 0030-0950/83/0004-0201 $2.00/0

FOOD RESOURCE PARTITIONING AND SELECTIVITY BY THE GREENSIDE, RAINBOW, AND FANTAIL DARTERS (PISCES: PERCIDAE)[1]

IHOR HLOHOWSKYJ[2] and ANDREW M. WHITE, Department of Biology, John Carroll University, University Heights, OH 44118

ABSTRACT. The diets and possible competitive interactions related to food were examined for greenside (*Etheostoma blennioides*), rainbow (*E. caeruleum*), and fantail (*E. flabellare*) darters from the Chagrin and Grand Rivers of northeastern Ohio. All 3 species fed heavily upon chironomid larvae in all seasons. In the Chagrin, the chironomids consumed were primarily of the subfamily Orthocladiinae; in the Grand, the subfamily Chironominae was also important to the darters. *E. blennioides* fed most heavily upon chironomids in both streams in all seasons. *E. caeruleum* consumed fewer chironomids than did *E. blennioides* but more than *E. flabellare* (except in spring). Seasonally important prey taxa for *E. blennioides* included Simuliidae, Trichoptera, and Ephemeroptera; for *E. caeruleum*, Trichoptera and Ephemeroptera; for *E. flabellare*, Plecoptera (especially in winter), Trichoptera, and Ephemeroptera. *E. blennioides* exhibited greatest selection for *Simulium*, Orthocladiinae, and *Hydroptila; E. caeruleum* for *Hydroptila*, Orthocladiinae, and *Baetis*. *E. flabellare* selected for *Paracapnia, Baetis, Hydropsyche*, and *Stenonema*. Greatest seasonal dietary overlap was between *E. blennioides* and *E. caeruleum*. Lowest overlap was between *E. caeruleum* and *E. flabellare*. In both streams, overlap between *E. blennioides* and *E. caeruleum* was greatest in winter, lowest in summer. Overlap between either of these darters and *E. flabellare* was greatest in spring, lowest in winter. Heavy reliance upon the abundant chironomid larvae by the darters may aid in reducing competition and increasing foraging efficiency. Competitive interactions resulting in habitat shifts may result in reduced and different foraging areas for these fishes, which may further decrease competition between these darters.

OHIO J. SCI. 83 (4): 201–208, 1983

INTRODUCTION

Competition for a resource such as food might be expected to be more intense between closely related species in the same community since closely related species show the least amount of evolutionary divergence (specialization) from one another. Resource partitioning in fish communities has received considerable attention (Starret 1950, Keast 1966, Zaret and Rand 1971, Gillen and Hart 1980). These studies examined feeding habits of fishes and indicate that food resource partitioning is important in reducing competitive pressures between species. The communities examined, however, were composed primarily of unrelated or distantly related species occupying different niches. Fish communities composed primarily of closely related species with similar niches have received little attention. Those studies which have examined closely related species found various degrees of resource partitioning (Mendelson 1975).

In many eastern North American streams, darters of the genus *Etheostoma* (Percidae: Etheostominae) comprise naturally occurring communities of closely related species belonging to the same ecological guild. In many such streams, darters may represent the major vertebrate

[1]Manuscript received 7 September 1982 and in revised form 5 May 1983 (#82–24).

[2]Present Address: Department of Zoology, Miami University, Oxford, OH 45056

biomass component and dominant fish form of riffle communities. As such they represent a good system in which to examine food resource partitioning.

The feeding habits of a number of darter species have been studied (Forbes 1880, Turner 1921, Karr 1964, Adamson and Wissing 1977, Wynes 1979). These studies indicate that darters primarily forage on the benthic macroinvertebrate fauna. As a result, competition might be expected to be important between these coexisting species. The objectives of the present study were to examine the seasonal diets of coexisting, congeneric darters and to apply this data to a determination of resource partitioning among the greenside (*Etheostoma blennioides*), rainbow (*E. caeruleum*), and fantail (*E. flabellare*) darters.

