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FEEDING RELATIONSHIPS AMONG FOUR RIFFLE-INHABITING STREAM FISHES

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ABSTRACT

The diel feeding period, dietary composition, and prey size relative to fish size were compared between four riffle-inhabiting stream fishes, *Cottus carolinae* (banded sculpin), *Etheostoma caeruleum* (rainbow darter), *E. flabellare* (fantail darter), and *E. spectabile* (orangethroat darter) in Illinois. The darters exhibited similar diurnal feeding patterns, while *Cottus* showed a crepuscular feeding pattern. Diet compositions of the darters were more similar to each other than to *Cottus*, based on cluster analysis of percentage similarity measures. These data also suggested that feeding habitat may differ in stream flow, with *Cottus* being the most rheophyllic, decreasing in the darters, *E. flabellare* and *E. caeruleum*, and *E. spectabile* having the most lentic diet. Significant but weak correlations were found between prey size and fish gape width in all fish species. The correlation was strongest in *Cottus*, which has the broadest fish size range of the four species examined. This suggests that in natural populations with naturally broad body size variation, prey size and fish size may be strongly correlated, allowing effective food resource partitioning among species and size classes within species.

INTRODUCTION

The study presented here was conducted to investigate the extent of overlap in resource utilization, particularly feeding period, prey size, and dietary composition among four small coexisting freshwater stream fishes. These species, including three darters (Percidae) and the banded sculpin (Cottidae), occur syntopically in riffle habitats of cool upland streams throughout much of the highland region of the eastern U.S. (Lee et al. 1980). Much literature has accumulated over the years on the biology of darters, including two recent books on their systematics and biology

(Page 1983, Kuehne and Barbour 1983). Several studies have been conducted on the food and feeding behavior of various darter species (e.g., Forbes 1880, Turner 1921, Winn 1958, Scalet 1972, Schenck and Whiteside 1977), including many life history studies which contain food habit information (Page 1983 and references therein). However, relatively little information has been published on the feeding periodicity and comparative feeding relationships of syntopic species (Mathur 1973, Adamson and Wissing 1977, Smart and Gee 1979, Cordes and Page 1980, Bek and Surat 1982, Matthews et al. 1982, Paine et al. 1982, Hlohowskyj and White 1983). Less information is available on the biology and feeding habits of freshwater sculpins (Koster 1937, Bailey 1952, Zarbock 1952, Northcote 1954, Daiber 1956, Patten 1962, Minckley et al. 1963, Straskraba et al. 1966, Pasch and Lyford 1972, Novak and Estes 1974, Mason and Machidori 1976, Daniels and Moyle 1978), which often co-inhabit cool, rocky riffles with darters in areas of range overlap.

In this study the diel feeding relationships of 4 riffle-inhabiting fish species were investigated in Hutchins Creek in southern Illinois. Species studied are the rainbow darter (*Etheostoma caeruleum*), fantail darter (*E. flabellare*), orangethroat darter (*E. spectabile*), and banded sculpin (*Cottus carolinae*). Diel feeding periodicities, diet compositions and prey size relative to fish size were determined for each species and compared between species. At the study area these species and the slender madtom (*Noturus exilis*) represent the riffle ichthyofauna. Trophic habits of the nocturnal *N. exilis* were presented earlier by Mayden and Burr (1981).

Study Site

Hutchins Creek is a 3rd order spring-fed stream draining primarily oak-hickory forests, with some pastured and cultivated land within the watershed. Stream habitats include gravel riffles and gravel and slate-bedded pools separated by gravel raceways. Stream width ranges from 1.5 to 7.5 m; water depth from 4 cm in riffles to about 2 m in pools. Annual stream temperatures range from 1° C in January to 32° C in July. Stream flow is continuous. The sample site consisted of two consecutive riffle areas (approx. 2.4 m × 3.6 m each and approx. 30 m apart), located 4 mi NW of Anna; SW ¼ of Sec. 25, R3W, T11S, Union Co., Illinois.

Materials and Methods

About five specimens each of *C. carolinae*, *E. caeruleum*, *E. flabellare* and *E. spectabile* were collected every 2 hr over a 24-hr period 27-28 September 1979 (Fig. 1). Fishes were killed in 10% formalin and preserved in 70% ethyl alcohol. In the laboratory the standard length (SL) and gape width (GW) of each fish were recorded. Gape width was measured as the transverse distance across the oral groove, with mouth closed (Hubbs and Lagler 1947). Stomach contents of each fish were examined, food items identified and maximum lengths and widths measured on intact food items using an ocular micrometer. Animal food items were identified to lowest possible taxon. Numeric indices describing the degree of digestion of food in stomachs (1-5; 1 indicating least, 5 indicating most, digestion) and degree of fullness of stomach (1-5; 1 = least, 5 = most, full) were assigned to each fish. The latter index used stomach distention and relative thickness of the stomach wall as indicators of fullness.

