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RESOURCE PARTITIONING AND MECHANISMS OF COEXISTENCE
OF BLACKCHIN AND BLACKNOSE SHINERS
(_NOTROPIS_: CYPRINIDAE)

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Leni Ann Wilsmann

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Earl E Werner
Major professor

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RESOURCE PARTITIONING AND MECHANISMS OF COEXISTENCE OF BLACKCHIN AND BLACKNOSE SHINERS (<u>NOTROPIS</u>: CYPRINIDAE)

By

Leni Ann Wilsmann

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ABSTRACT

RESOURCE PARTITIONING AND MECHANISMS OF COEXISTENCE OF BLACKCHIN AND BLACKNOSE SHINERS (*NOTROPIS*: CYPRINIDAE)

By

Leni Ann Wilsmann

Food and habitat utilization of the blackchin (*Notropis heterodon* Cope) and blacknose (*N. heterolepis* Eigenmann and Eigenmann) shiners were studied in Lawrence Lake, Michigan in 1977 and 1978. Habitat use was determined by underwater censuses at midday and dusk. Food utilization was investigated across the growing season (April through September) and within the diel cycle.

Shiners occurred in heterotypic schools over dense vegetation during the day but occuppied a wider range of habitats, including less densely vegetated regions, at twilight. No habitat segregation between species or among size classes within species was observed during the day and analyses of gut contents indicated that the fish fed very little at that time. Peak feeding periods were morning and evening twilights and prey taken at these times indicated the two species segregated by habitat when foraging. Blackchin foraged in a broader range of habitats than did the blacknose. Blackchin fed primarily upon open water prey with prey from the surface, benthos and vegetation approximately equally represented in the remainder of the diet. Blacknose fed primarily on benthic prey, very little on open water prey and not at all on surface prey; vegetation prey were particularly important to smaller blacknose. Total dry weight of food consumed and mean prey size declined across the summer in both species indicating resources were limited during that time.

Differences in habitats foraged were consistent with differences in mouth morphology of the shiners. The blackchin has a terminally positioned mouth whereas the blacknose has a subterminal mouth common to many species which forage the benthos.

Small bluegills ($\leq$ 50 mm Total Length) were also confined to dense vegetation during the day and exhibited a twilight migration to open habitats. Unlike the shiners, though, bluegills remained within the vegetation rather than above it during the day and foraged there throughout the day.

The results suggest that the greater success of the blackchin relative to the blacknose in Lawrence Lake may be due to its ability to opportunistically forage a wider range of habitats under low resource conditions. Predation is implicated both as an important constraint to ecological segregation by the shiners as well as an ameliorating factor to competition. The decline in food intake by the shiners across the summer, though, indicates that predation was not severe enough to maintain shiner populations below levels at which food was limiting.

To mdf

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INTRODUCTION

In an environment of finite resources, species with the capacity to reproduce at remarkable rates should face resource limitations at some time. Those species that do coexist must have evolved mechanisms by which available resources are partitioned in order to persist in the face of competition. Such mechanisms would be expected to be most refined in similar species -- that is, in those species whose requirements are most similar. These mechanisms may be multifaceted, but those bearing directly on survival and reproduction, which are the components of fitness, should be particularly well defined.

G. E. Hutchinson's (1957) definition of the niche as an n-dimensional hypervolume and his classic question concerning the diversity of life (1959) in conjunction with MacArthur's warbler study (1957) formed the basis for the development of "niche theory" approach to the study of the partitioning of resources among competing species. This approach routed ecologists to thinking about how similar species can be and still coexist, and what the mechanisms behind that coexistence are, in direct contrast to the monotonous attempts to disprove "Gauses's Principle" of competitive exclusion. Extensive sophistication of the theory has ensued (May, 1973, 1974; MacArthur, 1972; Roughgarden, 1974 a,b; Schoener, 1974a: etc. but major insights have come from uniting theory with the field (Werner, 1978).

To explore the mechanisms of coexistence among species, one must first ask which of the n dimensions that describe a species niche are expected to be most critical? The concept of the niche has been operationalized from n dimensions to two or three major dimensions for purposes of applying the theory to real systems. In animals, these dimensions are frequently taken to be some measure of food and space, two important environmental commodities over which competition is likely to occur and necessitate some mechanism for resource partitioning to enable coexistence of the competitors. Schoener (1974 b) has reviewed the literature concerning important resource dimensions and found segregation on habitat dimensions more frequently than on food dimensions over a wide range of animals.

Partitioning of resources alone may not account for coexistence of potential competitors. Predation upon competitors may reduce competitive pressures by maintaining the superior competitor or all competitors at population levels below critical levels for competitive exclusion (Connell, 1975; Paine, 1966). At present, the influence of predation on competitive interactions in many systems is not well understood (Schoener, 1974 b). The timimg of important life history stages, especially reproduction (Hutchinson, 1959) can also play an important role in determining both intra- and interspecific interactions. The understanding of the interplay of resource partitioning, predation, and life history characteristics in the maintenance of species coexistence in natural communities are essential to our understanding of community structure.

THE PROBLEM

A pilot study of the littoral fish communities of two Michigan lakes (Werner, et al, 1977) revealed the apparent lack of habitat segregation during the day between two similar shiner species, the blackchin shiner (Notropis heterodon Cope) and the blacknose shiner (N. heterolepis Eigenmann and Eigenmann) and their striking segregation with small size classes of the bluegill (Lepomis macrochirus Rafinesque), the dominant species in both lakes. These patterns raised several questions concerning the coexistence of these three species and the mechanisms which permitted it.

The small maximum size, general morphological similarity but differences in trophic sturctures, and high abundances of the shiners raised the question of whether these two species were competing for resources, and to what extent partitioning of food and/or habitat resources permitted coexistence. Since there appeared to be little habitat complementarity, at least during the day, food type and/or size segregation was expected. Secondly, was there an interactive basis for the apparent habitat segregation of shiners and bluegills? An thirdly, what role did predation play to facilitate or constrain coexistence between the shiners?

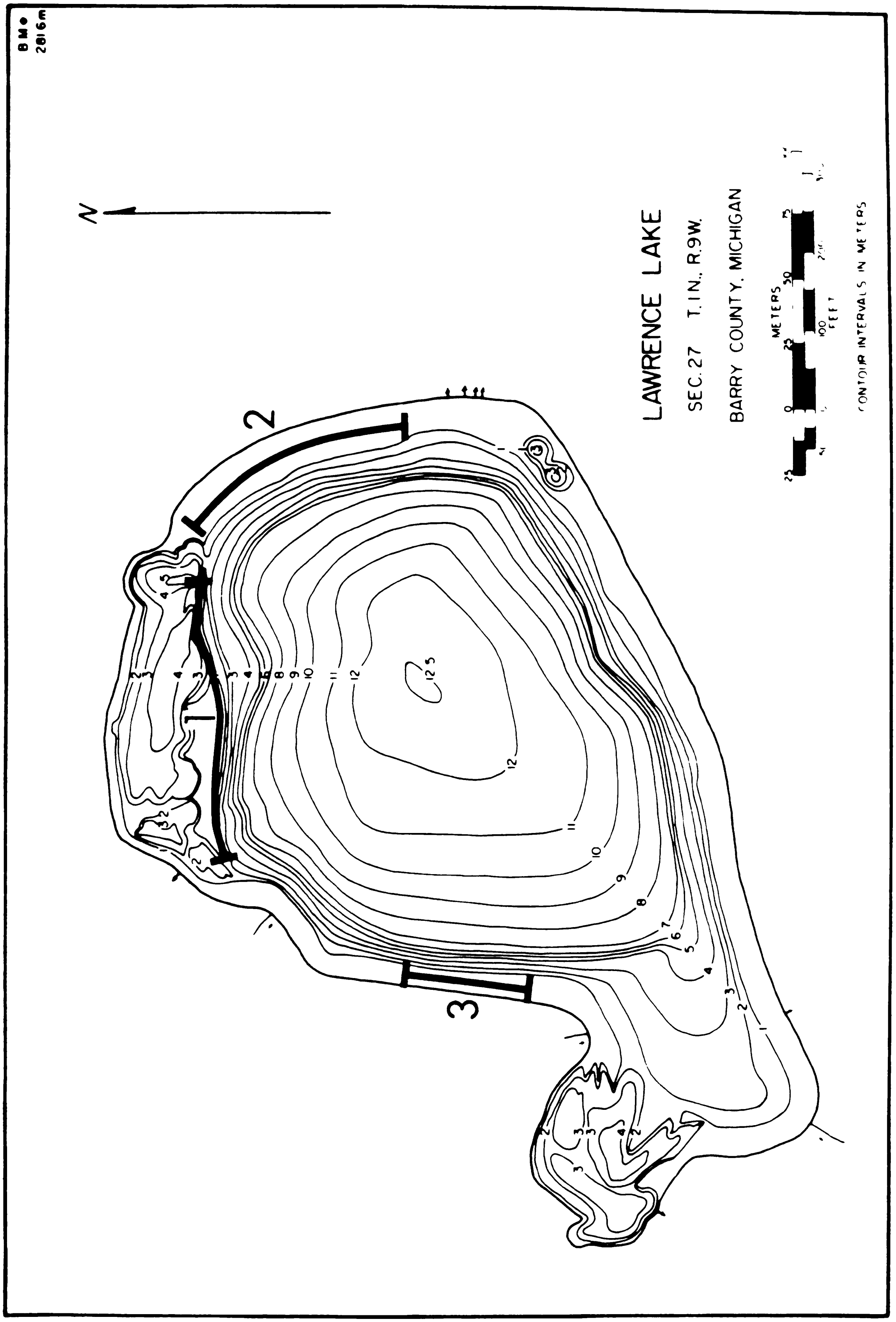
The study detailed below is an observational investigation in which food and habitat were assumed to be of primary importance to small fish in a seasonal and variable environment. Patterns of resource utilization across diel and seasonal cycles were expected to yield insight into the nature of interspecific interactions. In particular, differential capabilities of the species to acquire resources during times of low resource levels should indicate unequal competitive abilities. Basic life history and morphological data were also collected on the shiners to supply a necessary perspective for evaluating interspecific interactions.

THE SYSTEM

The Lakes

Southwestern Michigan contains many small, glacially formed, kettle hole lakes (Dorr and Eschman, 1970) that vary in their chemical relationships and aquatic vegetation but contain a fairly constant complement of fish species. One of these lakes, Lawrence Lake, was chosen as the primary study site. It contains a simple vegetational community, moderately diverse habitat types, only two common species of small shiners, and the fish community has been previously studied (Werner, et al, 1977; Hall and Werner, 1977). Lawrence Lake (Figure 1) is located 2.1 km east of Hickory Corners, Barry County, Michigan (T.1N, R.9W, Sec. 27). It is a mesotrophic, alkaline, hardwater lake, 4.9 ha in surface area with a maximum depth of 12.6 m (Rich, 1970; Wetzel, 1975). The major inlets to the lake are two small streams. Drainage from the lake flows into a smaller lake then through a marsh into Augusta Creek (Rich, 1970). Basin morphometry is characterized by a broad marl bench extending up to 15 - 20 m from shore to a depth of 1.25 m, followed by a steeply sloping drop-off to 7 m. Major artificial depressions about 4 m deep, due to marl dredging principally in the first half of this century (Rich, 1970), are located in the north and southwest areas of the lake. The lake is ice-covered from December to late March, but the lower hypolimnion becomes anoxic only at the end of summer stratification (Wetzel, personal communication).

Figure 1. Bathymetric Map of Lawrence Lake, Michigan. Transect locations are indicated (after Rich, 1970).


BM•
2816m
N
LAWRENCE LAKE
SEC. 27 T.1N., R.9W.
BARRY COUNTY, MICHIGAN
METERS
25 0 25 50 75
100 200
FEET
CONTOUR INTERVALS IN METERS
1
2
3
1 2 3 4 5 6 7 8 9 10 11 12
12.5

The dominant vegetation in Lawrence Lake is the perennial submersed macrophyte, Scirpus subterminalis (79% of total macrophyte biomass (Rich, et al, 1971)), which occurs from 0.5 m to approximately 6 m depth and resembles tall grass in appearance. There is little tall vegetation (e.g. Myriophyllum or Potamogeton) on the lower slope. Shallow bench regions are bare in wind swept areas but contain a mixture of Chara, Najas flexilis, and Utricularia in more protected areas. The west shore and shallow southern bay contain dense stands of Nuphar with scattered patches of Nymphaea ordorata.

Underwater visibility is usually very good in Lawrence Lake. Shiners can be identified at a distance of 2 to 3 m. However, algal blooms and marl precipitation occasionally reduce visibility to about half the usual condition.

Fishing pressure is very light because the lake is privately owned. So, except for occasional stocking of pike by one landowner, the fish community is little disturbed.

Two other lakes, Three Lakes II and Pine Lake, were chosen for corroboration and comparison of some of the findings from Lawrence Lake. Three Lakes II, 22 ha in surface area with a maximum depth of 8 m (Haney and Hall, 1975; Humphrys and Colby, 1965) is located 3.2 km southeast of Richland, Kalamazoo County, Michigan (T.1S, R.10W, Sec. 25,26), and contains 3 small shiner species. The dominant vegetation on the bench and upper part of the slope is a very dense mat of Chara, which is only occasionally interspersed with Najas or Potamogeton. Also, there are no areas of bare sediment on the bench as there are in Lawrence Lake. In stark contrast to Lawrence Lake, dense stands of taller vegetation begin developing at about 2.5 m depth in late spring and extend to within

0.25 m of the surface in some areas by mid to late June. Initially, Potamogeton's dominate the lower slope, but by midsummer, Myriophyllum has taken over. Fishing pressure in Three Lakes is relatively heavy on centrarchids.

Pine Lake, 3.6 km north of Cloverdale, Barry County, Michigan (T.2N, R.9W, Sec. 8), has a surface area of 27 ha with a maximum depth of 10 m (Humphrys and Colby, 1965). It is a marl lake but more productive than Lawrence Lake, due in part to nutrient input from homes on the west shore. The vegetational diversity in Pine Lake is greater than that in Lawrence, with discrete patches of different types of vegetation (e.g. Scirpus subterminalis, Chara, Myriophyllum, Eleocharis, Nuphar, Nymphaea, Bresinia, Sagittaria, etc.) scattered around the littoral. But here too, as in Lawrence, there are great expanses of bare marl bench. However, Scirpus subterminalis is present only in patches, the lip of the bench is ringed by Myriophyllum or Nuphar or a combination of the two, and the slope contains tall Potamogeton's and/or Myriophyllum. Fishing pressure is moderate.

The Fish Community

Local fish communities are dominated, both in number and biomass, by sunfishes (Centrarchidae), with shiners and minnows (Cyprinidae) comprising the second most abundant group. The within-lake relative abundances of most fish species are very similar across the three study lakes (Table 1); differences in community composition are usually attributable to presence or absence of rare species.

The blackchin and blacknose shiners are the most abundant cyprinids in the study lakes. In spite of this, relatively little is know about the general biology of these species. In contrast, there is considerably more

Table 1. Relative Abundances of Fishes in the Study Lakes. V = Very Abundant; A = Abundant; C = Common; R = Rare; - = Absent; X = Reported but extremely rare; ? = Genus reported but species not identified.

