. microperca*, and is therefore less manoeuverable and less able to take active prey. Sprawlers such as *Caenis*, and the tub
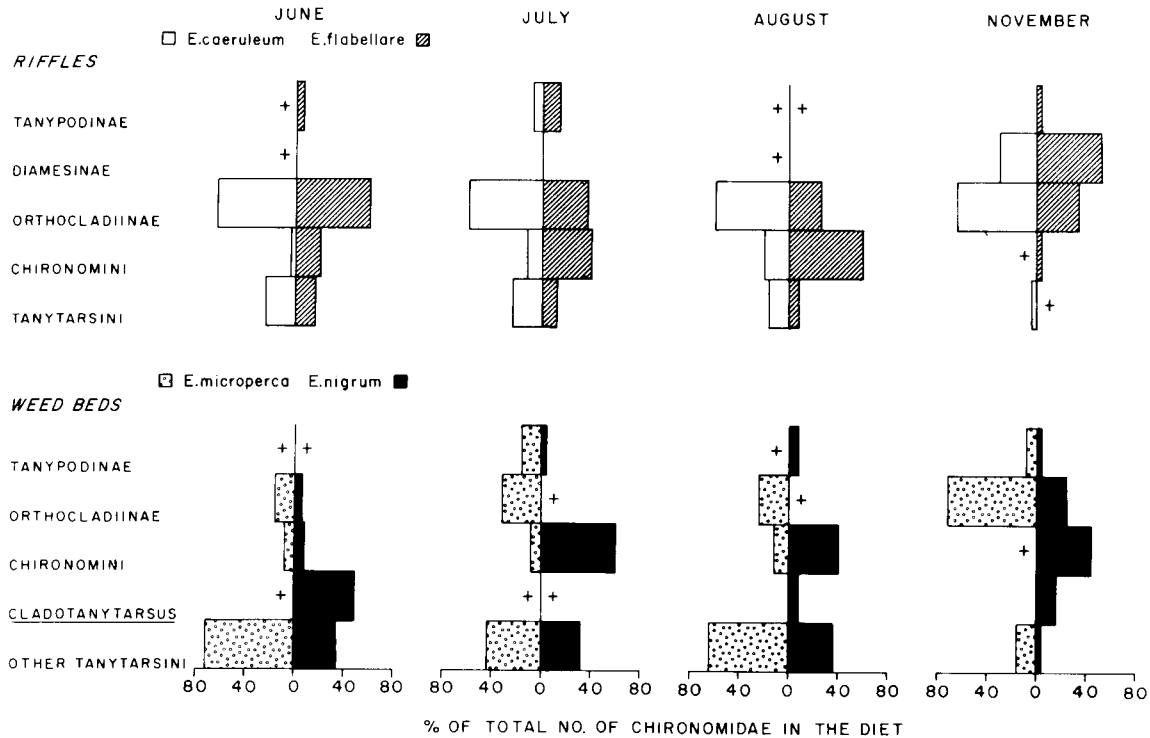
Fig. 4. The monthly composition of the Chironomidae found in the diets of *E. caeruleum* and *E. flabellare* from riffles and *E. microperca* and *E. nigrum* from weed beds; n, as in Fig. 3; +, relative abundance of items of less than 2% of the total number of Chironomidae in the diet.

TABLE 2. Morphological characteristics of the four *Etheostoma* species

Characteristic	Species				Significant pair-wise comparisons
	E.c.	*E.f.*	*E.m.*	*E.n.*	
Standard length (mm)					
Mean	41.5	34.8	23.6	37.2	Not measured
Range	30–52	21–52	16–30	23–49	
Relative caudal peduncle length	0.217	0.222	0.321	0.279	All pairs but *E.c.–E.f.*
Relative pectoral fin length	0.260	0.220	0.279	0.258	*E.f.–E.c., E.f.–E.m., E.f.–E.n.*
Flatness index (depth/width)	1.42	1.19	1.63	1.24	All pairs but *E.f.–E.n.*
Relative mouth height	0.0375	0.0455	0.0305	0.0338	All pairs
Mouth position	S	T	T	S	—
Protrusible premaxillae	—	—	—	+	—

NOTE: Interspecific morphological differences were significant for each quantitative characteristic (ANOVA, F-test, $p < 0.05$). Pairwise comparisons were done using Tukey's test (level of significance, $p < 0.05$). Abbreviations: *E.c., E. caeruleum; E.f., E. flabellare; E.m., E. microperca; E.n., E. nigrum;* T, terminal; S, subterminal.

dwelling Chironomini (Merritt and Cummins 1978) formed a major part of the diet of *E. nigrum*. The obvious adaptations of *E. nigrum* for bottom feeding have been suggested, and confirmed, by Lotrich (1973) and Smart and Gee (1979). The evidence seems strong enough to make an inference about the habits of *Cladotanytarsus*. Merritt and Cummins (1978) do not list any habits for this genus, but it was eaten by *E. nigrum* and not by *E. microperca*, suggesting that the

species of *Cladotanytarsus* present in Irvine Creek are benthic tube-dwellers or sprawlers.