Dietary composition was compared between fish species by calculating percentage similarity indices followed by dendrogram cluster analysis (CLUSTAN, Wishart 1978) based upon the percentage similarities. Percentage similarity among diets of each fish species was calculated using the following equation:

$$PS = 1 - 0.5 \sum_{i=1}^{s} \mid (p_{ai} - p_{bi}) \mid = \sum_{i=1}^{s} \min (p_{ai} \text{ or } p_{bi})$$

where p_a is the proportion of the total diet of fish species *a* comprised by a prey species, p_b is the proportion of the diet of fish species *b* comprised by the same prey species, and *s* is the total number of prey species common to both diets (Schoener and Gorman 1968, Linton et al. 1981). Taxonomic richness (number of species) of diet was also compared between fish species.

Data were tested for univariate normality using N-scores correlation analysis of normality as described by Ryan et al. (1980). Appropriately transformed data were then tested for significant differences in mean size of food items between fish species using two-sample t-test. Prey and fish size data were tested for significant relationship within species using correlation analysis. Fish gape width and standard length relationships were explored using linear regression.

Results and Discussion

Body size. — A combined total of 229 specimens of the 4 fish species were examined (Table 1). *Cottus carolinae* was the largest species examined with the broadest range for SL and GW, while *Etheostoma caeruleum, E. flabellare* and *E. spectabile* were very similar in size and range of both measurements (Table 1). Relationships between standard length and gape width of the darter species and *Cottus* were also dissimilar. At a given body length, all darter species had a similar gape width, which was less than one-half the gape width of a *Cottus* of that length (comparisons based on linear regressions using data summarized in Table 1). Equations describing the linear relationship between GW and SL are: *Cottus* GW = – 2.92 + .244 SL, R^2 = .871; *E. caeruleum* GW = –1.16 + .096 SL, R^2 = .672; *E. flabellare* GW = –.547 + .0847 SL, R^2 = .775; *E. spectabile* GW = –.628 + .0929 SL, R^2 = .867. All linear regressions of gape width on standard length were significant ($p < .001$ for all species).

Diel feeding periodicity. — Mean number of food items found in stomachs of fish of each species collected over 24 hr are presented in Figure 1. Based upon this measure, the three darters exhibited diurnal feeding activity patterns (Fig. 1), while *Cottus carolinae* showed a primarily crepuscular feeding pattern (Fig. 1A). Mean stomach fullness index (Fig. 2) and mean food digestion index (Fig. 3) corroborate these interpretations of feeding activity in most cases. Stomach fullness shows a positive correlation with number of prey ingested in *C. carolinae* (Figs. 1A, 2A), *E. caeruleum* (Figs. 1B, 2B), and *E. spectabile* (Figs. 1D, 2D), however, no clear pattern is exhibited in the fullness index curve of *E. flabellare* (Fig. 2C). Generally, mean digestion index (Fig. 3) was negatively correlated with food abundance (Fig. 1) and stomach fullness (Fig. 2), though not strongly so except in *C. carolinae* (Figs. 1A, 2A, 3A). The strong dip between 1600 hr and 2200 hr in the latter species' mean digestion curve (Fig. 3A), coupled with pronounced rise in fullness from 1800-2400 hr (Fig. 2A), suggests that highest feeding activity may occur in the evening in this species. Comparing the feeding periodicities of these riffle-inhabiting species with *Noturus exilis* (Mayden and Burr 1981), *C. carolinae* shows strong overlap in time of feeding. Both species exhibit greatest activity during crepuscular periods of the diel cycle.

Diet comparisons: composition. — A total of 25 prey taxa occurred in the stomachs of all fish species combined (Table 2). Chironomid larvae were by far the most important food item in the diets of the darters, but were less important than the mayfly nymph, *Centroptilum*, in the diet of *Cottus*. The diet of *Cottus* also differed from those of the darter species in the absence of microcrustacea and the presence of fish (*Campostoma anomalum*). Percentage similarities of diet composition (Table 3) compared using dendrogram cluster analysis (Fig. 4) again illustrate the similarity in diets of the *Etheostoma* species, primarily due to the dominance of chironomid larvae. Dietary similarity among darters is probably exaggerated by the lack of resolution in this prey group. *Cottus* was much less similar in diet to each darter species (Table 3) and all darters as a group (Fig. 4A) than the darters were to each other.