	Lawrence L.	Three L.	Pine L.
CENTRARCHIDAE			
Lepomis macrochirus, Bluegill sunfish	V[1]	V	V
L. gibbosus, Pumpkinseed sunfish	C	A	C
L. cyanellus, Green sunfish	R	C	C
L. gulosus, Warmouth	R	C	R
L. megalotis peltastes, N. longear sunfish	C	-	C
Micropterus salmoides, Largemouth bass	A	A	A
Pomoxis nigromaculatus, Black crappie	C	C	C
Ambloplites rupestris, Rockbass	X	-	-
PERCIDAE			
Perca flavescens, Yellow perch	C	C	C
Etheostoma exile, Iowa darter	R	R	-
E. microperca, Least darter	-	R	-
CYPRINIDAE			
Notrpois heterodon, Blackchin shiner	V	V	V
N. heterolepis, Blacknose shiner	V	A	V
N. anogenus, Pugnose shiner	X	C	R
N. cornutus, Common shiner	X	C	X
N. stramineus, Sand shiner	-	R	-
Notemigonus crysoleucas, Golden shiner	C[2]	C	C
Pimephales notatus, Bluntnose minnow	X	-	V
Semotilus atromaculatus, Creek chub	-	X	-
Cyprinus carpio, Carp	-	R	-
CATOSTOMIDAE			
Erimyzon sucetta, Lake chubsucker	R	C	R
Catostomus sp., Sucker	X	-	X
ESOCIDAE			
Esox lucius, Northern pike	R	R	R
Esox americanus vermiculatus, Grass pickerel	R	R	R
UMBRIDAE			
Umbra limi, Central mudminnow	R	X	-
ICTALURIDAE			
Ictalurus natalis, Yellow bullhead	X	?	X
GASTEROSTEIDAE			
Culaea inconstans, Brook stickleback	-	X	-

Table 1 (cont'd.).

	Lawrence L.	Three L.	Pine L.
CYPRINODONTIDAE			
Fundulus notatus, Blackstripe topminnow	-	C	-
F. diaphanus menona, W. banded killifish	-	C	-
ATHERINIDAE			
Labidesthes sicculus, Brook silverside	-	C	C
AMIIDAE			
Amia calva, Bowfin	R	R	R
LEPISOSTEUS			
Lepisosteus sp., Gar	-	R	-
SALMONIDAE			
Salmo gairdnerii, Rainbow trout	-	R	-

[1] Qualitative relative abundances are based on published quantitative estimates (Werner, et al, 1977; Hall and Werner, 1977), seine haul returns and underwater observations from this study, and discussions with local fisherman. Species identifications were made with the aid of various freshwater fish keys (Trautman, 1957; Hubbs and Lagler, 1964; Scott and Crossman, 1973; Hubbs and Cooper, 1936).

[2] Golden shiners were rare in Lawrence Lake in 1976, but abundant in 1978.

information available on the bluegill sunfish, the dominant centrarchid, because of its prominence as a sport fish. A summary of available life history information on these species is presented below.

The blackchin shiner (Notropis heterodon)is distributed throughout the northcentral portion of the United States and southern Canada in the Great Lakes basin and tributary watersheds (Scott and Crossman, 1973). It is a small, elongate fish with a silvery body and prominent black lateral stripe that continues anteriorly across both the upper and lower lip. It has a small, terminally positioned mouth, and attains a maximum total length of approximately 75 mm. Reports based on length determinations indicate that most blackchin do not survive beyond Age I, i.e. not longer than 2 years (Scott and Crossman, 1973; Trautman, 1957).

The blacknose shiner (N. heterolepis) occupies a wider geographic range than the blackchin shiner and is widely distributed between the Hudson Bay, Iowa, Missouri, Tennessee and New England (Scott and Crossman, 1973). In appearance it is similar to the blackchin but has a ventro-terminal mouth and the black lateral stripe extends across only the upper lip. Maximum size is approximately 75 mm total length. Blacknose shiners reportedly do not survive beyond their second summer (Emery and Wallace, 1974).

Both Notropis species prefer heavily vegetated areas in lakes and low gradient streams, and are intolerant of polluted or silted conditions. The geographical range of each species is presently smaller than originally reported due to adverse habitat changes, principally due to the effects of farming on watersheds (Bailey and Allum, 1962; Harlan and Speaker, 1969; Scott and Crossman, 1973; Trautman, 1957). Both species are late spring-early summer breeders, presumably of the broadcast type (Breder and Rosen, 1966), although the blacknose breeds earlier than the blackchin (see below).

One striking characteristic of both species is their schooling behavior. Shiners are usually found in dense, heterotypic, non-polarized, mobile schools during the day, but the schools disperse after dark (personal observation). This behavior is exhibited throughout the entire lifetime of an individual. In contrast, of the size classes of bluegills associated with vegetation, only small, young-of-the-year fish are found in dense schools (personal observation). Further, bluegill schools are relatively sedentary, with relatively little movement of individuals within the school and of the school as a whole.

Literature reports of the diets of the blackchin and blacknose usually are based on few fish and are reported in very general terms. The general pattern is that both species consume Cladocera and insect larvae and pupae; the blackchin may also take surface prey (Forbes and Richardson, 1920; Keast, 1965, 1970; Pearse, 1915). Identification of prey items in the gut is very difficult because prey are frequently broken into small pieces by the action of well-developed pharyngeal teeth common to all cyprinids.

Analysis of morphological characteristics of the blackchin and blacknose shiners lends insight into the relative metabolic requirements and foraging potential (prey size, microhabitat, etc.) of the two species. Length-weight regressions demonstrate that blackchin and blacknose are virtually identical in body weight (mg dry weight) at a given standard length (mm) ($W = 1.35 \times 10^{-7} SL^{3.87}$, $R^2 = 0.99$, blackchin; $W = 9.80 \times 10^{-8} SL^{3.94}$, $R^2 = 0.99$, blacknose). Maximum size attained is also very similar (Trautman, 1957; personal observation). Metabolic requirements should therefore be relatively similar for individuals of similar length of both species.

On the other hand, mouth size and position differ between the blackchin and blacknose. The blackchin's upper jaw length (Figure 2) relative to body length is larger and increases more rapidly with increasing body length than the blacknose's ($P < 0.002$, comparison of slopes of regression equations by 1-tailed F-test; Li, 1964; Snedecor and Cochran, 1967). The subterminal position of the blacknose's mouth necessarily restricts the length of the upper jaw. This is especially obvious when it is compared to the terminally positioned mouth of the blackchin. Differences in mouth width (Figure 2) are not as straightforward, for although the slopes of the regressions of mouth width on standard length for the two species are different, the lines intersect at approximately 30 mm standard length. Thus, over the range of standard length of major interest in this study (approximately 15 - 45 mm), expected mouth widths of the two shiners are very similar. For example, the ratio Blacknose:Blackchin of expected mouth widths at 15 mm standard length is 1.096; at 45 mm, Blackchin: Blacknose for mouth width is 1.077. Based on mouth morphology, the blackchin should be more of a food generalist than the blacknose since its mouth is consistently larger, at least in one dimension, thus allowing larger prey to be eaten. Also, the blackchin mouth position is less specialized than that of the blacknose, permitting prey to be taken from a wider variety of positions in the environment.

Lengths and densities of gill rakers on the first pharyngeal arch were examined qualitatively in several species to determine their relative potential for prey retention. The blackchin's rakers are somewhat more developed than those of the blacknose, but both have rather short, widely spaced rakers. Gillrakers of the golden shiner (Notemigonus crysoleucas), an open water planktivore, were much longer and more finely spaced than the

Figure 2. Relation of Upper Jaw Length (UJL) and Mouth Width (MW) to Standard Length (SL). Measurements are in mm.

<u>KEY</u>

BLUEGILL

— - - — $MW = 0.3751 + 0.0999\ SL,\ r = 0.98$

— — — $UJL = 0.185 + 0.0975\ SL,\ r = 0.99$

BLACKCHIN

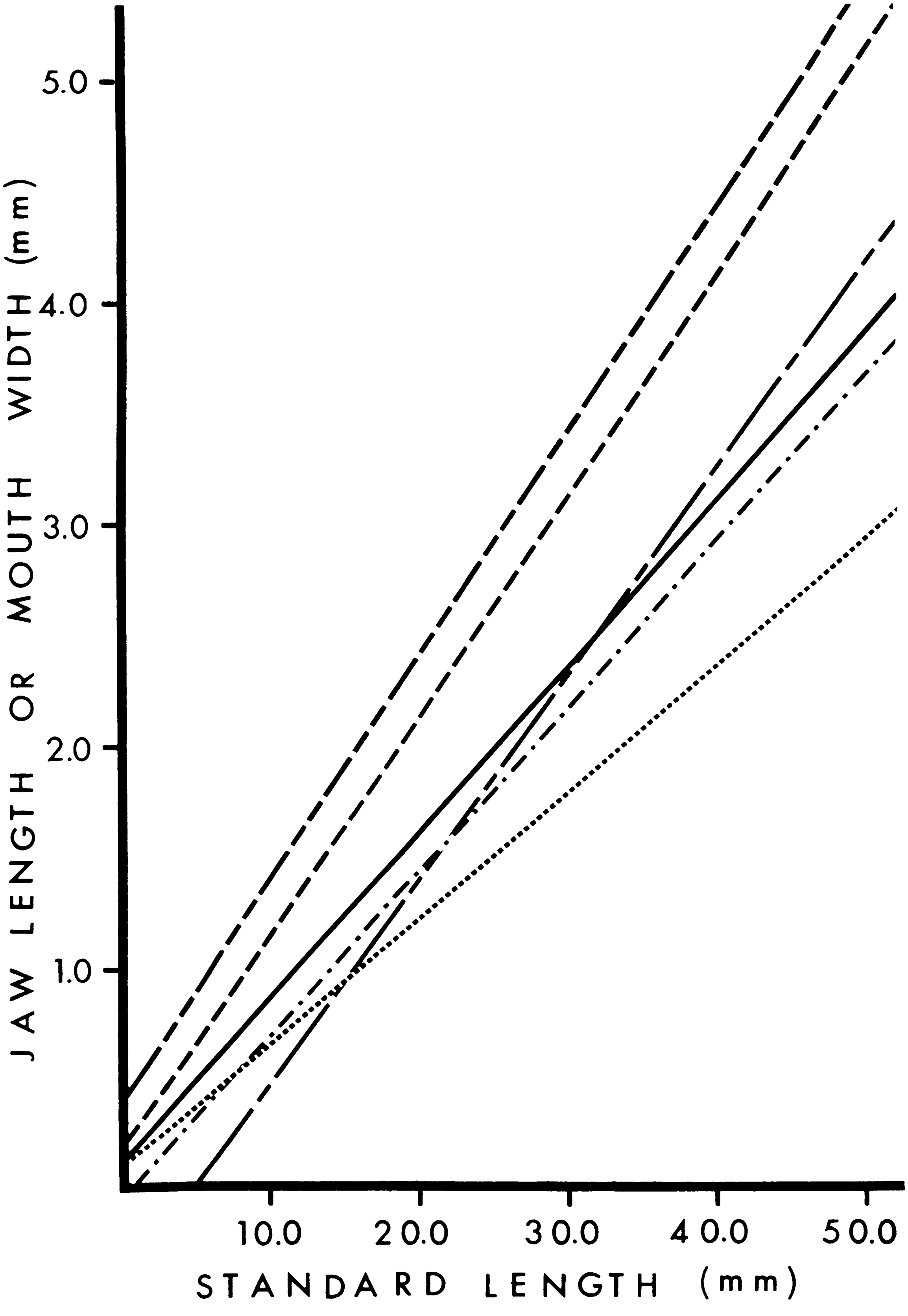
- —— - $MW = -0.0171 + 0.0862\ SL,\ r = 0.98$

— - — - $UJL = -0.0390 + 0.0734\ SL,\ r = 0.99$

BLACKNOSE

——— $MW = 0.123 + 0.0738\ SL,\ r = 0.97$

- - - - - $UJL = 0.0762 + 0.0563\ SL,\ r = 0.97$


JAW LENGTH OR MOUTH WIDTH (mm)
5.0
4.0
3.0
2.0
1.0
10.0
20.0
30.0
40.0
50.0
STANDARD LENGTH (mm)

Notropis rakers. Similarly, gill rakers of the bluegill were much longer and finer than those of the shiners. The rakers of both *Notropis*, then, are relatively generalized and do not confer specialized prey handling abilities on either species.

The bluegill sunfish occurs naturally over the eastern half of the United States, but it has been introduced almost everywhere else in the country (Scott and Crossman, 1973). The bluegill is a morphological, habitat, and food generalist in comparison to many other centrarchids (Keast, 1965; Keast and Webb, 1966; Werner, et al, 1977; Werner and Hall, 1976, 1977), but small size classes are usually found in heavily vegetated areas (Hall and Werner, 1977; Werner, et al, 1977). Onshore movements of larger size classes at dusk have been reported (Baumann and Kitchell, 1974; Werner, et al, 1977), but diel habitat changes of smaller individuals have not been studied. Newly hatched fry spend their first 8 - 10 weeks of life in the open limnetic zone (Faber, 1967; Werner, 1967, 1969) and return to the vegetated littoral at 20 - 25 mm total length.

The bluegill has a larger mouth than either the blackchin or blacknose in both mouth size parameters (Figure 2). The slope of the regression for upper jaw length increases more rapidly with standard length in the bluegill than in either of the shiners ($P < 0.0001$). And although regression slopes for mouth widths are not significantly different between the bluegill and shiners ($P > 0.05$), the bluegill intercept is significantly higher (2-tailed F-test, $P < 0.0001$). The bluegill, then, not only has a larger mouth than the shiners at a given standard length, but jaw length increases more rapidly with increasing size than it does in the shiners. Therefore, for a similar increment of additional body length, the bluegill should be able to add larger prey to its diet than the shiners.