The diet differences between the two riffle species may also be related to morphological differences. *Etheostoma caeruleum*, with its subterminal mouth, can take prey from rock surfaces. This species is also laterally compressed, and therefore manoeuverable, and may be able to take active prey, provided it remains within the area of reduced flow just above the substrate.

Clingers and climbers such as Tanytarsini (e.g., *Tanytarsus*, *Paratanytarsus*, *Rheotanytarsus*), Orthocladiinae (primarily *Cricotopus*), *Antocha*, and Hydroptilidae (Merritt and Cummins 1978) were more important for *E. caeruleum* than for *E. flabellare*. *Etheostoma flabellare*, with a terminal mouth, would have to orient itself vertically, risking downstream displacement, to graze on rock surfaces. *Etheostoma flabellare* could, however, remain in the reduced flow layer while feeding on prey under or between rocks. Sprawlers and burrowers such as Chironomini, Diamesinae (primarily *Potthastia*), and Ephemeroptera (*Caenis*, Heptageniidae) (Merritt and Cummins 1978) were important in the diet of *E. flabellare*.

The feeding styles of the two riffle species presented above, while consistent with the observed diet differences between the two species, are not supported by evidence from the literature. Adamson and Wissing (1977) found little difference between the diets of these two species in an Ohio stream, indicating little difference in feeding styles. In the present study, however, it should be noted that diet overlaps were consistently higher for the riffle species than for the weed bed species. The feeding styles of the two riffle species have not been examined in the laboratory, but personal observations indicate that in aquaria, *E. caeruleum* remains largely on top of, and *E. flabellare* beneath, rocks. *Etheostoma flabellare* males hold territories under rocks (Winn 1958), and therefore may restrict *E. caeruleum* to foraging on rock surfaces.

Body form characteristics previously identified as good indicators of habitat preference do not appear related to the distribution of the four species studied. Only one morphological characteristic, caudal peduncle length, clearly separates riffle from weed bed species. *Etheostoma caeruleum* and *E. flabellare* have significantly shorter peduncles than either *E. microperca* or *E. nigrum*, but caudal peduncle length is difficult to relate to habitat preference. If peduncle length is related to straight-ahead swimming ability, a long peduncle would obviously aid weed-bed species in evading predators and pursuing prey, but would also enable riffle species to maintain or regain position in a current. Gatz (1979a) found little correlation between peduncle length and habitat preference in stream fishes.

Gatz (1979a) considered long pectoral fins, associated with low-speed manoeuvering, and lateral compression, associated with lateral manoeuverability, characteristic of fishes inhabiting slower waters. This was not the case in this study. Pectoral fin length does not differ significantly among three of the species studied, but *E. flabellare* does have significantly shorter pectoral fins than those three species. The pectoral fins of all four darter species may function in vertical movement, as well as in low speed manoeuvering, as these fish lack a swim bladder. Selachians and some

bladderless teleosts utilize their pectorals largely to provide lift (Alexander 1967). Vertical movement would not be of benefit in fast water, but pectoral fins can also be used for braking (Alexander 1967), and may be used to maintain position in strong currents. Therefore, the multiple functions of the pectorals make pectoral fin length an equivocal habitat indicator for the bladderless darters.

If lateral compression is characteristic of slow water fish, and roundness (which reduces drag) characteristic of fast water fish, as Gatz (1979a) and Alexander (1967) suggest, then the two compressed species (*E. caeruleum, E. microperca*) should dominate the weed beds, and the two rounded species (*E. flabellare, E. nigrum*) should dominate the riffles. However, one rounded and one compressed species occurred in each habitat.

There are several explanations for the lack of a relationship between morphology and habitat utilization. First, morphological characteristics other than those measured may be important. Second, many structures (i.e., pectoral fins) have multiple functions, and may represent a compromise adaptation to more than one habitat variable (Bock 1977). Bock argues further that structures do not function independently of each other, limiting the occurrence of direct relationships between single structures and single environmental variables. Third, availability of suitable prey may override other considerations, such as predator avoid' ance, in determining distribution and dominance. Fo. example, *E. nigrum* may be uncommon in riffles, despite its rounded body, because sedentary benthic prey may be less abundant there than in weed beds.

Gorman and Karr (1978) and Gatz (1979a, 1979b) consider that stream fishes are habitat, not feeding, specialists, and Mendelson (1975) and Gibbons and Gee (1972) found habitat partitioning to be more important than food partitioning for coexisting Cyprinidae. Coexisting darter species, however, appear to segregate by partitioning food resources in the same habitat (Lotrich 1973; Smart and Gee 1979). In this study, food partitioning was as important as habitat partitioning in segregating the four darter species. The relative importance of habitat partitioning versus food partitioning may be difficult to assess. Darters are primarily benthic and nonmobile, and their foraging habitat may be identical to their microhabitat. In this study, if the weed bed habitat had been divided into strata, we might have found that the two dominant species segregated by partitioning the habitat vertically, thus occupying different strata.

In summary, the four darter species in Irvine Creek showed morphological differences which allowed them to partition food resources. The morphological characteristics measured were not closely related to habitat utilization. Food partitioning appeared to be as important as habitat partitioning for the four species, but tl

two types of resource partitioning may be difficult to separate.

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