METHODS AND MATERIALS

Sampling sites were located in 2 northeastern Ohio streams; the Chagrin and Grand Rivers. Both streams flow through rolling agricultural lands of the Glaciated Allegheny Plateau and then enter urbanized areas of the Lake Erie Lake Plain. The Chagrin River is 77.53 km long, has an average fall of 3.01 m per km, and drains 691.53 km^2. It flows primarily in a northerly direction, draining portions of Geauga, Portage, Lake, and Cuyahoga Counties (ODNR 1960). It enters Lake Erie at the city of Eastlake in Lake County. The Grand River is 158.59 km long, has an average fall of 1.06 m per km, and drains 1844.34 km^2 (ODNR 1960). It flows in a northeasterly direction and enters Lake Erie at the city of Fairport in Lake County. It drains portions of Geauga, Trumbull, Lake, and Ashtabula counties.

Two riffles, ranging from 10 to 20 m in width, 30–65 m in length, and 10–55 cm in depth, were sampled in each drainage. Bottoms were composed primarily of gravel, cobble, and boulder with filamentous algae (*Cladophora*) present in spring and summer. Darters (*E. blennioides* and *E. caeruleum* in the Chagrin River; *E. blennioides*, *E. caeruleum*, and *E. flabellare* in the Grand River) and benthic macroinvertebrates were collected in August 1979, January 1980, and March 1980. Other fish species collected from the riffles included *Rhinichthys atratulus*, *Semotilus atromaculatus*, *Pimephales notatus*, *Campostoma anomalum*, *Notropis cornutus*, *Hypentilium nigricans*, *Catostomus commersoni*, *Noturus flavus*, and *E. nigrum*.

Darters were collected with a 1.22-m × 2.44-m minnow seine (0.63-cm^2 mesh) and immediately preserved in 10% formalin. Stomach contents were removed in the laboratory, identified to genus when possible, enumerated and the percent numerical contribution calculated. Due to the difficulty in identifying chironomid larvae to genus, these were identified only to subfamily. Seasonal benthic prey availability was determined by taking 15 0.1-m^2 Surbur samples at each site on each collection date. Five Surbur samples were taken along each of 3 transects, one across the base, middle, and head of the riffle. Benthic organisms were sorted and then handled in the same manner as the stomach contents. Fish and benthos were collected between noon and 3 p.m. on each collection date. A total of 448 stomachs were examined: 223 *E. blennioides*, 165 *E. caeruleum*, and 60 *E. flabellare*.

Food overlap between species pairs of adult darters was determined using an index of overlap (Horn 1966). The index is calculated as:

$$C = 2\frac{\sum_{i=1}^{s} X_i Y_i}{\sum_{i=1}^{s} X_i^2 + \sum_{i=1}^{s} Y_i^2}$$

where: C = index of overlap, x_i = proportion of total diet of species x taken from prey taxon i, and y_i = proportion of total diet of species y taken from prey taxon i. Overlap values may range from none (0.0000) to all (1.0000) prey taxa shared and consumed in equal proportions.

Preferential selection for or against certain food items was measured using the Index of Electivity (Ivlev 1961), calculated as:

$$E = \frac{r_i + p_i}{r_i - p_i}$$

where: E = electivity index, r_i = proportion of prey taxon i in the ration, and p_i = proportion of prey taxon i in the environment.

Values may range from −1.000 (lack of utilization of a prey taxon) to +1.000 (preferential selection for a prey taxon). A value of 0.000 indicates that a prey taxon is consumed in the same proportion in which it occurs in the environment.