Differences between the sculpin and the darters in time of feeding and/or microhabitat within riffles may account for two diet dissimilarities (Chironomidae, *Centroptilum*). Differences between the darters and sculpin in gill raker morphology most likely explains the dietary dissimilarity in the number of microcrustacea consumed. In fact, the 3 darter species have very similar number and arrangement of gill rakers, with 10-15 well-developed rakers on the first gill arch. *Cottus* has reduced gill rakers (nubs) on the first gill arch and so is not equipped to filter small food items. The presence of fish prey (*Campostoma anomalum*) in the diet of the sculpin, and the absence of such prey in the darters, most likely reflects differences between the sculpin and darters in maximum size. Fish were present only in the diets of the largest *Cottus* individuals (59.0-72.6 mm SL), larger than the largest individuals of any of the *Etheostoma* species examined. Figure 4A also shows *E. flabellare* to be less similar in diet to the other darter species than they are to each other, which reflects the greater importance of *Cheumatopsyche* and *Centroptilum* in the diets of *E. flabellare* and *Cottus*. Thus, *Cottus* and *E. flabellare* may at times feed in similar microhabitats, perhaps more rheic than the other darters, given the highly rheophyllic habits of *Cheumatopsyche* (Merritt and Cummins 1978).

To refine comparison between the diets of the darters, percentage similarities were calculated between them, excluding Chironomidae (Table 3) and these values were used in dendrogram cluster analysis (Fig. 4B). *Etheostoma caeruleum* and *E. flabellare* were more similar in diet to each other than either was to *E. spectabile* (Table 3, Fig. 4b). This most strongly reflects the high proportion of the more lentic taxa such as Cladocera, Copepoda, Ostracoda and Ceratopogonidae (Merritt and Cummins 1978, Pennak 1978) in the diet of *E. spectabile* relative to the other darters (Table 2). Further, the highly rheophyllic caddisfly larva, *Cheumatopsyche* was found in a much lower proportion in the diet of *E. spectabile* than the other darters. The more lentic diet of *E. spectabile* may be explained by its broad habitat use, including stream pools as well as riffles and riffle margins, compared to *E. flabellare* and *E. caeruleum* which are restricted to riffle habitats (Cross 1967, Pflieger 1975, Smith 1979).

One inference that can be drawn from the above diet comparisons is that during this study period the four species varied in feeding habitat from *Cottus* being most rheophyllic, followed by *E. flabellare* and *E. caeruleum*, to the more lentic *E. spectabile*. The diet of *Noturus exilis* (Mayden and Burr 1981) shows similarity to all of the species studied here, but is especially similar to *C. carolinae* and *E. flabellare* in the high number of Ephemeroptera and rheophyllic Trichoptera (*Cheumatopsyche*) present in the gut. This suggests that the slender madtom may also inhabit the more rheic microhabitats while feeding. Page (1983) suggests that feeding microhabitat may be the primary cause of dietary separations among darter species. However, experimental tests of this hypothesis are generally lacking in published food habit studies.

Comparisons of taxonomic richness of diet (S) are presented in Table 2. The low S value for *Cottus* relative to the darters again most strongly reflects general fish species size and gill raker morphology. *Cottus* generally cannot retain microcrustacea and other characteristically or seasonally small organisms, which effectively reduces the potential taxonomic richness of its diet compared to the darters. Differences in S between the darters most likely reflects behavioral and feeding microhabitat differences between species.

Diet comparisons: prey size. — A total of 1,124 food items from the 4 fish species was measured (Table 1). Log-transformed prey maximum widths and fish gape widths were tested by two-sample t-test between fish species (Table 4). Mean prey width was much larger in *Cottus* than any of the darters, corresponding to the much larger mean gape width in *Cottus* (Table 4). Among the darters there was no difference in mean gape widths, but mean size of prey of *E. flabellare* was significantly larger than that of either *E. spectabile* or *E. caeruleum* (Table 4). Mean prey size of the latter species did not differ significantly. Because of the very large sample sizes of measured food items (Table 1), the tests were sensitive to slight consistent differences between species (less than 1 mm, see Table 1). It was therefore difficult to interpret the biological significance (if any) of the prey size differences between darter species. Comparisons between *Cottus* and darters, however, likely reveal biologically significant fish and associated prey size differences, which may be important in resource partitioning among these species.