METHODS

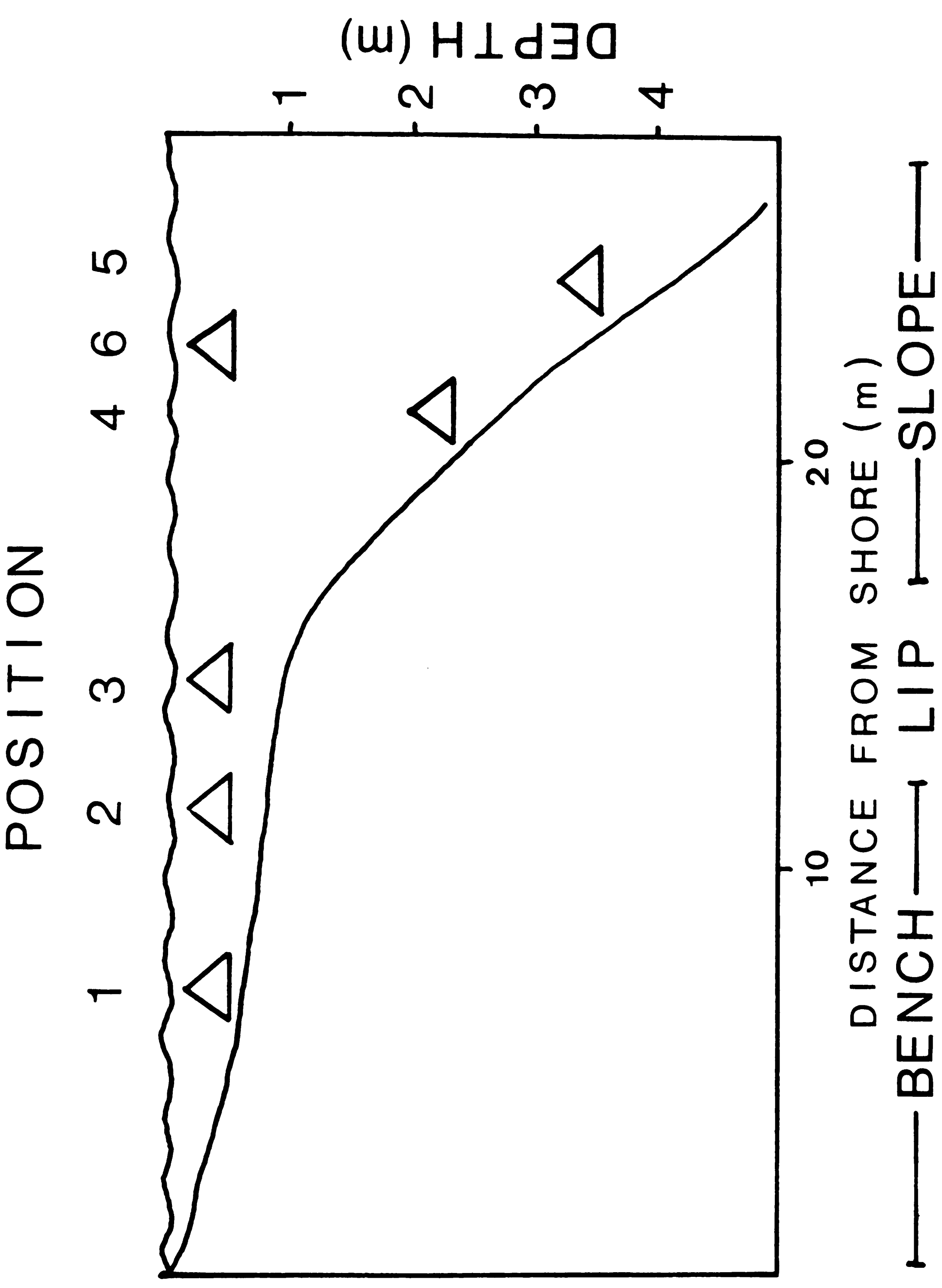
Field Methods

Habitat Censuses. Daytime habitat distributions and relative abundances of blackchin and blacknose shiners in Lawrence Lake were investigated during mid-summer, 1977, by means of transect censuses. Three transects were established (Figure 1) to include the range of habitat types in which the "shiner complex" (blackchin and blacknose not distinguished as separate species) was found in a previous study (Werner, et al, 1977). The transects differed primarily in their bench vegetation; lip and slope positions were comprised of primarily dense *Scirpus subterminalis* in all three cases. Position 2 (Bench) was barren, partially vegetated, and completely vegetated on Transects 1, 2, and 3, respectively. Refer to Appendix 1 for habitat descriptions.

I swam two to three parallel positions, one at a time, using face mask and snorkel, on each transect in order to census different vegetational areas and/or depths; these positions are designated Bench (Position 2), Lip (Position 3), and Slope (Position 4) in Figure 3. I censused a distance of approximately 1 m on each side of me at each position. The census technique used was a modification of the one developed by Werner, et al (1977) and Hall and Werner (1977).

Censuses were conducted between 27 July and 23 August 1977, between the hours of 1300 and 1700; fish on each transect were counted no more than once each day. All shiners encountered were identified to species (blackchin or blacknose) and size class (small ≤ 25 mm total length;

Figure 3. Schematic Profile of Lawrence Lake Littoral Zone.
Triangles represent positions of observers.


POSITION
1
2
3
4
6
5
DEPTH (m)
1
2
3
4
10
20
DISTANCE FROM SHORE (m)
BENCH
LIP
SLOPE

medium 26 - 40 mm; Large 41 - 55 mm; and extra-large > 55 mm). With some practice it was possible to distinguish between even the smaller individuals of the two species, both from a side and dorsal view. Counts were recorded on underwater paper. Counts differed by 4 to 26% of the mean between replicate censuses (Appendix 2).

Diel changes in habitat and microhabitat distributions as well as relative abundances of blackchin and blacknose shiners, bluegills, and largemouth bass (Micropterus salmoides (Lacépède)), were studied in Lawrence Lake during the summer of 1978. This work was conducted in conjunction with Gary G. Mittelbach and James F. Gilliam who were studying bluegills and bass, respectively. The team of three observers allowed us to census multiple habitats simultaneously (3 positions at a time rather than 1 position as in 1977), something which was of utmost importance in the evening when observation time was limited.

Midday and dusk habitat distributions were censused in 1978 in a manner similar to that described for 1977. Transect 2 was chosen for intensive study because the range of habitats there was greater than on Transects 1 or 3. All six positions (Figure 3) were censused once on each of 2 consecutive days during the afternoon (1300 - 1600 h), three times during the summer (7, 8 July; 26, 27 July; and 14, 15 August). The Bench and Lip (Positions 1, 2, and 3) were censused on the evening of the first day of censusing and the Slope (Positions 4, 5, and 6) was censused the second evening, thus only daytime counts were replicated within each sampling period. Dusk censuses began approximately 15 minutes before sunset and lasted 35 - 50 minutes.

The transect was divided into three parts for Bench and Lip habitats based on vegetational changes at Position 2 in order to more accurately assess the associations of the fish with habitat types (see Appendix 1 for habitat details). Wires marked with reflective tape were placed on the shore at habitat boundaries for reference after dark. Slope positions (4 - 6) were not subdivided because the habitat was fairly homogeneous for the entire length of the transect. Observers at Positions 4 and 5 used SCUBA gear.

Microhabitat position, species (except shiners, see below), and size class were determined for each fish in the 1978 habitat censuses. Microhabitat categories on the bench were: lower vegetation, upper vegetation, 0 - 0.25 m, 0.25 - 0.50 m, 0.50 - 1.0 m, and 1.0 - 1.5 m above the vegetation. Categories on the slope were in 0.5 m intervals. The observer at Position 6 counted all fish above the vegetation at Position 4 and from 0.5 m above the vegetation at Position 5. Position counts are included in those reported for Positions 4 and 5 and are not reported independently.

Shiners were not identified to species because it was impossible to keep track of all species of fish, size classes, microhabitat designations and carefully identify shiners at the same time. Identification of shiners to species was possible in 1977 because microhabitats were not distinguished and species other than shiners were not counted. Two size classes of shiners were recognized, Age 0 and Age I, and are reported as Blackchin 0, Blackchin I, Blacknose 0, etc. Corresponding standard lengths for these age classes changed across the summer but maximum size for Age 0 was approximately 35 mm. Bluegills were assigned to size classes in intervals of 25 mm total length. For purposes of comparison with the shiners in this discussion, bluegills ≤25 mm TL are referred to as Bluegill 0 and those 26 - 50 mm TL as Bluegill I.

After dusk (2110 - 2130 h) censuses of fish in open habitats of

Transect 2 (Regions A and B; see Appendix 1) were conducted on two occasions (14 and 15 August 1978). Observers used flashlights and fish identification and size class designations were as described above.

One transect was established in Three Lakes on the south shore (187 m), which in contrast to Lawrence Lake, had dense vegetation from the shoreline to a depth of 3 m and an extensive overstory from about 3 to 4 m on the slope. Bench positions were similar to those in Lawrence Lake, but the slope positions ranged from 4 to 6 down the slope without a midwater observer similar to Position 6 in Lawrence Lake. This arrangement of observers was necessary to adequately census the broad slope region in Three Lakes. Once again, daytime censuses were replicated within sample periods, but evening runs were not.

For comparison with 1977 data and to determine the relative species abundances of the shiners that corresponded with 1978 microhabitat data, Transects 1, 2, and 3 were censused twice on 22 August 1978, by a single observer. Methods followed those outlined above for 1977.

Habitat Descriptions. Lawrence Lake transect vegetation was described once, at the end of the summer, in 1977. In 1978, Transect 2 was described twice and the single Three Lakes transect, once. Data were collected from a boat in Lawrence Lake in 1977 and on the Three Lakes bench in 1978, in order to get a more accurate picture of the dense vegetation. Other data were collected by swimmers. Six to eight estimates were made for each 100 m of transect at each position. At each stop, the observer blindly dropped a ½ x ½ m (0.25 m^2) metal square and recorded percent cover of each plant species, plant height, and water depth found within the square. Habitat descriptions are provided in Appendix 1.

Fish Collections. Fish were collected in Lawrence Lake for gut content analysis and size-frequency distributions every 2 to 4 weeks from 16 July to 13 September in 1976, and 23 April to 28 September in 1977. Collections were made a 0900 - 0930 h in 1976 and usually within one hour after sunrise in 1977. In 1978 fish were collected coincident with each of the three habitat census episodes to determine the relative amounts of prey captured by the fish in daytime and evening habitats. Fish were collected at 1500 h, 1 hour before sunset and 1 hour after sunset on the day following the last evening census for that sample period. On 31 July 1978, pre-sunrise and post-sunrise collections were also made following a standard series of evening collections on 30 July. In general, fish were collected from dense *Scirpus* beds with a 50', ¼" mesh bag seine.

Fish were killed in cold 10% formalin (1976 and 1977) or in MS-222 and then transferred to 10% formalin (1978). After several days, the fish were soaked in water for 2 days then transferred to 70% ethanol. All length and morphological measurements were made after the fish had been transferred to ethanol.

Laboratory Methods

Fish Gut Content Analysis. Analyses were performed on fish from Lawrence Lake from all three years of the study, but the number of gut sections examined varied among years. All three parts of the S-shaped gut of cyprinids were examined in 1977 fish, similarly for most 1976 fish, but only the first section (referred to here as the stomach but it is actually the first 1/3 of the intestine, since cyprinids lack a true stomach) was analyzed in 1978 fish.

Standard procedure was to determine the standard length and sex of the animal, remove the intestine, and cut it into three sections corresponding to the three parts of the "S" in cyprinids, or four parts (stomach and 3 intestinal loops) in small centrarchids. Usually only stomach contents were examined in larger centrarchids. Contents were examined at 25X or 50X with a Wild dissection microscope. The entire content of each section was enumerated and measurements were made, with the aid of an ocular micrometer, of the first 15 - 20 individuals of each prey taxon encountered. Usually head width or body length was measured on prey items, but some species were so badly pulverized by the shiner's pharyngeal teeth that other structures, such as postabdomens, postabdominal claws, or mandibles were measured.

Fish were selected for analysis based on size. An attempt was made to sample five fish within each 10 mm size class present for each species. However, sample sizes were quite variable due to changes in population size structures across the summer and small numbers of fish collected in the original seine hauls. Results are reported in terms of size classes of fish where the size class corresponds to the 10 mm range within which the standard lengths occurred. For example, size class 4 (SC4) represents fish for which $40 \leq SL \leq 49$ mm and SC2 represents $20 \leq SL \leq 29$ mm, etc. Size classes of a species are designated by the appropriate number following the species name, e.g. Blackchin 4 is size class 4 of the blackchin shiner.

Seasonal patterns in amount, size, and types of prey taken were determined for blackchin, blacknose, and bluegills collected in 1977 within 75 minutes after sunrise. This time limit was established to minimized differences across the season in amount of food digested and eliminated by the fish between feeding and subsequent capture. Previous analyses indicated that intestines were consistently mostly empty before periods of intense feeding activity, so feeding could continue for quite a while before food from the foraging bout would begin to be eliminated. Analysis of the entire gut also helped to minimize possible errors due to sampling time differences between dates that might occur if only stomachs were examined.

Diel feeding patterns were studied in fish collected in 1978. Only the stomach or first intestinal loop was examined. Seasonal data from 1977 correspond in time of collection to those for morning twilight feeding bouts in 1978.

Total dry weight of gut contents of each fish was determined by summing the dry weight of each prey item. Dry weights of prey items were computed from length-weight regressions. Regression equations were obtained from the literature (Burns, 1969; Costa, 1967; Dumont, et al, 1975; Frey, 1973; Ivanova and Klekowski, 1972; Sergeev, 1973; Smirnov, 1962) and from unpublished data of several investigators. Habitat affiliations assigned to prey taxa were also based on literature accounts (Berg, 1949, 1950; Mrachek, 1966) and unpublished data. Data analysis was performed on the Hewlett-Packard 2100 computer at W. K. Kellogg Biological Station.

Dry weights of fresh (unpreserved) fish were determined for one set each of blackchin and blacknose shiners. The fish were taken from Lawrence Lake on 23 August 1978 and dried for 48 h at 68° C in a forced draft oven.

RESULTS

Distribution and Life History

Blackchin and blacknose shiners were found widely distributed in local lakes. Of 12 lakes sampled by seining, blackchin and blacknose occurred in 12 and 11 of them, respectively (Table 2). In the study lakes, blackchin were usually more abundant than blacknose (Table 3). Other small cyprinid species (pugnose shiner, Notropis anogenus and bluntnose minnow, Pimephales notatus) were neither as widely distributed (Table 2) nor locally as abundant (personal observation) as the blackchin and blacknose. The golden shiner, a larger species, occurred in most lakes.

Size-frequency distributions of Lawrence Lake, Pine Lake and Three Lakes populations of blackchin and blacknose shiners and bluegill are presented in Figures 4, 5, and 6, respectively. (Note that fish less than approximately 18 mm standard length are under-represented due to seine mesh size on all dates except 19 August 1977 in Pine Lake. On that date a smaller mesh seine was used which prevented small fish from escaping). Year classes 0 and I were well separated in all species and most shiners did not live beyond Age I. Blackchin, however, appeared to be more variable than blacknose in maximum lifespan.

Blacknose reproduced before blackchin in all lakes, based on the size of the smaller year class (Age 0) of the two species. This interpretation is supported by the fact that small blacknose were regularly found in the littoral zone before small blackchin. Also,

Table 2. Distribution of Shiners in Twelve Southwestern Michigan Lakes. Numbers in parentheses are lake areas in hectares. + = present; - = absent; ? = collection not extensive enough to conclude the species is absent.

	Blackchin	Blacknose	Pugnose	Bluntnose	Golden
Bassett (17.8)	+	+	-	+	+
Deep (13.1)	+	+	-	+	+
Fair (96.4)	+	+	-	+	+
Fine (13.0)	+	+	-	+	+
Hamilton (16.2)	+	-	-	+	+
Head (39.2)	+	+	+	+	+
Lawrence (4.9)	+	+	*[1]	*[2]	+
Palmatier	+	+	+	-	?
Pine (27.0)	+	+	+	+	+
Tamarack (2.0)	+	+	-	-	?
Three Lakes (21.9)	+	+	+	*[3]	+
Wall (218.6)	+	+	-	+	?
Frequency (%)	100	92	33	66	75(+)

*[1] One fish captured in 1978; none in 1976 or 1977.

*[2] Reported by Keen and Kantor (1977) captured in 1969; none found in 1976-1978.

*[3] One bluntnose minnow seen in Three Lakes in 1978. With the heavy fishing pressure on the lake, it is notable that a common bait minnow like the bluntnose is not reported more frequently.

Table 3. Relative Abundances (%) of Blackchin and Blacknose Shiners in the Study Lakes. Proportions are based on seining in multiple habitats (S) or underwater counts (U). Sample size = 400 to 2400 fish.