RESULTS

PREY UTILIZATION. Chironomid larvae of the subfamily Orthocladiinae were the major prey taxon consumed by *E. blennioides* in any season in either drainage (table 1). Orthocladiinae numerical importance was highest in winter and lowest in summer. Chironomids of the subfamily Tanypodinae were not important prey items, while chironomids of the subfamily Chironominae were important only in the Grand River. Chironominae importance

TABLE 1

Seasonal percent numerical contribution of major benthic invertebrate taxa to the diets of E. blennioides *(blen),* E. caeruleum *(caer), and* E. flabellare* *(flab) from the Chagrin and Grand Rivers.*

	Winter			Spring			Summer		
Taxa	blen	caer	flab	blen	caer	flab	blen	caer	flab
				CHAGRIN RIVER					
DIPTERA									
Chironomidae									
Orthocladiinae	95.47	89.00	—	89.95	73.16	—	69.10	46.13	—
Tanypodinae	0.04	nc**	—	nc	0.08	—	nc	0.55	—
Chironominae	0.08	0.40	—	nc	4.41	—	nc	0.27	—
Simuliidae	0.31	0.39	—	0.03	0.42	—	15.95	14.66	—
Diptera pupae	0.56	1.19	—	3.67	5.76	—	0.91	1.55	—
Other Diptera	2.27	3.41	—	2.23	3.56	—	2.09	0.54	—
TRICHOPTERA	0.67	1.17	—	2.31	8.07	—	9.65	10.40	—
EPHEMEROPTERA	0.15	0.48	—	2.11	3.01	—	3.73	25.66	—
PLECOPTERA	nc	4.83	—	0.06	0.94	—	0.17	1.23	—
MISCELLANEOUS	0.11	0.18	—	0.14	3.65	—	0.44	0.08	—
				GRAND RIVER					
DIPTERA									
Chironomidae									
Orthocladiinae	96.91	70.37	44.07	84.26	64.44	74.39	75.46	65.03	31.79
Tanypodinae	0.15	nc	nc	nc	0.72	2.84	0.01	0.34	31.79
Chironominae	nc	1.85	1.69	1.95	2.17	17.07	19.69	18.53	35.76
Simuliidae	0.22	nc	nc	10.30	12.80	2.32	0.66	0.59	0.61
Diptera pupae	0.22	1.61	nc	2.61	4.45	nc	0.41	0.91	0.23
Other Diptera	0.37	3.79	nc	0.30	0.55	nc	nc	0.22	0.31
TRICHOPTERA	5.37	14.09	13.42	0.59	1.47	3.80	4.44	12.80	20.38
EPHEMEROPTERA	5.00	6.52	8.93	0.17	0.54	0.74	0.39	5.33	10.01
PLECOPTERA	0.14	2.17	32.20	0.04	0.27	nc	nc	0.09	0.16
MISCELLANEOUS	nc	2.17	nc	0.05	6.63	0.25	0.12	0.08	0.23

*Not collected from the Chagrin River
**nc — not consumed

was lowest in winter (0.00%) and greatest in summer (19.69%). The Simuliidae were important in summer in the Chagrin River and in spring in the Grand River.

E. blennioides exhibited considerable variation in its utilization of Ephemeroptera between the 2 streams. Ephemeroptera contribution to the diet increased from winter to summer in the Chagrin, while in the Grand this prey taxa was important only in winter. The Plecoptera never exceeded more than 0.44% of the diet in any season in either stream.

The diet of *E. caeruleum* was also heavily comprised of Orthocladiinae. Importance of this prey item was less than that for *E. blennioides* in any season in both streams, but followed a similar trend; greatest in winter, lowest in summer (table 1). The Chironominae however, were important to the diet of *E. caeruleum*, particularly in spring in the Chagrin and in all seasons in the Grand. The seasonal importance of Simuliidae was similar between *E. caeruleum* and *E. blennioides* in each stream. The Diptera pupae comprised a significant portion of the diet of *E. caeruleum* only in summer and only in the Grand. Other Diptera were more important to the diet of *E. caeruleum* than to *E. blennioides* except in summer in the Chagrin. In the Grand, they comprised from 0.22% of the diet in summer to 3.79% in winter.