The results of correlation analysis of prey width (PW) and prey length (PL) each with gape width within each fish species are as follows: *E. caeruleum*, Correlation Coefficient$_{PW}$ (CC_{PW}) = 0.15, $p < 0.01$, $CC_{PL} = 0.10$, $p = 0.05$; *E. flabellare*, $CC_{PW} = 0.19$, $p < 0.01$, $CC_{PL} = 0.27$, $p < 0.01$; *E. spectabile*, $CC_{PW} = 0.22$, $p < 0.001$, $CC_{PL} = 0.32$, $p < 0.001$; *C. carolinae*, $CC_{PW} = 0.52$, $p < 0.001$, $CC_{PL} = 0.51$, $p < 0.001$. Although statistically significant correlations between gape width and prey width, and gape width and prey length, are indicated for all fish species, the correlations are generally very weak. *Cottus* shows the best correlation between food size and gape width, which may reflect the greater size range of *Cottus* collected compared to the darter species (see Table 1), making the trend between predator and prey size more apparent. These results suggest that in natural populations with naturally broad body size variation, size of food consumed may be strongly correlated with size of feeding individual. This intuitively logical relationship sets up a food availability gradient that may be important in resource partitioning within and between some fish species. Although predator-prey size relationships are thought to have potential importance in the coexistence of similar predator species (Schoener 1974, Hespenheid 1975 and references therein) relatively few fish studies have addressed this question (Northcote 1954, Werner 1974, Mathur 1977, Ross 1977, Schenck and Whiteside 1977, Gatz 1979a, 1979b, 1981, Mathews 1982, Mathews et al. 1982, Miller 1983). Several of these studies (Gatz 1979a, 1979b, 1981, Matthews 1982) have demonstrated that morphological characters may be important variables in defining resource use patterns between gross fish community functional groups (e.g., trophic guilds, habitat guilds). Others (Ross 1977, Schenck and Whiteside 1977, Matthews et al. 1982, Miller 1984) have indicated that morphological characters, especially mouth and head size, may be important in defining within-guild resource partitioning. Miller (1984) cautions, however, that the relative position of a fish population on the resource use axis can change seasonally, due to asynchronous demographic patterns in the populations within the community (e.g. reproduction, which lowers the mean gape size of a fish population during a given season). For this reason, the resource use patterns described here for *E. caeruleum*, *E. flabellare*, *E. spectabile*, and *C. carolinae* are more comparable with similar studies conducted during the fall than other seasons.

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Table 1. Total number of specimens and morphometric means and ranges for *Cottus carolinae, Etheostoma caeruleum, E. flabellare,* and *E. spectabile* and their prey.

	Fish Species			
Measurement	*C. carolinae*	*E. caeruleum*	*E. flabellare*	*E. spectabile*
No. of Specimens	57	61	62	49
Standard length (mm)				
range	24.5-72.6	31.7-50.8	26.0-40.9	24.5-47.5
mean	39.7	40.2	35.4	33.6
Gape Width (mm)				
range	1.7-15.3	1.7-4.4	1.7-3.2	1.7-4.2
mean	6.8	2.7	2.5	2.4
No. Food Items				
total	332	1320	627	978
measured	68	460	228	368
Prey Length (mm)				
range	0.96-48.00	0.16-6.32	0.18-8.96	0.14-13.60
mean	4.58	1.57	1.82	1.33
Prey Width (mm)				
range	0.16-9.60	0.08-3.84	0.12-1.60	0.08-1.36
mean	1.24	0.29	0.34	0.28

Table 2. Total diet determined from stomach contents of all specimens of *Cottus carolinae*, *Etheostoma caeruleum*, *E. flabellare*, and *E. spectabile*, including total number of each prey taxon, percentage of total prey abundance that each prey taxon comprises, and prey taxonomic richness (S) in the diet of each fish species.

	Fish Species							
	C. carolinae		*E. caeruleum*		*E. flabellare*		*E. spectabile*	
Prey Taxon	No.	%	No.	%	No.	%	No.	%
Cladocera	0	0.0	3	0.2	2	0.3	48	4.8
Copepoda	0	0.0	3	0.2	3	0.5	51	5.2
Ostracoda	0	0.0	1	0.1	0	0.0	8	0.8
Hydracarina	0	0.0	50	3.8	25	3.9	61	6.2
Ephemeroptera								
Baetidae								
Centroptilum sp.	164	49.4	44	3.3	80	12.5	20	2.0
Heptageniidae								
Stenonema tripunctatum	1	0.3	1	0.1	2	0.3	2	0.2
Caenidae								
Caenis spp.	1	0.3	12	0.9	6	0.9	18	1.8
Plecoptera								
Perlidae								
Neoperla clymene	2	0.6	2	2.2	2	0.3	0	0.0
Coleoptera								
Psphenidae								
Psphenus herriki	16	4.8	3	0.2	1	0.2	16	0.2
Megaloptera								
Corydalidae								
Corydalus cornutus	0	0.0	0	0.0	0	0.0	1	0.1
Diptera								
Tipulidae	0	0.0	1	0.1	0	0.0	0	0.0
Psychodidae								
Pericoma sp.	0	0.0	0	0.0	0	0.0	1	0.1
Ceratopogonidae								
Atrichopogon sp.	0	0.0	1	0.1	0	0.0	1	0.1
Palpomyia	0	0.0	2	0.2	0	0.0	3	0.3
Stilobezzia	0	0.0	0	0.0	0	0.0	6	0.6
Simuliidae	2	0.6	3	0.2	7	1.1	2	0.2
Chironomidae	115	34.6	1139	86.3	467	72.9	739	74.7
Tabanidae								
Tabanus sp.	0	0.0	0	0.0	1	0.2	0	0.0
Empididae	0	0.0	3	0.2	0	0.0	0	0.0
Dipteran pupae	3	0.9	35	2.9	8	1.2	13	1.3