	LAWRENCE LAKE				PINE LAKE		THREE L.
	1976 S	1977 U	1978 U	1978 S	1976 S	1977[1] S	1976 S[2]
BLACKCHIN	46.6	54.5	75.3	78.2	66.6	80.3	82.7
BLACKNOSE	53.4	45.5	24.7	21.8	33.4	19.7	17.3
BC / BN	0.9	1.2	3.0	3.6	2.9	4.1	4.8

[1] This is the only collection made with a small mesh seine that prohibited the escape of young-of-the-year blackchin.

[2] Figures based on the entire season of seining; others are from a single day of collecting or observing.

Figure 4. Size-frequency Distributions of Fish from Lawrence Lake. A. Bluegill, B. Blacknose, and C. Blackchin. ——— 30 August 1976, ---- 23 April 1977.

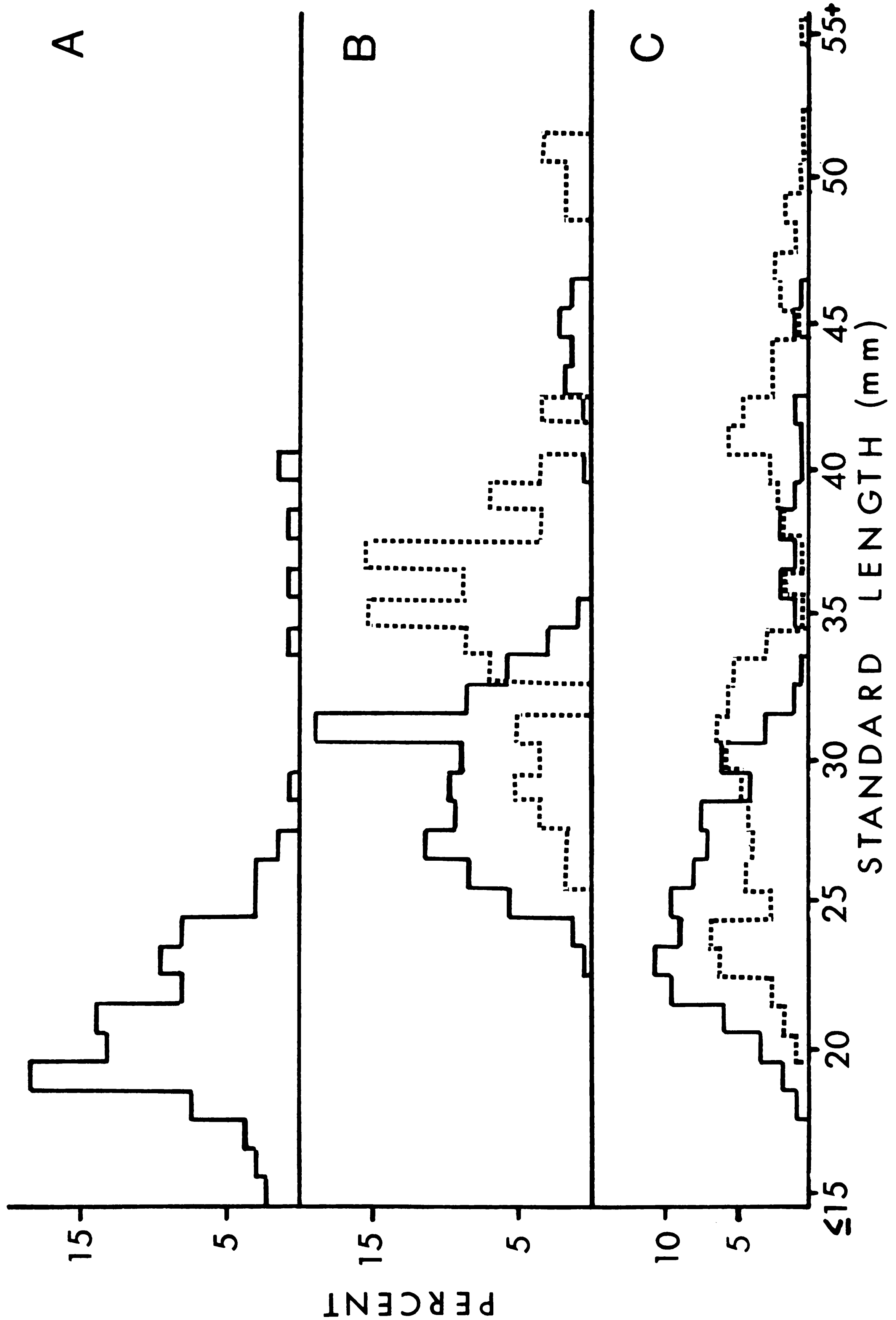

A
B
C
PERCENT
15
5
15
5
10
5
STANDARD LENGTH (mm)
≤15
20
25
30
35
40
45
50
55+

Figure 5. Size-frequency Distributions of Fish from Pine Lake, 19 August 1977. A. Bluegill, B. Blacknose, and C. Blackchin.

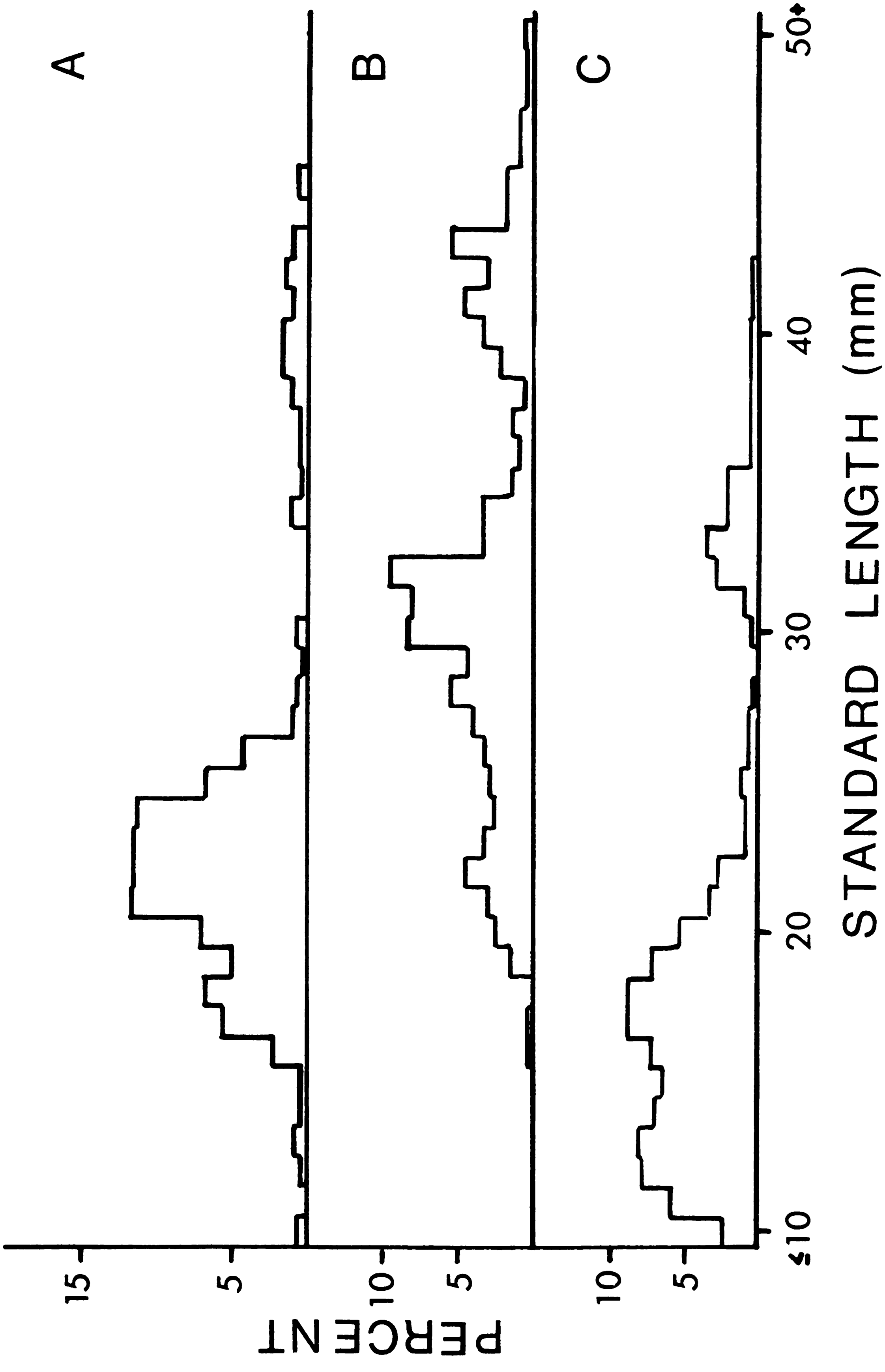
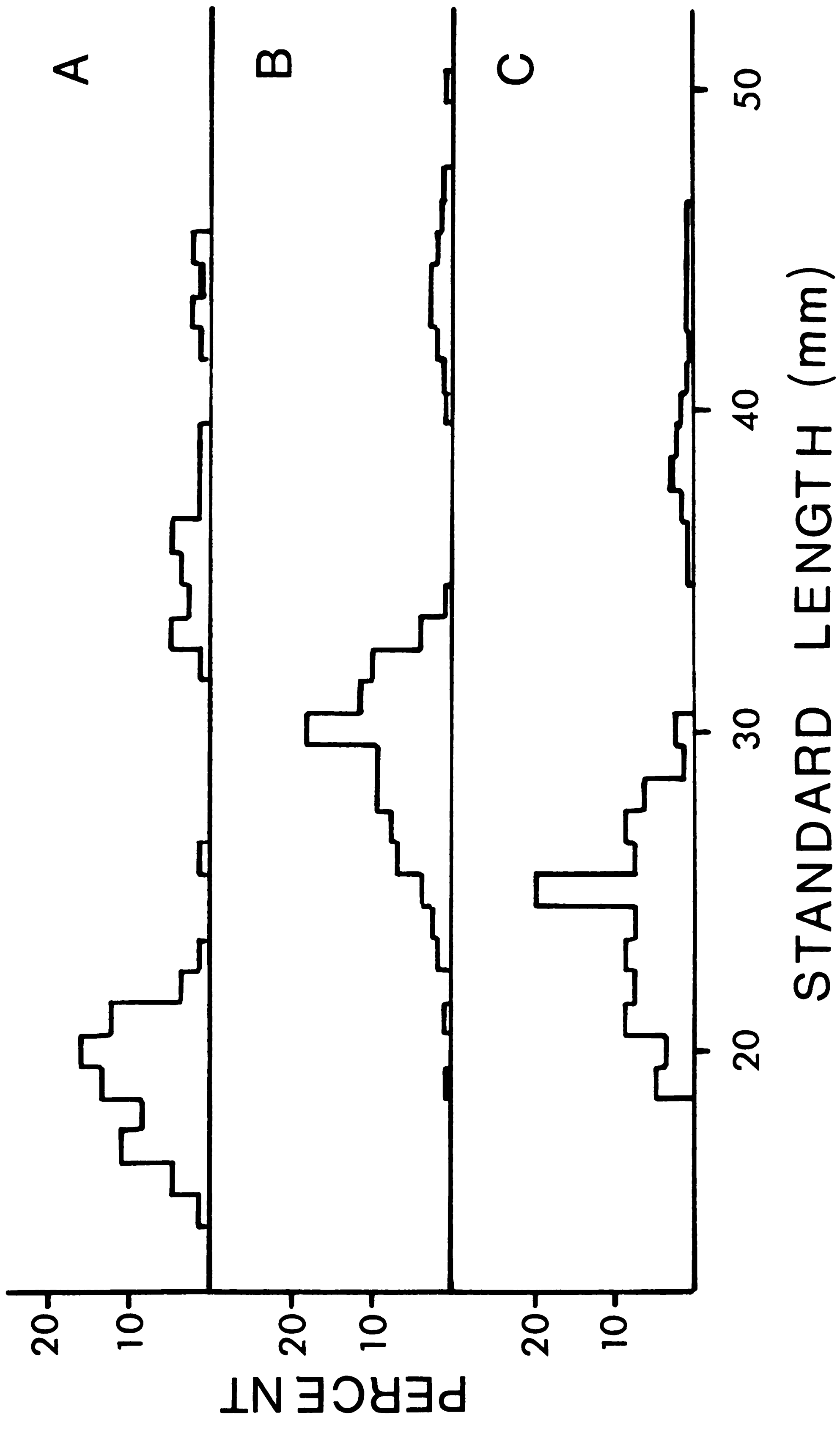

A
B
C
PERCENT
15
5
10
5
10
5
≤10
20
30
40
50+
STANDARD LENGTH (mm)

Figure 6. Size-frequency Distributions of Fish from Three Lakes, 16 August 1976. A. Bluegill, B. Blacknose, and C. Blackchin.


A
B
C
PERCENT
20
10
20
10
20
10
20
30
40
50
STANDARD LENGTH (mm)

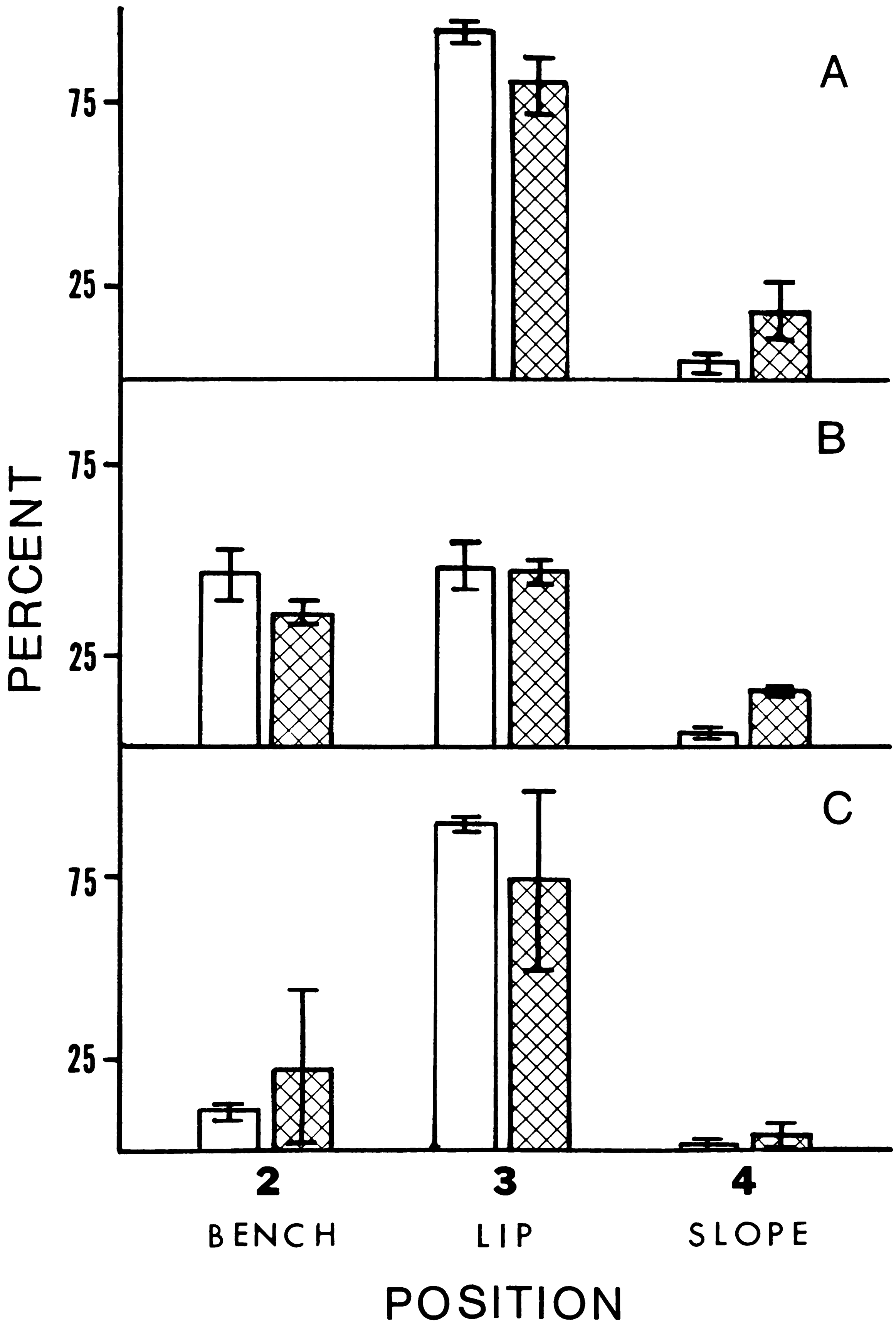
inspection of ovaries indicated that female blacknose matured ova and became spent before blackchin females.