The Trichoptera was a very important prey taxon in all seasons for *E. caeruleum*. In the Chagrin, dietary importance of Trichoptera increased from winter to summer. Trichoptera represented the second largest portion of the diet in spring and the third largest portion in summer. In the Grand, Trichoptera importance was greatest in winter and summer and lowest in spring. Ephemeroptera importance was similar to that of Trichoptera in both streams. In the Chagrin, importance increased from winter to summer when they were the second most important prey taxa consumed, comprising over 25% of the diet. Plecoptera, which were not important to the diet of *E. blennioides*, represented large portions of the winter diet of *E. caeruleum* in both streams.

E. flabellare also fed heavily on Orthocladiinae. This darter consistently consumed a smaller percentage than *E. blennioides* in all seasons but consumed a greater percentage than *E. caeruleum* only in spring (table 1). The Chironominae were more important to *E. flabellare* than to either of the other darters. Chironominae were least important in winter, increasing to more than 35% of the diet by summer.

E. flabellare relied less heavily upon Simuliidae in any season than the other darters. Simuliidae exceeded 1.00% of the diet only in spring. Trichoptera were important in all seasons as prey items. In summer they comprised over 20% of the diet. At their lowest level of use they still represented almost 4.00% of the diet. Ephemeroptera were important prey items in winter and summer, but in spring they accounted for less than 1.00% of the diet. Plecoptera were major prey items for *E. flabellare* in winter, when they comprised the second largest component of the diet (32.20%).

The miscellaneous category was important only for *E. caeruleum*. This prey category was important in winter in the Grand and in spring in both streams. In winter, this category included mites, daphnids, gammarids, and oligochaetes; in spring, fish eggs represented the major portion of this prey category.

ELECTIVITY INDICES. For calculating the electivity indices, 2 assumptions were made. First, prey taxa that represented less than 1.00% of the macroinvertebrate community and were not consumed were not included in the calculations. If included, these values would have been −1.000, indicating strong avoidance. Rather than avoidance, we are assuming that these prey taxa are so rare that they are not encountered frequently by the darters and therefore are not consumed. Second, prey taxa that comprised less than 1.00% of the macroinvertebrate community but were consumed are included in the calculations.

In the Chagrin River, *E. blennioides* exhibited positive selection for 6 of the prey taxa consumed. In the Grand River, this darter selected for only 4 of the prey taxa that it consumed. The largest value was for *Psephenus* in the Grand River. This, however, was due to a few individuals consumed and none collected in the macroinvertebrate community. In the Chagrin River, greatest selection was expressed for *Simulium* larvae and the Orthocladiinae. In the Grand River, excluding *Psephenus*, greatest selection was for the Orthocladiinae and *Simulium* larvae (table 2).

E. caeruleum exhibited positive selection for more of the prey taxa than did *E. blennioides*. In the Chagrin River, 8 of the 22 prey taxa were selected positively. Greatest selection was exhibited for *Paracapnia*, a result of a few individuals being consumed and none being found in the macroinvertebrate community. Excluding *Paracapnia*, greatest selection was for *Allocapnia*, *Hydroptila*, and Orthocladiinae. In the Grand River, 6 of the 17 prey taxa were selected positively. Greatest selection was for *Baetis*. Also selected for were *Stenonema*, *Hydropsyche*, Orthocladiinae, and *Simulium* larvae and pupae (table 2).

Positive selection was exhibited by *E. flabellare* for 8 of the 17 prey taxa. Greatest selection was for *Paracapnia* and

TABLE 2

Mean electivity indices for Etheostoma blennioides *(blen),* E. caeruleum *(caer), and* E. flabellare *(flab) and mean percent numerical contribution of the benthos (ben) from the Chagrin and Grand Rivers.*