Trichoptera								
Hydropsychidae								
Cheumatopyche sp.	25	7.5	16	1.2	37	5.8	5	0.5
Hydroptilidae								
Hydroptila hamata	0	0.0	1	0.1	0	0.0	0	0.0
Gastropoda								
Ferrisidae								
Ferrissia sp.	0	0.0	1	0.1	1	0.2	0	0.0
Physidae								
Physa sp.	0	0.0	0	0.0	1	0.2	8	0.8
Osteichthyes								
Cyprinidae								
Campostoma anomalum	3	0.9	0	0.0	0	0.0	0	0.0
Total	332	100.0	1322	100.0	642	100.0	989	100.0
Taxonomic Richness (S)	10		20		15		18	

Table 3. Percentage similarity of diet between riffle-inhabiting fishes. Lower half of table inclusive of all species and prey taxa. Upper half calculated between darter species only, with Chironomidae excluded from diets.

	Fish Species			
Fish Species	*C. carolinae*	*E. caeruleum*	*E. flabellare*	*E. spectabile*
C. carolinae	—			
E. caeruleum	40.77	—	62.12	53.28
E. flabellare	55.05	84.27	—	38.83
E. spectabile	38.97	84.50	83.06	—

Table 4. Results from two-sample t-tests comparing gape widths (upper half of table) and prey maximum width (lower half) among four riffle-inhabiting fish species.

	Fish Species			
Fish Species	*C. carolinae*	*E. caeruleum*	*E. flabellare*	*E. spectabile*
C. carolinae	—	****	****	****
E. caeruleum	****	—	n.s.	n.s.
E. flabellare	****	*	—	n.s.
E. spectabile	****	n.s.	***	—