Habitat Use -- Daytime

Shiners in Lawrence Lake schooled in relatively shallow, heavily vegetated areas during the daytime and exhibited no interspecific habitat segregation within transects. The proportion of each species found at different positions on each transect is presented in Figure 7. Note especially the extensive overlap in daytime habitat utilization between the two species. Proportions represented in Figure 7 were based on #/m only for habitats occupied by shiners during the day. This distinction is important only in the case of the Bench, Transect 2, where shiners were found on only 38 m of the 95 m transect, i.e. in the dense Scirpus area. On all the transects the greatest density of fish was found at the Lip, with an equal proportion of fish found at another position only for blackchin on the Scirpus Bench of Transect 2. Here, in essentially identical habitats of the Bench and Lip (dense Scirpus subterminalis), #/m were not significantly different (t-test, $P > 0.85$). No segregation of shiner size classes by habitat was found on any transects or among transects.

A greater proportion of the blacknose than blackchin population occurred below 1.0 m depth. On all three transects the percent blacknose found on the slope was significantly greater than the percent of blackchin (t-test on arcsin transformed data, $P < 0.001$). Replicate counts in 1978 were obtained separately for parts of Lip Transect 1 which were above and below 1.0 m. Again the proportion of blacknose found on the deeper section was significantly greater than the proportion of blackchin ($P < 0.001$). In spite of these differences, shiners were not found below

Figure 7. Mean Percent of Blackchin and Blacknose Populations at Transect Positions, Lawrence Lake, 1977. A. Transect 1, B. Transect 2, and C. Transect 3. Open bars are blackchin, shaded bars are blacknose, and vertical lines are ± 1 S.E.


A
B
C
75
25
75
25
75
25
PERCENT
2
BENCH
3
LIP
4
SLOPE
POSITION

the upper 2 m of the slope. Those observed on the upper slope were usually in small, inactive groups settled into the upper reaches of the *Scirpus* and represented on average less than 10 - 15 % of the population.

Differences among transects in shiner densities appear to be due to bench habitat differences. Transects with vegetation on the bench supported more blackchin than those without vegetation. Blackchin were most dense on Transect 3 which offered the only bench vegetated for its entire length (2-tailed t-test, $P < 0.05$). Transect 2, which was only partially vegetated, supported marginally more blackchin than Transect 1 ($0.10 > P > 0.05$), which had an unvegetated bench. Blacknose densities, in contrast, were correlated with open bench area. Blacknose were least dense on Transect 3 which had a completely vegetated bench, and they were equally dense on Transects 1 and 2 ($P > 0.9$) when blacknose/m were calculated based on the length of open bench on each transect. The dichotomy between the two species in relative densities on the three transects may be a reflection of differences in day and evening habitat requirements.

Total number of fish counted was not significantly different between 1977 and 1978 (2-tailed t-test, $P > 0.30$; d.f. = 2) based on a comparison of means of the replicated transect counts on 22 August 1978 with means for the last 2 dates in August 1977. However, mean number of blackchin encountered in 1978 was significantly greater than in 1977 ($P < 0.03$). These changes in relative abundances of blackchin and blacknose along with the small sample size (2 samples, 1 date) make comparison of 1977 and 1978 counts difficult, but some patterns are still discernable. Blacknose were still least abundant on the completely vegetated transect. Blackchin were distributed more evenly across transects in 1978 but total number/m on Transects 2 and 3 were still greater than on Transect 1 ($P < 0.04$ and 0.002, respectively).

In Pine Lake, shiners and small bluegill were also found principally in habitats characterized by dense, tall vegetation. Results from selective seining in five habitats indicated that fish numbers were positively correlated with stem densities of overstory vegetation (Figure 8) as well as with a combination of % horizontal cover and % vertical cover in the understory. Similarly, shiners and small centrarchids were never observed over open sediments in Three Lakes.

During the day then, shiners schooled only over densely vegetated areas of the bench, with very few individuals found on the upper slope. Habitat segregation between and within species did not occur. Differences in densities within species among transects were due to twilight habitat requirements.

Habitat Use -- Diel Changes

Shiners and bluegills in Lawrence Lake underwent diel changes in habitat and microhabitat utilization (all habitat utilization data in this section are from Wilsmann, Mittelbach, and Gilliam, unpublished data). Shiners and small bluegills were observed on sparsely vegetated and unvegetated sections on Transect 2 in Lawrence Lake after sunset. These areas contained very few fish during daylight hours. Less densely vegetated areas of Transect 2 (Positions 1 and 2, Regions A and B; see Appendix 1) were censused by a team of three swimmers using diving lights beginning 30 minutes after sunset on two successive nights, 14 and 15 August 1978. Results of these censuses (Table 4) and seine hauls in these areas indicated that small fish did move into less vegetationally structured habitats under cover of low light levels, and that centrarchids

Figure 8. Relation of Number of Fish to Plant Density in Pine Lake, 1977. Regressions are based on multiple seine hauls in each of five habitats. — — — — X Blacknose, · · · · △ Bluegill, - — - — O Blackchin, ——★ Total.

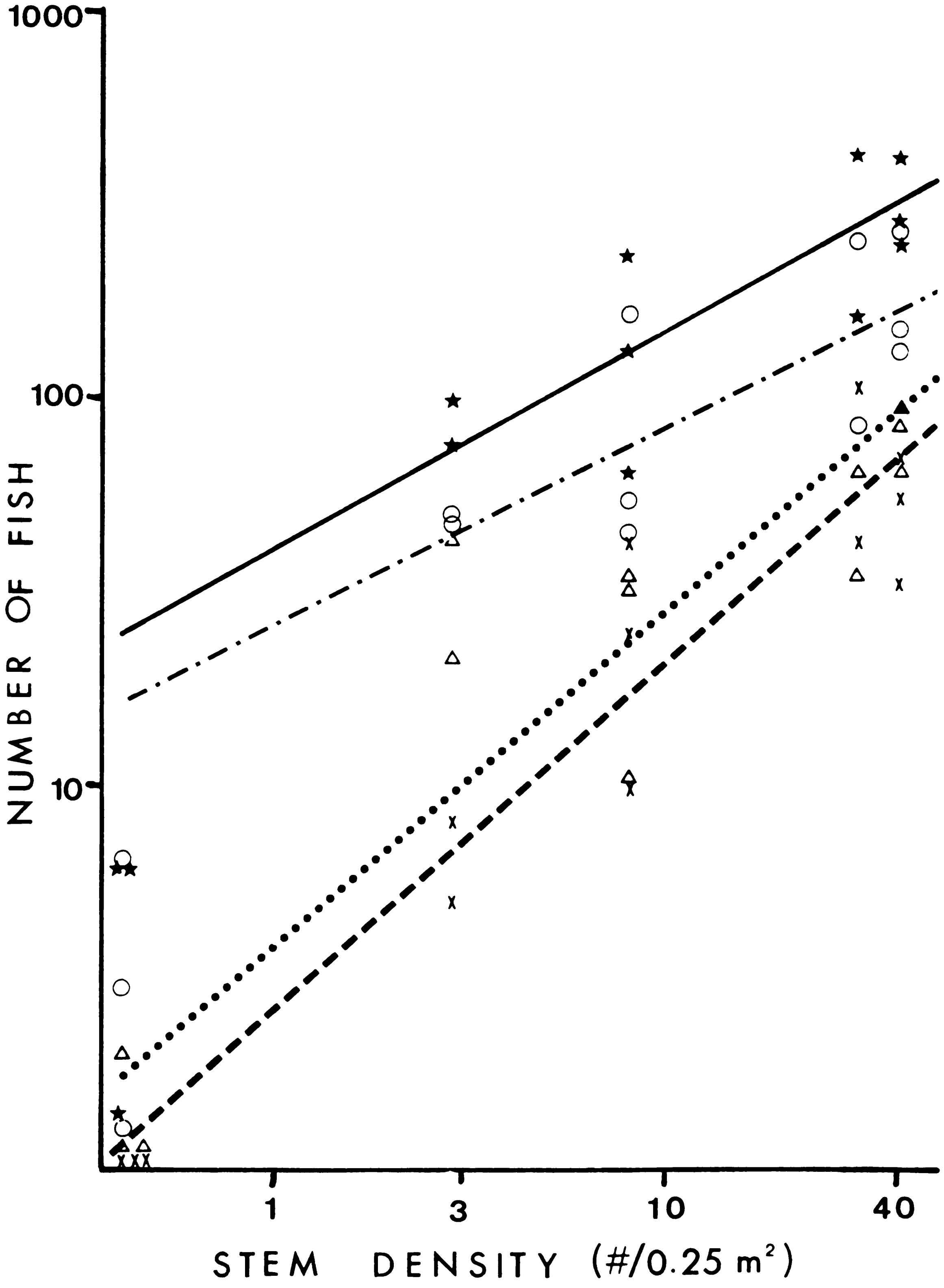

1000
100
10
NUMBER OF FISH
1
3
10
40
STEM DENSITY (#/0.25 m²)

Table 4. Fish Densities in Sparsely Vegetated Habitats of Lawrence Lake. Mean number of fish ± standard error for 14 and 15 August 1978 for small fish censused in open habitats of Lawrence Lake during the afternoon and after sunset in the evening.

	SHINER 0	SHINER I	BLUEGILL 0	BLUEGILL I
AFTERNOON	8.0 ± 8.0	0	0	2.0 ± 0
EVENING	97.5 ± 9.5	47.5 ± 3.5	16.5 ± 4.5	30.5 ± 7.5

preceded cyprinids into open areas by about 10 minutes (personal observation). Fish appeared to be active for about 50 - 60 minutes after sunset in these habitats.

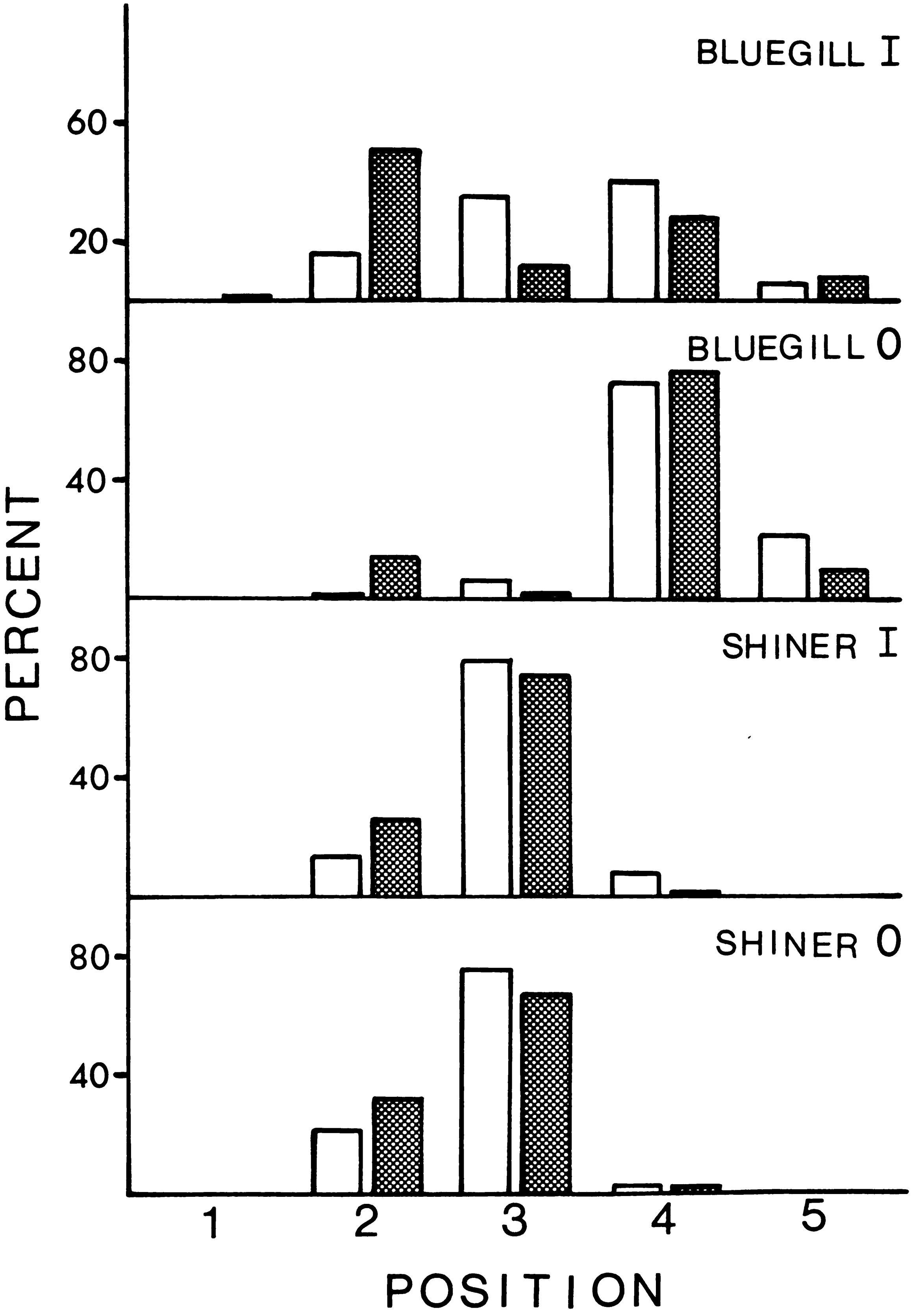
Habitat distributions of fish found by evening complete transect censuses represented transition distributions between daytime and after sunset habitat utilization patterns. Both shiners and bluegills exhibited a shoreward shift in distributions in the evening (Figure 9) which appeared to be a queuing of animals in dense Scirpus at Position 2 in advance of moving into the more open habitats at Positions 1 and 2.

The numbers of shiners and bluegills found in open habitats after sunset, although significantly greater than the number found there during the day, did not equal the numbers found in the Scirpus during the day. In light of this finding, the water column above the slope was examined by swimmers and by observers from a boat using flashlights. No shiners and only one small centrarchid were found there, indicating that if some fish move offshore at night, they were moving far offshore or were dispersing to very low densities. Other explanations for the discrepancy in numbers of fish counted are restricted field of view at night, that not the entire length of Transect 2 was censused, and that some fish may have stayed in the Scirpus, which was not censused after sunset.