	Chagrin River			Grand River			
Prey Taxa	ben	blen	caer	ben	blen	caer	flab
Baetis	3.67	−0.491	0.373	0.59	−0.641	0.530	0.722
Stenonema	5.56	−0.976	−0.775	1.11	−0.892	0.192	0.282
Caenis	0.31	nc*	−0.784	0.55	−0.894	−0.587	−0.006
Isonychia	1.05	nc	−0.695	0.63	nc	nc	nc
Acroneuria	1.72	−0.980	−0.532	0.79	nc	nc	nc
Allocapnia	0.01	0.11	0.892	nc	nc	nc	nc
Paracapnia	nc	nc	1.000	3.03	−0.801	nc	0.786
Hydroptila	0.69	0.389	0.427	1.22	−0.140	−0.285	−0.128
Hydropsyche	7.41	−0.801	−0.403	4.84	−0.564	0.028	0.444
Cheumatopsyche	10.41	−0.863	−0.647	4.74	−0.757	−0.218	0.168
Antocha	1.54	0.165	0.289	1.25	nc	nc	nc
Atherix	1.03	−0.878	−0.696	0.03	nc	nc	nc
Hexatoma	0.11	−0.099	−0.084	0.12	nc	−0.812	−0.217
Orthocladiinae	27.45	0.514	0.416	35.65	0.412	0.303	0.168
Chironominae	9.53	−0.138	−0.118	13.65	−0.373	−0.355	0.070
Tanypodinae	0.74	−0.873	−0.358	0.79	−0.881	−0.386	0.189
Simulium larva	0.68	0.572	0.270	0.75	0.222	0.315	−0.499
pupa	0.09	nc	0.196	2.02	0.095	0.314	−0.450
Diptera pupa	4.03	−0.439	−0.066	4.94	−0.494	−0.095	−0.875
Stenelmis larva	6.50	−0.996	−0.963	3.68	−0.994	nc	−0.941
Psephenus	4.54	−0.953	nc	nc	1.000	nc	nc
Miscellaneous	12.71	−0.964	−0.814	8.22	−0.985	−0.470	−0.962

*nc—either not consumed or not collected

Baetis. In contrast to *E. blennioides* and *E. caeruleum*, the high value exhibited for *Paracapnia* by *E. flabellare* was due to high levels of consumption of this stonefly. The mean electivity value for the Orthocladiinae expressed by *E. flabellare* was the lowest for this prey taxon by any of the 3 darter species. In contrast to *E. blennioides* and *E. caeruleum*, *E. flabellare* selected against both larvae and pupae of *Simulium* (table 2).

OVERLAP. The largest amount of overlap found between pairs of darter species was that for *E. blennioides* and *E. caeruleum*. Total (all seasons summed), mean, and seasonal overlaps between these 2 species were all high (>0.6000) except for summer in the Chagrin River. This was also the season of lowest Orthocladiinae importance to the diets of these darters. In both drainages, seasonal overlap followed a trend similar to that of the dietary importance of Orthocladiinae; greatest in winter and lowest in summer. Total, mean, and seasonal overlaps between *E. flabellare* and each of the other darter species were lower than those found between *E. blennioides* and *E. caeruleum*. Seasonal overlap between *E. flabellare* and the other 2 darter species did not exceed 0.6000, except in spring, when overlap was highest. Mean overlap of *E. flabellare* was lower with *E. caeruleum* than with *E. blennioides* (table 3).

DISCUSSION

Results of the diet analysis for the 3 darter species generally agreed with the findings of other investigators (Forbes 1880, Turner 1921, Lotrich 1973, Wehnes 1973). The diet of *E. flabellare* differed from some earlier accounts. Adamson and Wissing (1977) found caddisfly larvae to

TABLE 3

Coefficient of overlap values based upon the numerical contributions of each food type to the diets of Etheostoma blennioides *(blen),* E. caeruleum *(caer), and* E. flabellare *(flab) from the Chagrin and Grand Rivers.*

	Chagrin River	Grand River		
Season	blen × caer	blen × caer	blen × flab	caer × flab
Winter	0.9490	0.7936	0.5096	0.4118
Spring	0.8413	0.7762	0.7545	0.6323
Summer	0.3893	0.7087	0.5550	0.5068
Total	0.8061	0:8833	0.5898	0.5075
Mean	0.7265	0.7595	0.6063	0.5169

be the most important food item of this darter in Four Mile Creek in southwestern Ohio. Our data indicate that while caddisfly larvae represent a seasonally important food item, chironomid larvae and stoneflies (especially in winter) are more important to the diet of *E. flabellare* in northeastern Ohio.