*p <0.05
***p <0.001
****p <0.0001

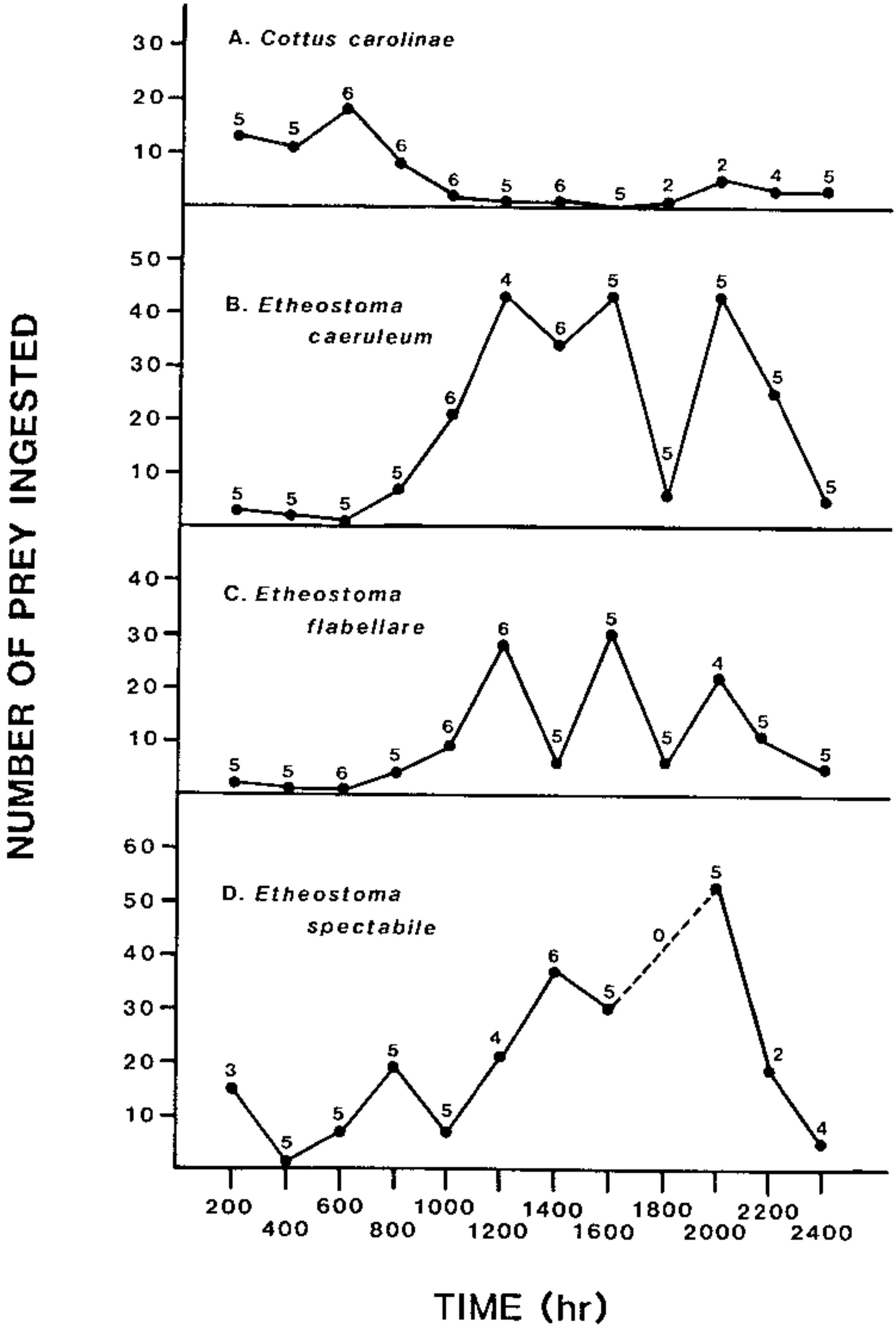

Figure 1. Mean number of food items found in the stomachs of fish collected from Hutchins Creek, Illinois, every two hr for 24 hr, 27-28 September 1979. Numbers above each collection time along the species curves represent number of fish collected at that time.