Diurnally, bluegills were more abundant at deeper positions than shiners (Figure 9). Young-of-the-year bluegills (Bluegill 0) displayed striking complementarity of habitat use with the shiners at both times of the day. Bluegill I (26 - 50 mm TL), although more evenly distributed across all positions than the other fish, overlapped with shiners in habitat use only about 50%.

Microhabitat utilization patterns of shiners and bluegills showed

Figure 9. Day and Evening Habitat Distributions of Shiners and Bluegills in Lawrence Lake, 1978. Open bars are day, and shaded bars are evening.


BLUEGILL I
60
20
BLUEGILL O
80
40
SHINER I
80
40
SHINER O
80
40
PERCENT
1
2
3
4
5
POSITION

a general increase at evening in height in the water column (Figures 10 and 11, respectively). Exceptions to this were Bluegill I and the few shiners on the slope. It should be noted that dense Scirpus on the bench restricted the available water column above the vegetation to less than 0.5 m in most places.

Relative abundances of shiners and small bluegills at bench and slope positions in Three Lakes on 18 and 19 August 1978, are presented for comparison with Lawrence Lake in Figure 12. In Three Lakes, where Position 1 was heavily vegetated and the slope was gradual, shiners were found primarily at the four shallow positions during the day. The bluegill-shiner habitat complementarity was once again very striking, particularly in Bluegill 0. This size class of bluegills actually became noticeably much more abundant at Positions 1 - 5 in the evenings than it was during the day (evening total = 3896; mean daytime total = 652), but this increase is hard to discern in Figure 12 because of the overwhelming number of small bluegills in the tall vegetation at Position 6. In contrast to Lawrence Lake, Bluegill I moved to deeper positions in the evening in Three Lakes. This may represent a shift toward more open habitats which in Three Lakes occurred on the slope.

Young-of-the-year bluegills appeared to change habitats as they grew. The smallest fry were found in dense schools in the upper portions of the tall vegetation at Position 6 in Three Lakes. Slightly larger fry were found in the lower vegetation there, and the largest fry were found on the bench and upper slope.

Diel microhabitat changes in Three Lakes (Figures 13 and 14) were similar to those in Lawrence Lake; all fish tended to be higher in the water column in the evening. This microhabitat change was especially

Figure 10. Day and Evening Microhabitat Distribution of Shiners in Lawrence Lake, 1978. A. Shiner 0, bench; B. Shiner 0, slope; C. Shiner I, bench; and D. Shiner I, slope. Open bars are day and shaded bars are evening. U = Upper and L = Lower Vegetation.

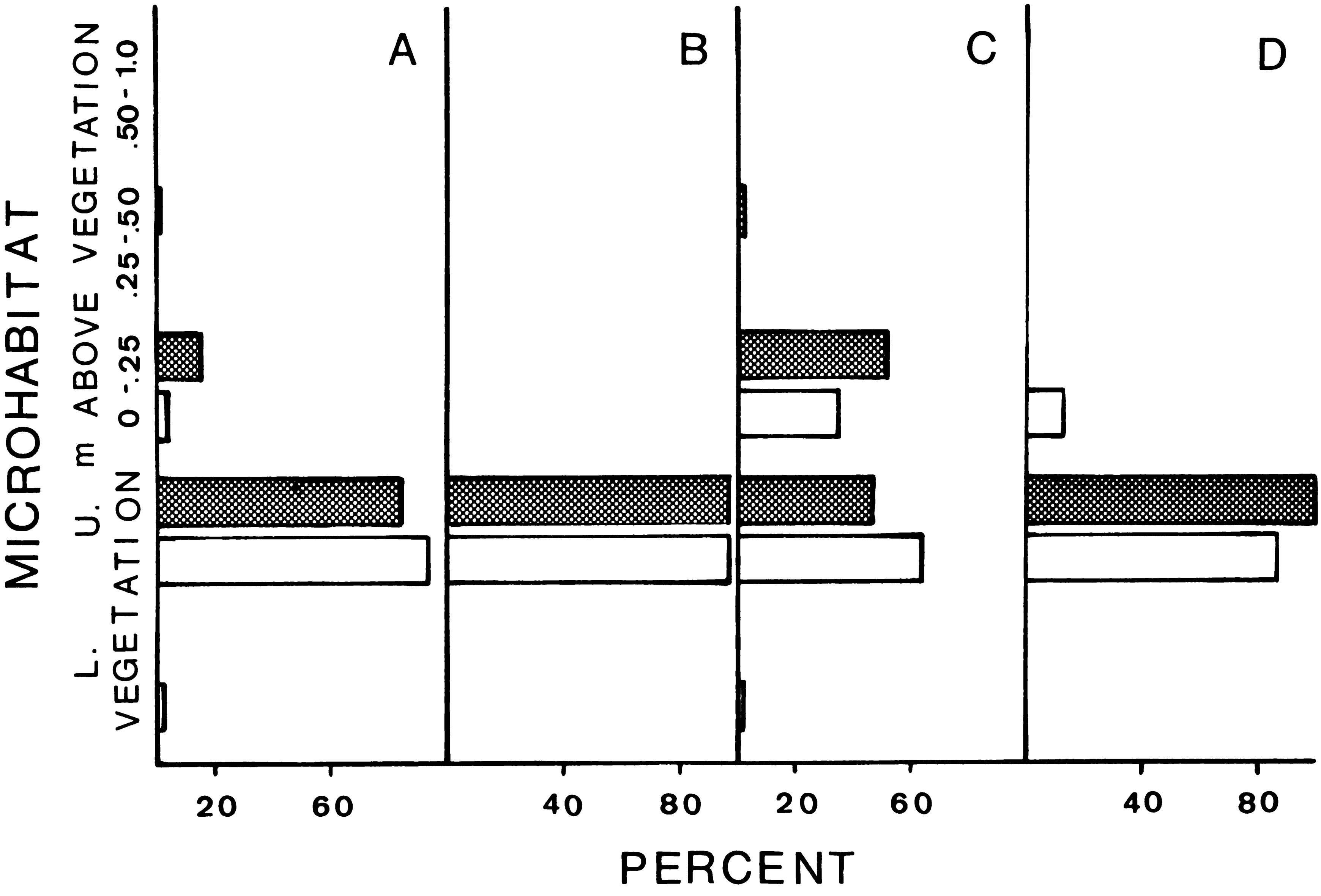

MICROHABITAT
L.
VEGETATION
U.
VEGETATION
m ABOVE VEGETATION
0 -.25
.25-.50
.50-1.0
A
B
C
D
20
60
40
80
20
60
40
80
PERCENT

Figure 11. Day and Evening Microhabitat Distribution of Bluegills in Lawrence Lake, 1978. A. Bluegill 0, bench; B. Bluegill 0, slope; C. Bluegill I, bench; and D. Bluegill I, slope. Open bars are day and shaded bars are evening. U = Upper and L = Lower Vegetation.

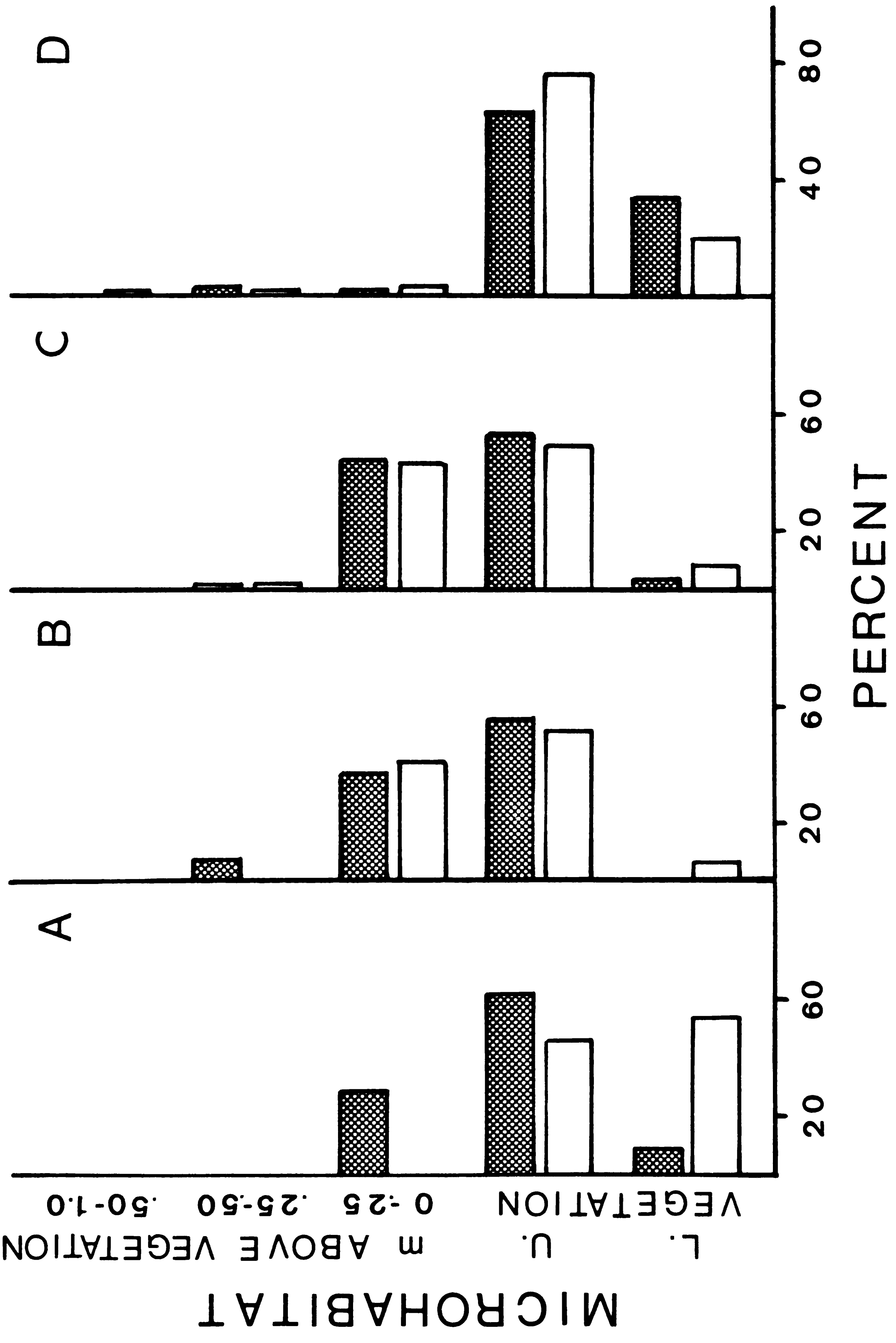

A
B
C
D
20
60
20
60
20
60
40
80
PERCENT
MICROHABITAT
m ABOVE VEGETATION
.50-1.0
.25-.50
0-.25
U.
L.
VEGETATION

Figure 12. Day and Evening Habitat Distributions of Shiners and Bluegills in Three Lakes on 18 and 19 August 1978. Open bars are day and shaded bars are evening.

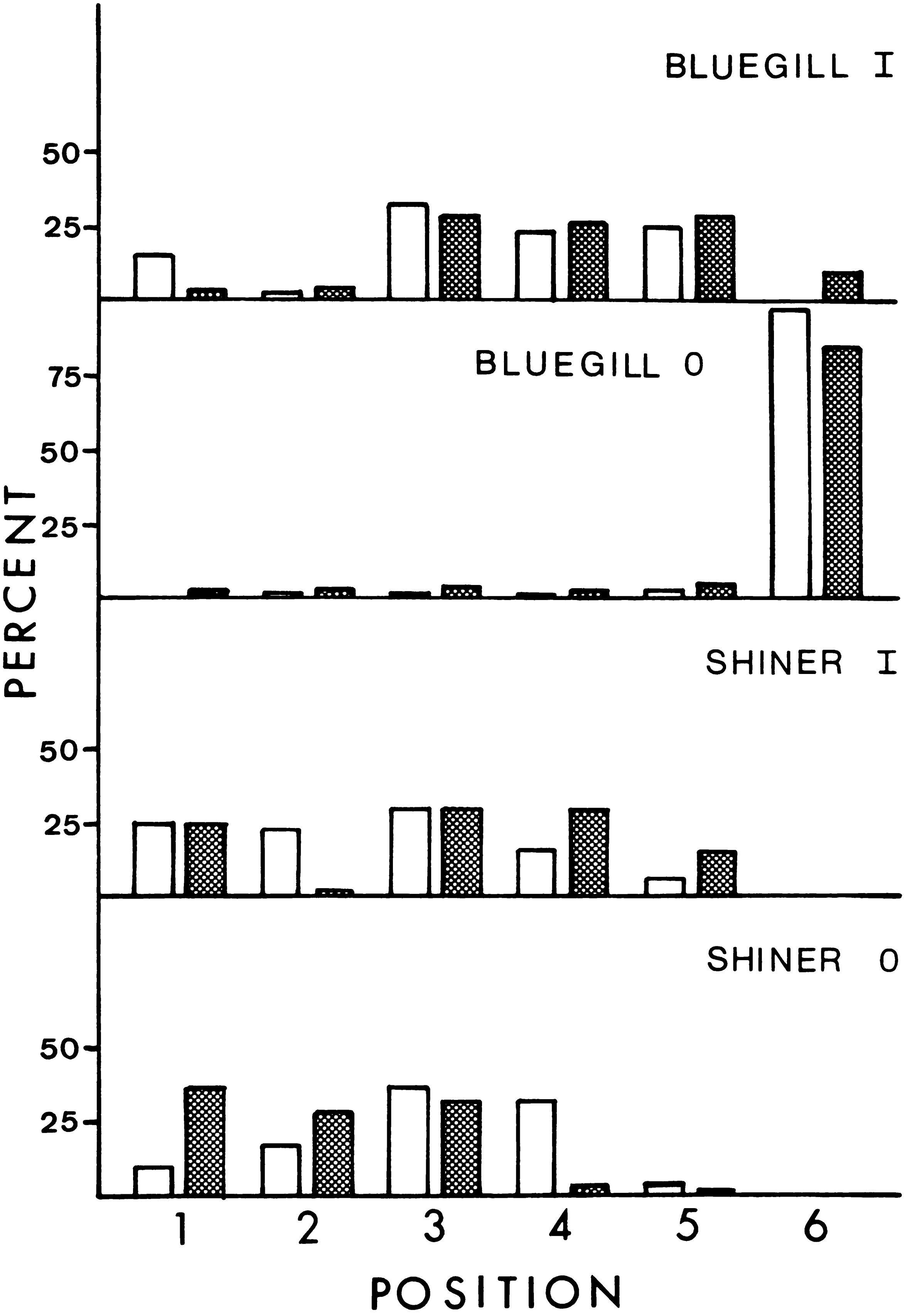

BLUEGILL I
BLUEGILL O
SHINER I
SHINER O
PERCENT
25
50
75
1
2
3
4
5
6
POSITION

Figure 13. Day and Evening Microhabitat Distributions of Shiners in Three Lakes on 18 and 19 August 1978. A. Shiner 0, bench; B. Shiner 0, slope; C. Shiner I, bench; and D. Shiner I, slope. Open bars are day and shaded bars are evening. U = Upper and L = Lower Vegetation.