Seasonal trends in the diets of the 3 darter species differed considerably. Even though the importance of Orthocladiinae larvae decreased in summer, they remained the most important food item in any season for *E. blennioides*. These data, along with the high electivity values exhibited for Orthocladiinae larvae, indicate the very specialized diet of this darter. *E. blennioides* also showed strong selection for *Simulium* larvae, which were never very abundant in the macroinvertebrate community. Other prey items varied seasonally in their importance but never approached the level of utilization that was expressed for Orthocladiinae.

E. flabellare exhibited distinct seasonal differences in its diet. These differences were primarily due to the increased importance of Plecoptera in the winter diet and to the more limited utilization of chironomids in most seasons. *E. caeruleum* was intermediate with respect to seasonal differences in its diet. Although *E. caeruleum* relied heavily upon chironomid larvae in all seasons, differences were evident in the non-chironomid portion of the diet, particularly in the utilization of Ephemeroptera and Plecoptera.

All 3 darter species fed upon similar food items, especially chironomid larvae. This would account for the very high overlap values obtained, and implies that competition is significant between these species throughout most of the year. Zaret and Rand (1971) considered overlap values greater than 0.6000 to represent significant competitive interactions within a community. Based on this value, the darters examined in this study are being subjected to significant competitive interactions. The extent of these interactions is variable both between species and between seasons. *E. flabellare* exhibited the least amount of overlap of any of the darters, with a high degree of overlap occurring only in spring. This is primarily due to the seasonal differences in the importance of chironomids in its diet.

While the high degree of overlap between the darters is indicative of competition, this may simply be an artifact of the index. Keast (1966) and Nilsson (1967) both state that similarity of diet (overlap) may sometimes be attributed to a very abundant food source. In such an instance, competition actually would be far lower than that indicated by the index of overlap. This appears to be the case in the darter communities studied. Chironomids comprised the largest component of the benthic macroinvertebrate community (30–72% by number) and were heavily utilized (especially the Orthocladiinae) by the darter community. Chironomids never represented less than 45% (by number) of all food items consumed in any season by any of the darters. Competition for the other food taxa probably exists but is reduced in terms of intensity by the heavy reliance upon abundant chironomid larvae.

This heavy use of the chironomid larvae by the darters appears to agree with optimum foraging theory (MacLean and Magnuson 1977). By feeding upon this abundant food source, darters may be maximizing the ratio between quantity and the energy expended to obtain each food item. By utilizing this food resource the darters could not only be reducing competition but also energy expenditure.

Competition, however, appears to play an important role in structuring the diets of these darters. This becomes evident in a comparison of the diets of *E. blennioides* and *E. caeruleum* between the 2 drainages. The benthic communities in these drainages did not differ dramatically in terms of either taxa present or densities. Yet, the number of prey taxa selected for by both these darters differed between the Chagrin and Grand Rivers. The major difference between the darter communities of these streams is the presence of *E. flabellare* in the Grand River. With the addition of *E. flabellare,* the number of positively selected prey taxa decreased from 5 to 3 (excluding *Psephenus*) for *E. blennioides* and from 8 to 6 for *E. caeruleum*. The number of shared prey taxa also decreased. Excluding the chironomid larvae and miscellaneous categories, the number of prey taxa shared by *E. blennioides* and *E. caeruleum* decreased from 14 to 9.