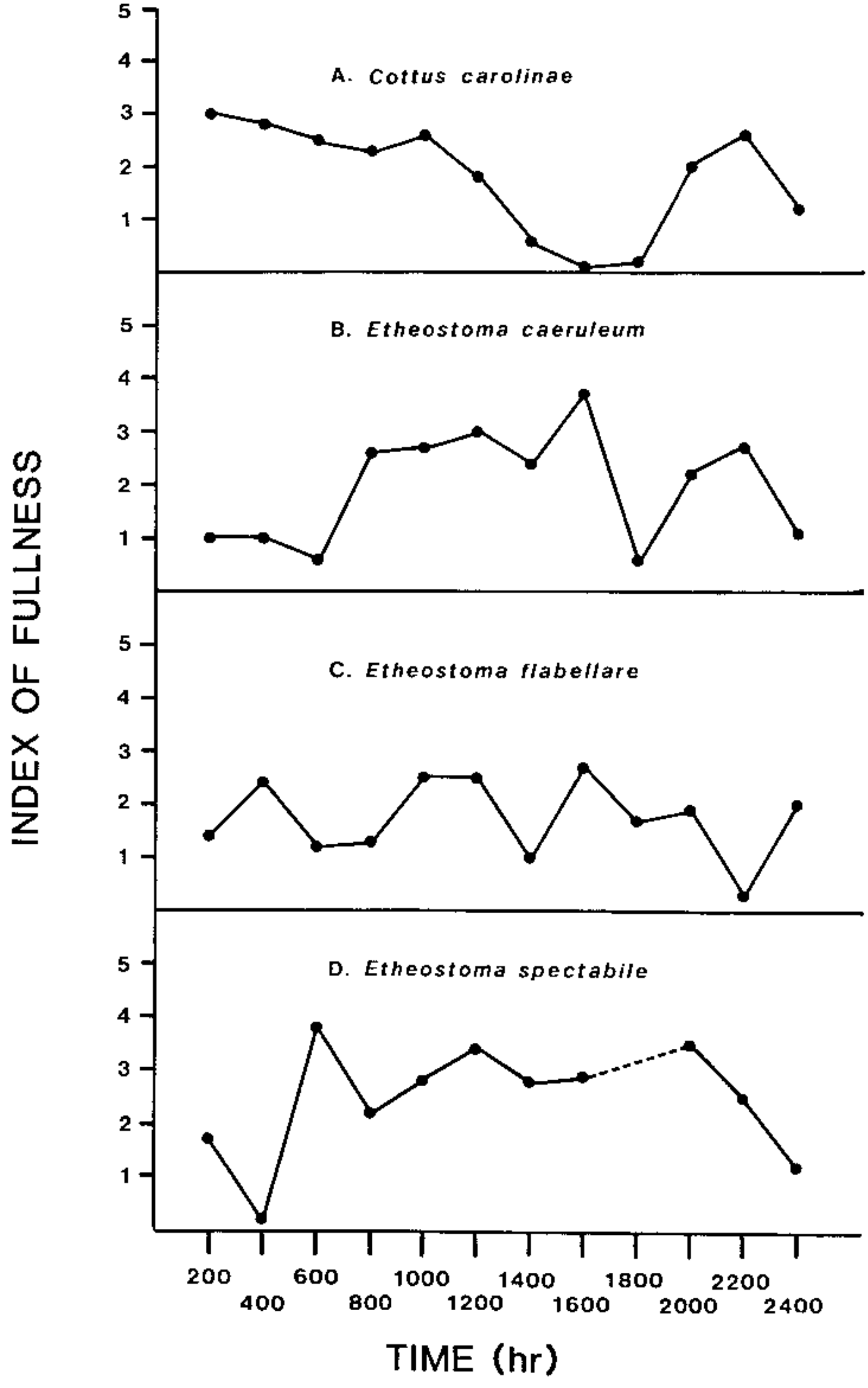

Figure 2. Mean stomach fullness index of four fish species collected every two hr for 24 hr from Hutchins Creek, Illinois, 27-28 September 1979. A fullness index of 1 indicates least full (empty) and 5 indicates most full.