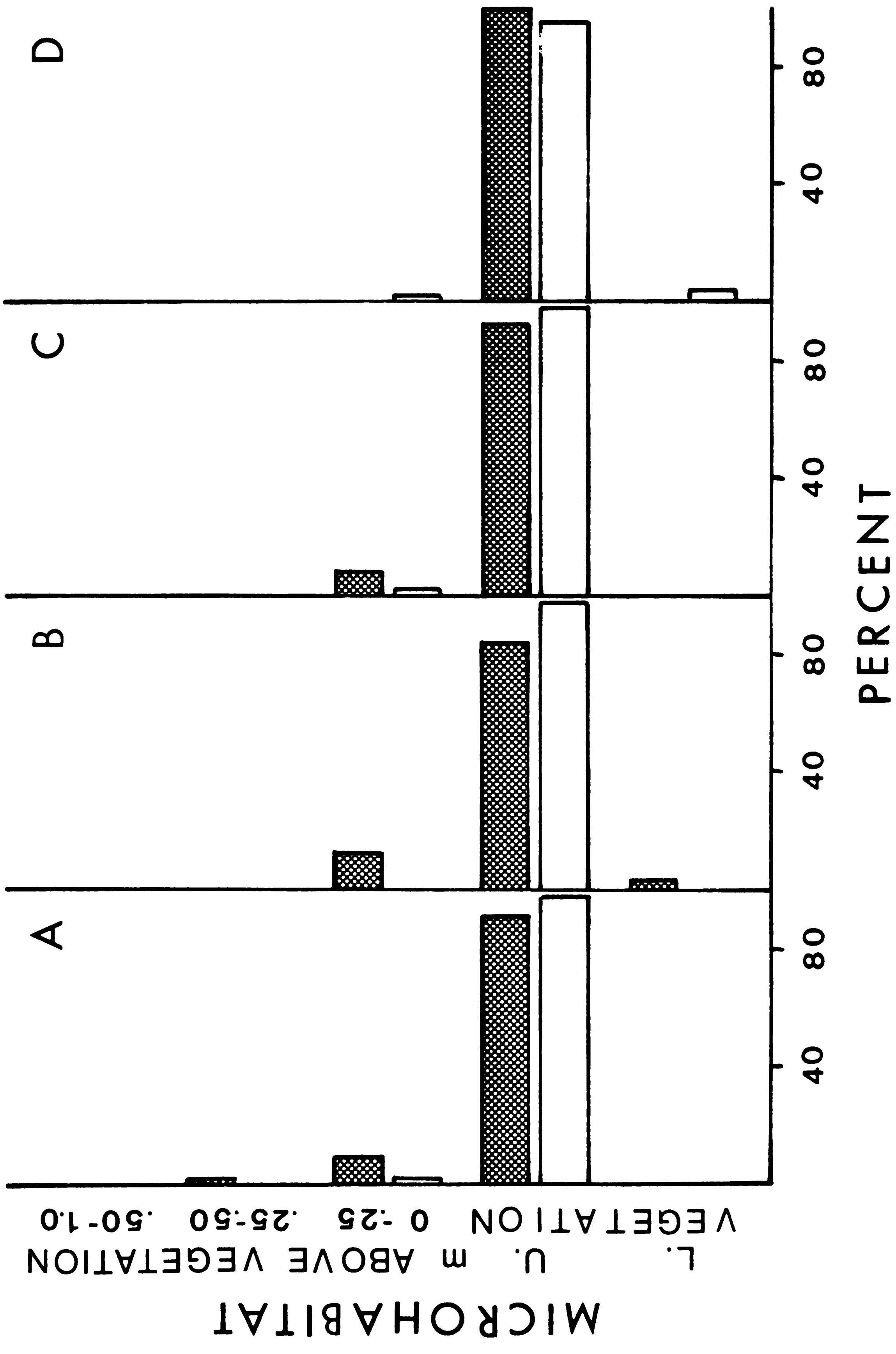
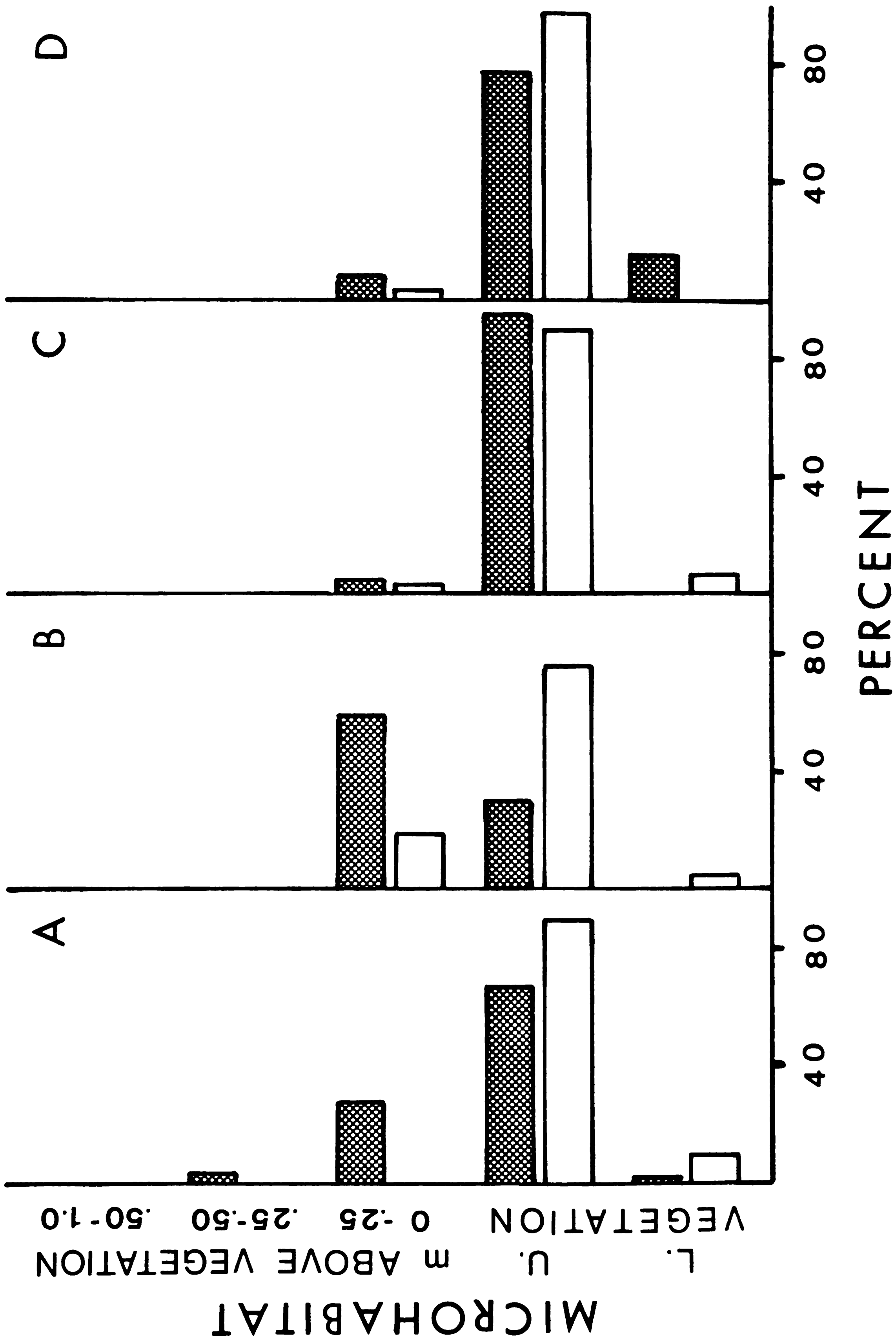

A
B
C
D
40
80
PERCENT
MICROHABITAT
L. VEGETATION
U. VEGETATION
m ABOVE VEGETATION
0 -.25
.25-.50
.50-1.0

Figure 14. Day and Evening Microhabitat Distribution of Bluegills in Three Lakes on 18 and 19 August 1978. A. Bluegill 0, bench; B. Bluegill 0, slope; C. Bluegill I, bench; and D. Bluegill I, slope. U = Upper and L = Lower Vegetation.


A
B
C
D
40
80
40
80
40
80
40
80
PERCENT
MICROHABITAT
L.
U.
VEGETATION
0 -.25
.25-.50
.50-1.0
m ABOVE VEGETATION

noticeable in Bluegill 0 in which the fish could be seen to almost imperceptibly rise out of the vegetation as light levels dropped. Bluegill I on the slope in Three Lakes spread out vertically, moving both higher and lower in the vegetation at dusk, in a pattern similar to that observed in Lawrence Lake.

In summary, both shiners and bluegills exhibited changes in both habitat and microhabitat utilization patterns between daytime and evening, moving into more open areas (unvegetated regions as well as open water column) as light levels declined. Bluegills, especially Age 0 fish, showed marked complementarity of habitat use with the shiners both in Lawrence Lake and in Three Lakes.

Diel Feeding Activity

Changes in feeding activity accompanied diel changes in habitat use of the shiners. Both species fed primarily at dusk and dawn and very little during the day (Figures 15 and 16). Shiners captured after sunset or before sunrise contained, in general, significantly more food in their stomachs than did fish captured before sunset and after sunrise, respectively (1-tailed t-test, $P < 0.05$; Table 5). It is evident that shiners fed very little prior to dusk or after dawn. This is corroborated by gut data from Lawrence Lake in 1976, in which fish collected later than noon were almost completely empty (Wilsmann, unpublished).

Bluegills fed in the vegetation during the day so an evening feeding peak was not evident as it was in the shiners (Figures 15 and 16). It is clear, though, that neither the bluegills nor the shiners fed through the night since all three species contained relatively little food an hour before sunrise.

Table 5. Statistical Comparisons of Diel Differences in Mean Total Dry Weight of Prey in Fish. Mean ± standard error (mg dry weight), degrees of freedom (df), and statistical significance (P) are presented for 1-tailed t-tests of pairs for fish taken (1) before sunset and (2) after sunset, or (1) after sunrise and (2) at sunrise. H_o: 1 = 2; H': 1 < 2. Means are presented graphically in Figures 15 and 16. Size classes are explained on page 25.

	7 July 1978	1 = Before Sunset	2 = After Sunset				
	BLACKCHIN 4	BLACKCHIN 3	BLACKNOSE 4	BLACKNOSE 1	BLUEGILL 3		
1	.271 ± .262	.290 ± .105	.022 ± .021	.022 ± .017	1.18 ± .348		
2	.404 ± .227	.207 ± .084	.536 ± .335	.065 ± .020	.737 ± .164		
df	9	7	7	6	8		
P	NS	NS	< .063	NS	NS		
	30 July 1978	1 = Before Sunset	2 = After Sunset				
	BLACKCHIN 4	BLACKCHIN 3	BLACKNOSE 4	BLACKNOSE 3	BLACKNOSE 2	BLUEGILL 3	BLUEGILL 1
1	.121 ± .073	.006 ± .005	.023 ± .018	.032 ± .012	.056 ± .013	1.81 ± .222	.309 ± .156
2	1.55 ± .444	.220 ± .207	1.09 ± .252	1.38 ± .117	.264 ± .083	1.70 ± .379	.00009 ± 0
df	8	6	8	8	8	8	4
P	< .01	NS	< .002	< .001	< .038	NS	NS
	31 July 1978	1 = After Sunrise	2 = At Sunrise				
	BLACKCHIN 4	BLACKCHIN 3	BLACKCHIN 2	BLACKNOSE 4	BLACKNOSE 2	BLUEGILL 3	BLUEGILL 1
1	2.64 ± .791	.237 ± .091	.164 ± .038	.618 ± .241	.121 ± .027	2.04 ± .392	.191 ± .039
2	4.17 ± .884	1.44 ± .396	.168 ± .060	3.09 ± .247	.354 ± .063	10.1 ± 1.82	.309 ± .309
df	8	8	8	8	8	8	9
P	NS	< .01	< .01	< .001	< .02	< .01	< .03

Figure 15. Shiner and Bluegill Feeding Pattern on 7 July 1978 in Lawrence Lake. Mg dry weight of food in the stomachs at 3 times of day are presented by fish size class (see page 25 for size class explanation). Statistical comparisons are presented in Table 5. ▲ Bluegill 3, ● Blackchin 4, ○ Blackchin 3, ■ Blacknose 4, □ Blacknose 3, and ★ Blacknose 2.