In the Chagrin River, *E. blennioides* was primarily taken from the deepest portions of the riffle with fewer individuals taken in the shallower areas. *E. caeruleum* was found principally in the shallower areas, with fewer individuals being collected in the deep, central portions of the riffle. In the Grand River however, the shallower regions of the riffles were occupied primarily by *E. flabellare*. As a result, *E. blennioides* was collected almost exclusively from the central, deep, swift portions of the riffles, and *E. caeruleum* occupied the areas between those occupied by *E. blennioides* and *E. flabellare*. Given the patchy characteristics of the benthic community, this may have resulted in reduced foraging areas for *E. caeruleum* and *E. blennioides* and, therefore, in a reduced number of accessible prey taxa. It is probable that *E. flabellare* partially is excluding *E. caeruleum* and *E. blennioides* from portions of the riffles that these darters would occupy in the absence of *E. flabellare*, thus indirectly causing a shift toward a more limited food base.

ACKNOWLEDGMENTS. The authors thank Bruce Colvin, Barry Kline, David Loucks, and Mark Potapczuk for their assistance with the collection of the darters and benthos, Daniel Keogh with aiding in the identification of the benthos, and Dr. Robert G. Sherman for constructively reviewing an early draft of the manuscript.

LITERATURE CITED

Adamson, S. W. and T. E. Wissing 1977 Food habits and feeding periodicity of the rainbow, fantail, and banded darters in Four Mile Creek. Ohio J. Sci. 77: 164–169.

Forbes, S. A. 1880 The food of darters. Amer. Natur. 14: 697–703.

Gillen, A. L. and T. Hart 1980 Feeding interrelationships between the sand shiner and the striped shiner. Ohio J. Sci. 80: 71–76.

Horn, H. S. 1966 Measure of "overlap" in comparative ecological studies. Amer. Natur. 100: 419–424.

Ivlev, V. A. 1961 Experimental ecology of the feeding of fishes. Yale Univ. Press, New Haven, CT. 302 p.

Karr, J. R. 1964 Age, growth, fecundity, and food habits of fantail darters in Boone County, Iowa. Proc. Iowa Acad. Sci. 71: 274–280.

Keast, A. 1966 Trophic interrelationships in the fish fauna of a small stream. Great Lakes Res. Div., Univ. Mich. Publ. 15: 51–79.

Lotrich, V. A. 1973 Growth, production, and community composition of fishes inhabiting a first-, second-, and third-order stream of eastern Kentucky. Ecol. Monogr. 43: 377–397.

MacLean, J. H. and J. J. Magnuson 1977 Inference on species interactions in percid communities. J. Fish. Res. Bd. Canada 34: 1941–1951.

Mendelson, J. 1975 Feeding relationships among species of *Notropis* (Pisces: Cyprinidae) in a Wisconsin stream. Ecol. Monogr. 45: 199–232.

Nilsson, N. A. 1967 Interactive segregation between fish species. *In:* S. D. Gerking (ed.), p. 295–314. The biological basis of freshwater fish production. J. Wiley and Sons, Inc., NY.

Ohio Department of Natural Resources (ODNR) 1960 Gazetteer of Ohio streams. Div. Water Rep. 12, Ohio Water Plan Inventory.

Starrett, W. C. 1950 Food relationships of the minnows of the Des Moines River, Iowa. Ecol. 31: 216–233.

Turner, C. L. 1921 The food of the common Ohio darters. Ohio J. Sci. 22: 41–62.
Wehnes, R. E. 1973 The food and feeding relationships of five sympatric darter species (Pisces: Percidae) in Salt Creek, Hocking County, Ohio. Unpubl. M. S. Thesis. Ohio State Univ., Columbus.
Wynes, D. L. 1979 Predator-prey relationships in riffle fish communities of the Little Miami River, Ohio. Unpubl. Ph.D. dissert. Miami Univ., Oxford, OH.
Zaret, T. M. and A. S. Rand 1971 Competition in tropical stream fishes: Support for the competitive exclusion principle. Ecol. 52: 336–342.