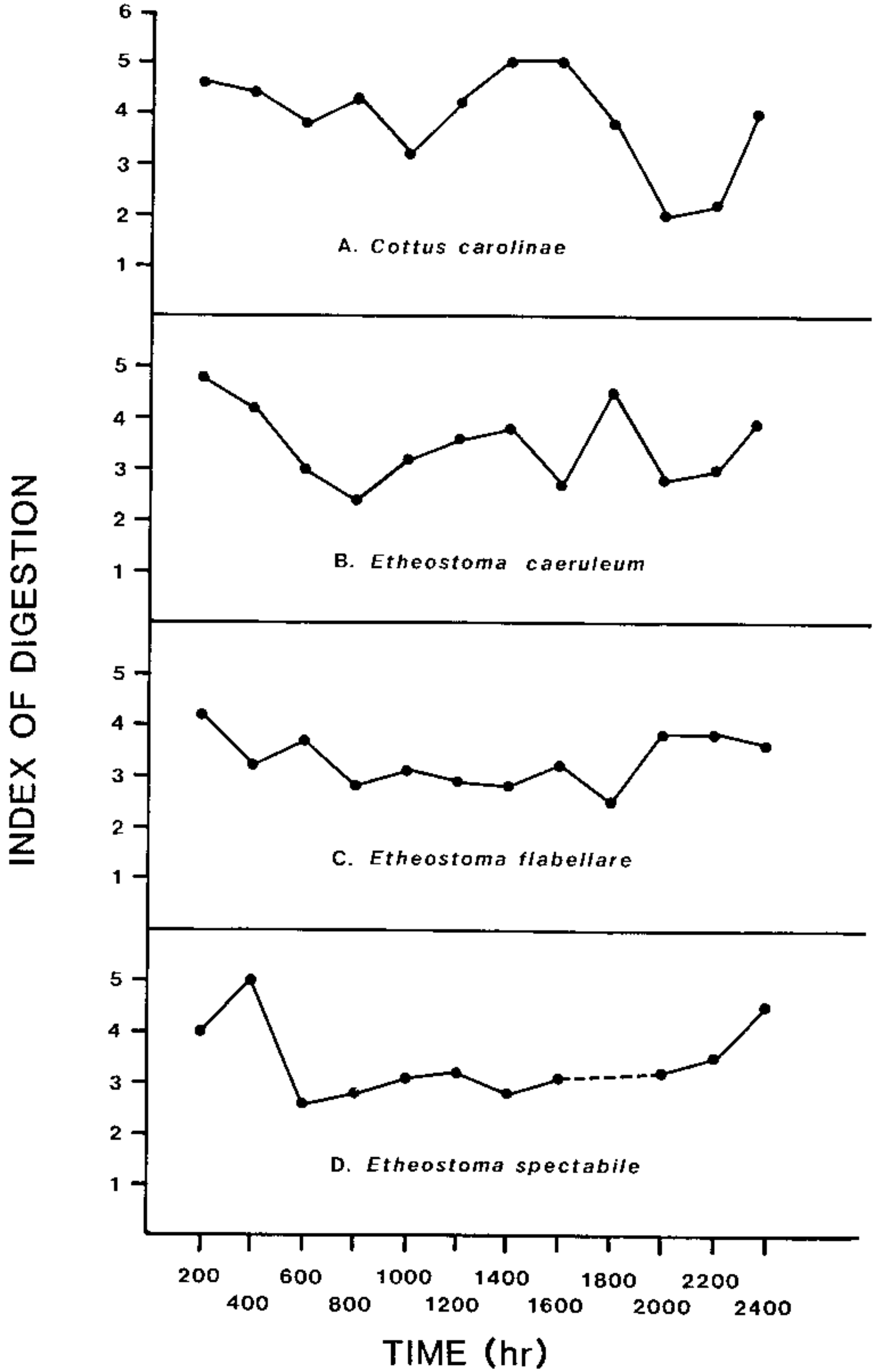

Figure 3. Mean index of digestion of stomach contents of four fish species collected every two hr for 24 hr from Hutchins Creek, Illinois, 27-28 September 1979. A digestion index of 1 indicates least apparent digestion and 5 indicates most apparent digestion of stomach contents.

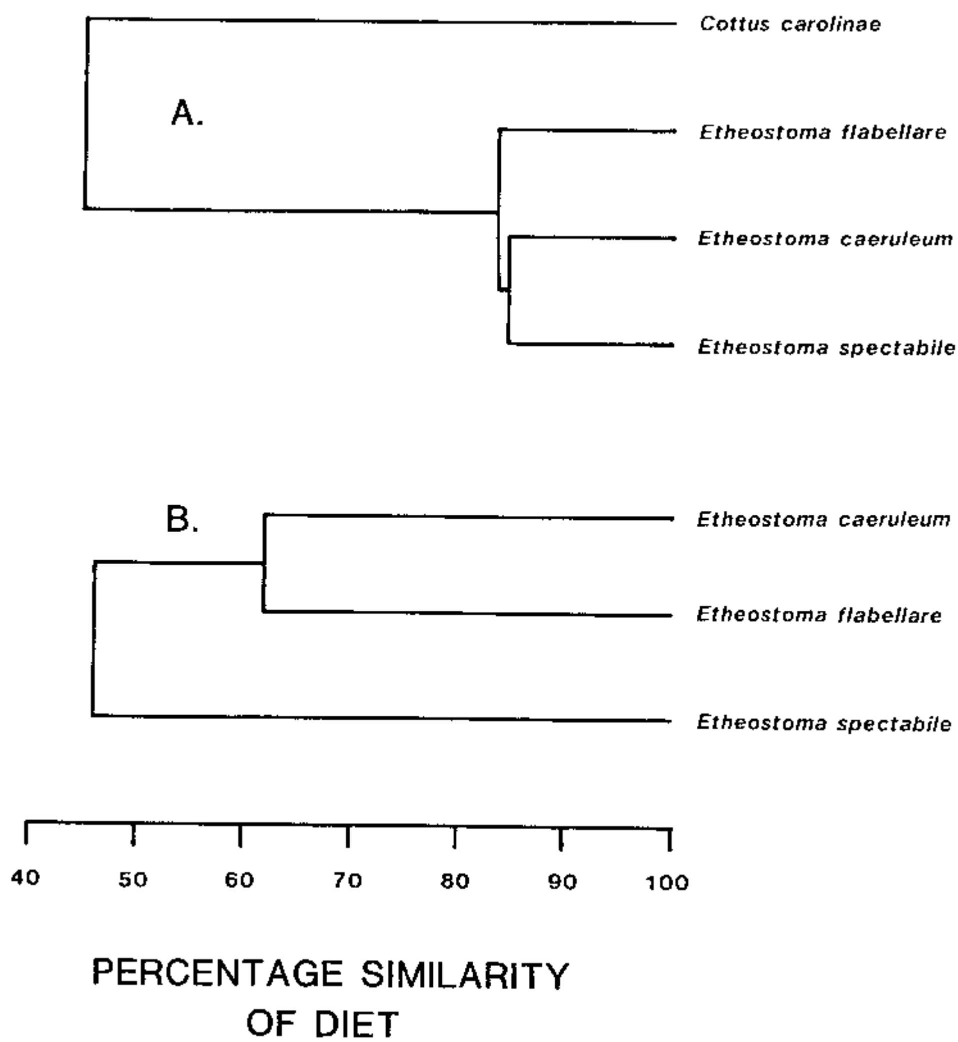

Figure 4. Dendrogram cluster analysis of diet composition of (A) all four riffle fish species, and, (B) the darter species only, excluding the chironomid prey component from the analysis.