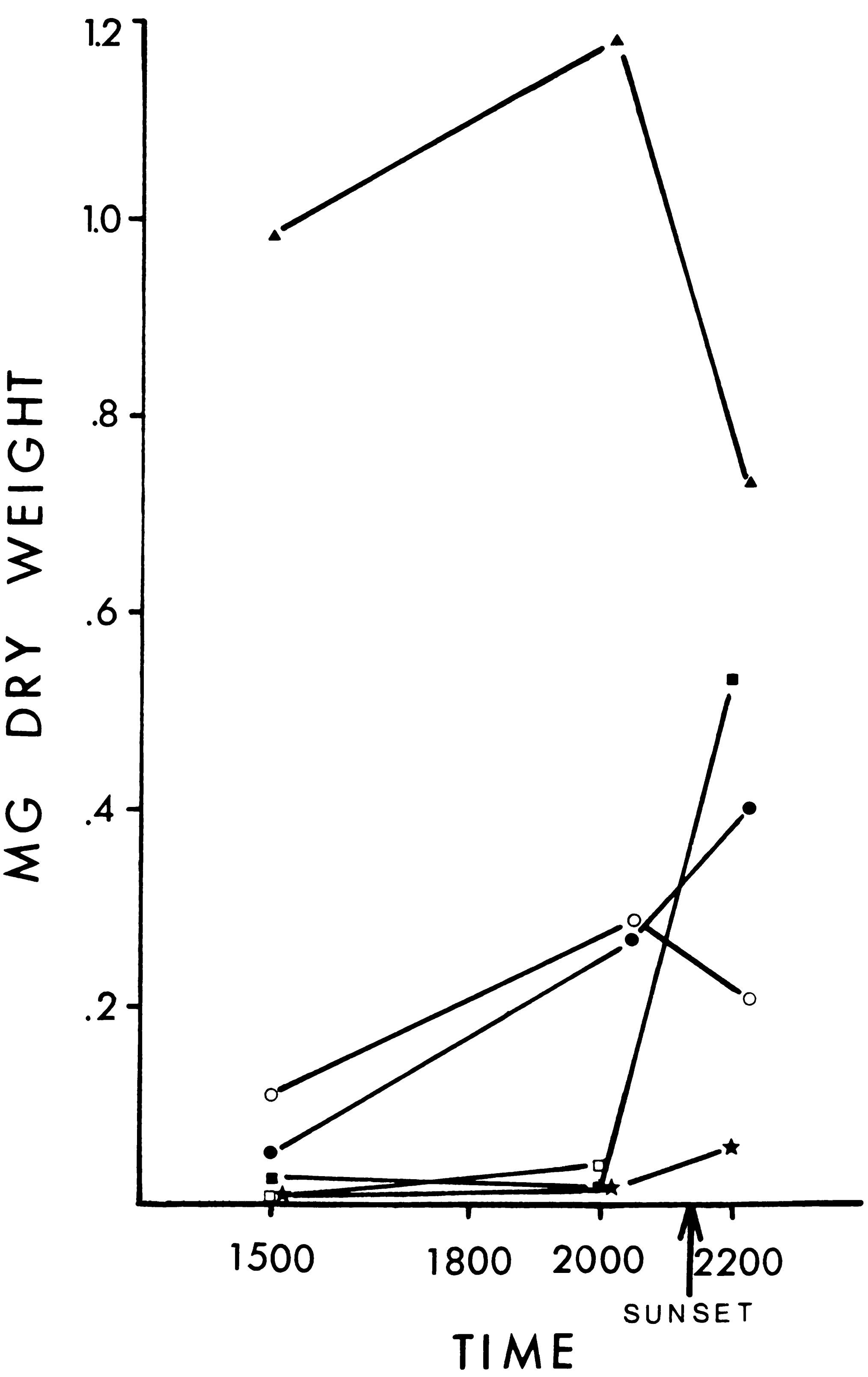
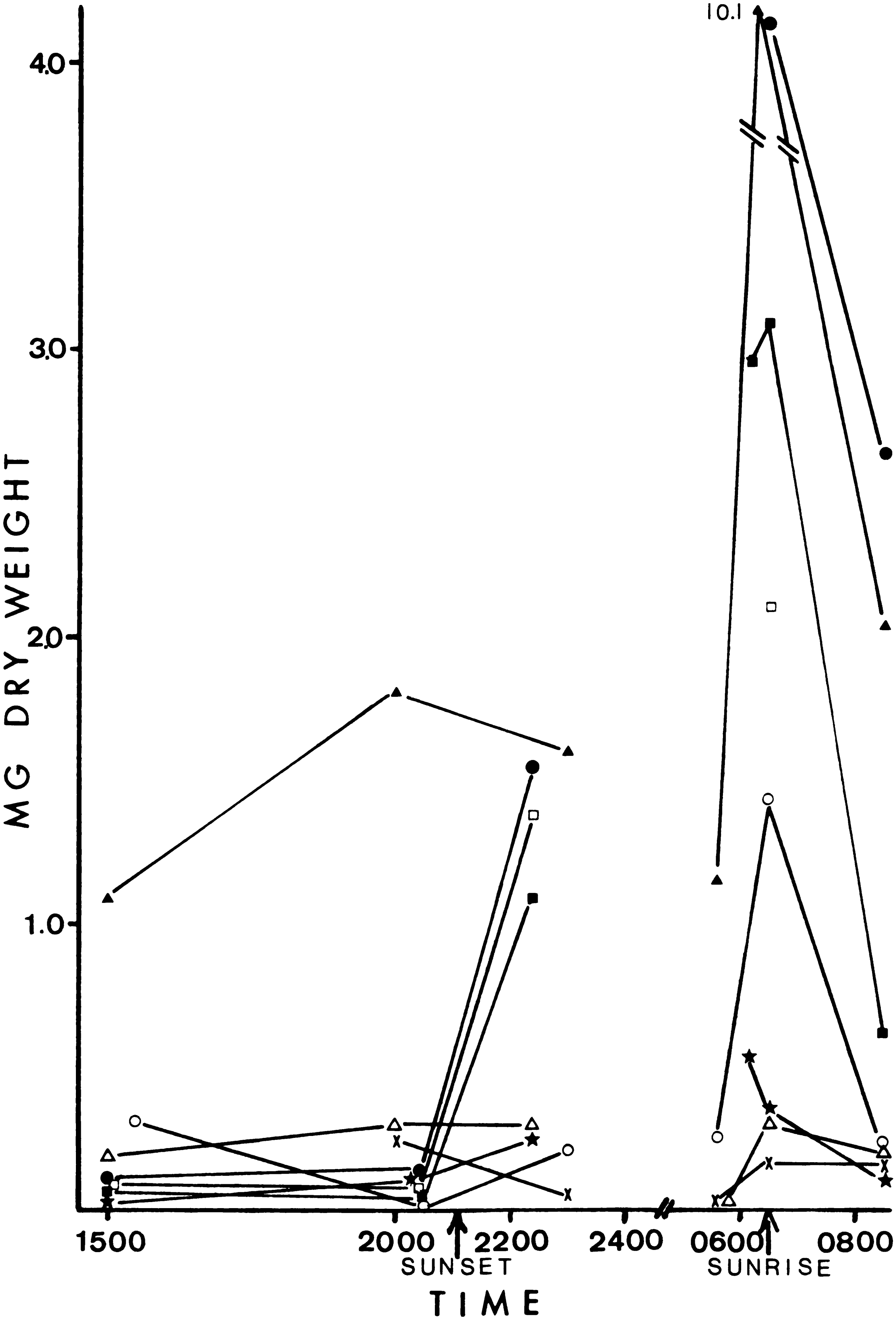

MG DRY WEIGHT
1.2
1.0
.8
.6
.4
.2
1500
1800
2000
2200
SUNSET
TIME

Figure 16. Shiner and Bluegill Diel Feeding Patterns on 30 and 31 July 1978 in Lawrence Lake. Mg dry weight of food in the stomachs at 6 sample times are presented by fish size class (see page 25 for size class explanation). Statistical comparisons are presented in Table 5. ▲ Bluegill 3, △ Bluegill 1, ● Blackchin 4, O Blackchin 3, X Blackchin 2, ■ Blacknose 4, □ Blacknose 3, ★ Blacknose 2.


MG DRY WEIGHT
4.0
3.0
2.0
1.0
10.1
1500
2000
2200
2400
0600
0800
SUNSET
SUNRISE
TIME

Seasonal Diet Patterns

Seasonal trends in total prey intake, mean prey size and similarity of diets among size classes were generally similar for blackchin and blacknose shiners. Both species exhibited overall declines in the total amount and size of prey captured, and diet similarities of size classes within species increased across the summer. Between species, diets became less similar across the growing season.

Total Prey Biomass. Mean total dry weight of food of blackchin and blacknose shiners generally decreased across the summer (Figures 17C and 18C, respectively). For most size classes, mean total dry weight of food consumed was significantly greater (1-tailed t-test, $P < 0.05$) at the beginning than at the end of the season. The only exception was blackchin size class 4 (Blackchin 4) which displayed an erratic seasonal pattern. (Refer to page 25 for definition of size class designations).

Mean total weight of food was expected to increase with increasing size class within each species due to higher metabolic demands of larger fish and their larger gut capacities. Among size classes of the blackchin, mean total weight of gut contents increased significantly with size class at the beginning of the season (6 May 1977) ($F_{2,12} = 5.961$; $P < 0.025$). On 28 September, mean total weight was not significantly greater in larger size classes ($F_{2,12} = 2.420$; $0.25 > P > 0.10$) and none of the pairwise comparisons were significantly different. In the blacknose size classes 3 and 4 were not different on 6 May (1-tailed t-test, $P > 0.12$). In September, although the overall relationship of increasing food with increasing size class was significant ($F_{2,12} = 4.083$; $0.05 > P > 0.025$), the only significant pairwise comparison was Blacknose 3 > Blacknose 2.

Figure 17. Blackchin Seasonal Diet Patterns. A. Number of prey types, B. Mean prey weight, and C. Total amount of food in the gut for fish by size class from Lawrence Lake, 1977. Statistical comparisons are discussed in the text. See page 25 for explanation of size classes. O Blackchin 4, ☐ Blackchin 3, △ Blackchin 2, and ● Total.

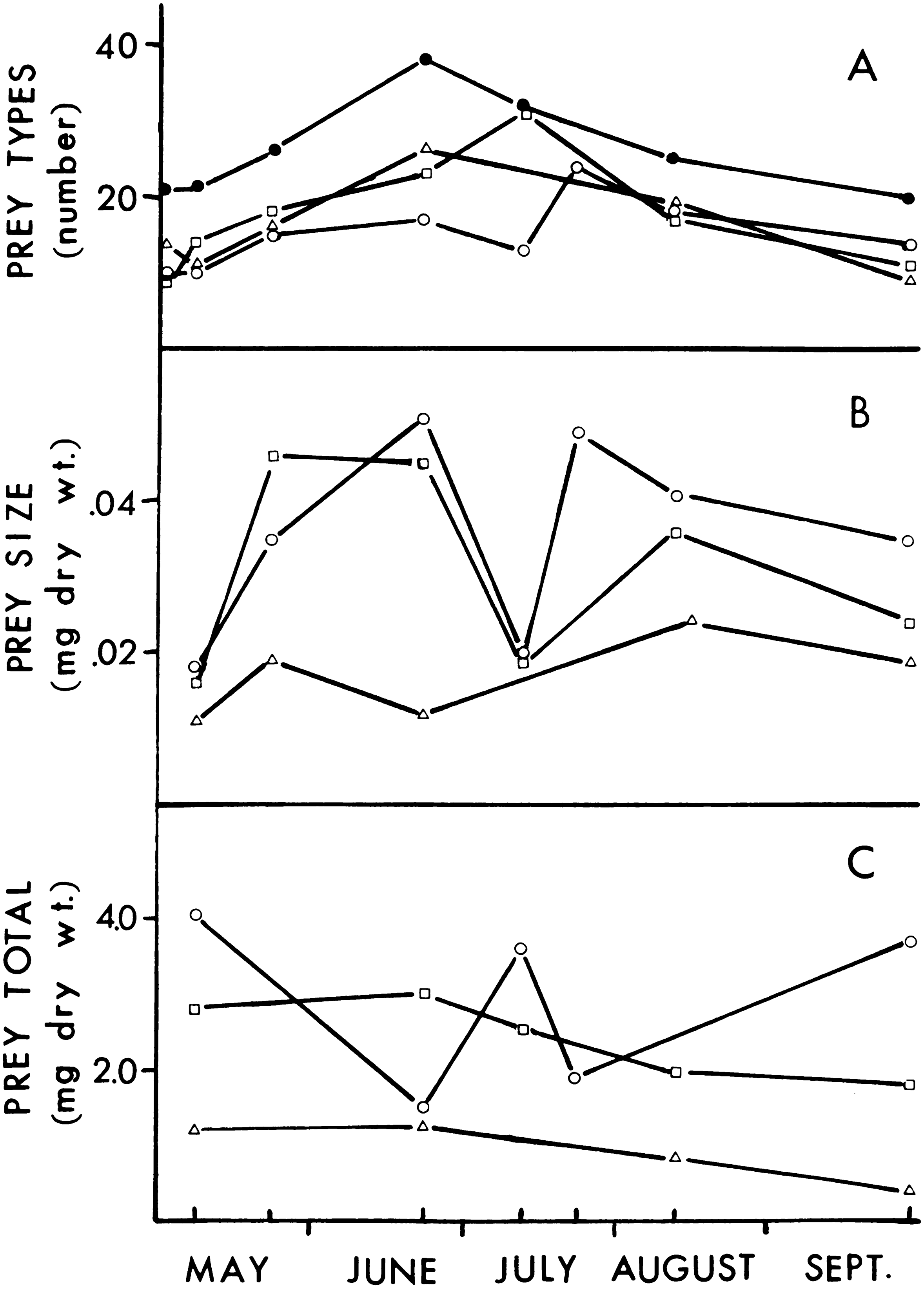
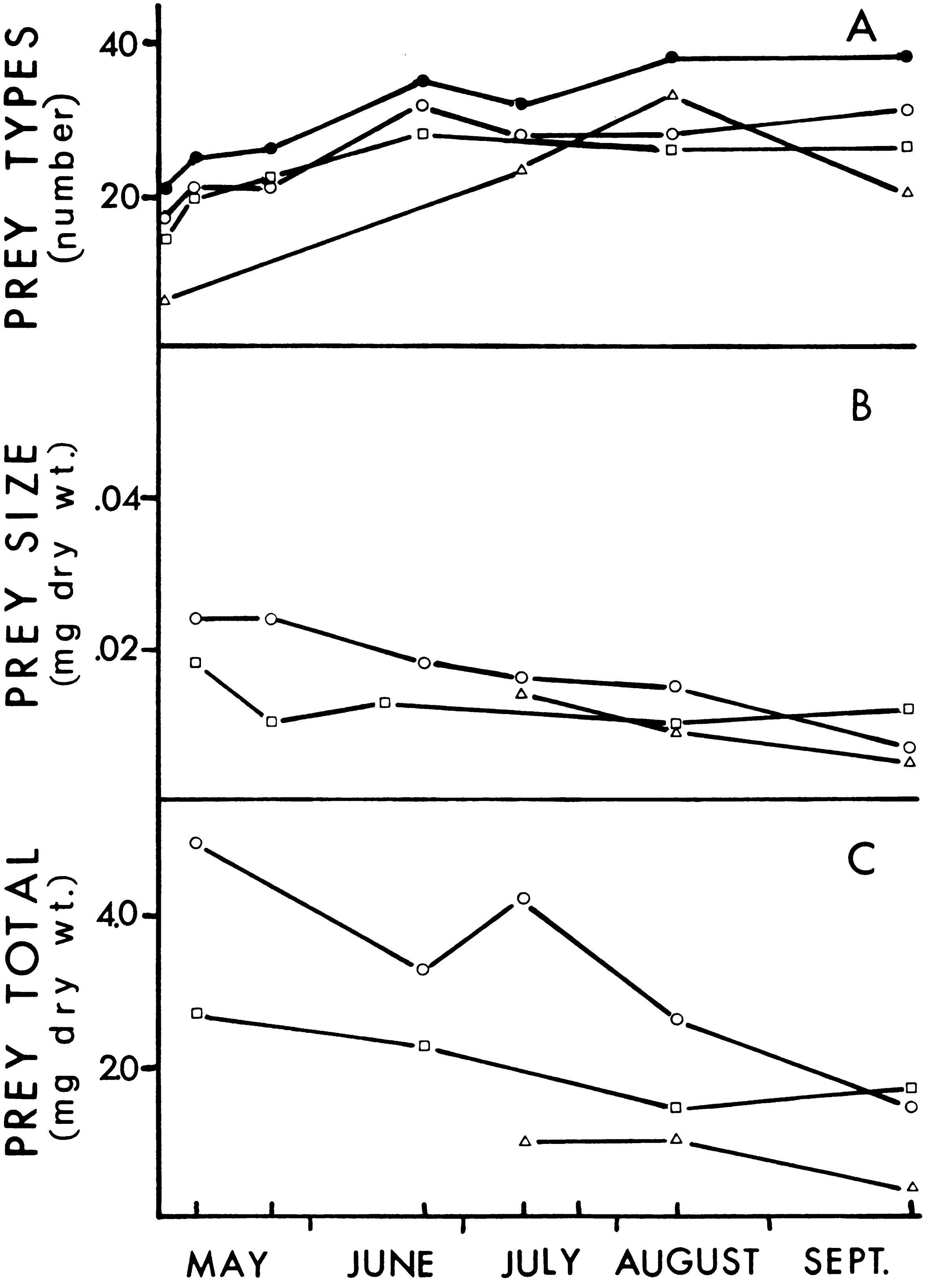

A
PREY TYPES (number)
40
20
B
PREY SIZE (mg dry wt.)
.04
.02
C
PREY TOTAL (mg dry wt.)
4.0
2.0
MAY
JUNE
JULY
AUGUST
SEPT.

Figure 18. Blacknose Seasonal Diet Patterns. A. Number of prey types, B. Mean prey weight, and C. Total amount of food in the gut for fish by size class from Lawrence Lake, 1977. Statistical comparisons are discussed in the text. See page 25 for explanation of size classes. ○ Blacknose 4, □ Blacknose 3, △ Blacknose 2, and ● Total.


A
B
C
PREY TYPES
(number)
PREY SIZE
(mg dry wt.)
PREY TOTAL
(mg dry wt.)
40
20
.04
.02
4.0
2.0
MAY
JUNE
JULY
AUGUST
SEPT.

In contrast to the shiners, young-of-the-year bluegills (YOY = size class 1) showed an increased food intake across the last half of the summer (Figure 19). Larger bluegills (size class 3) exhibited an erratic midsummer pattern similar to Blackchin 4.

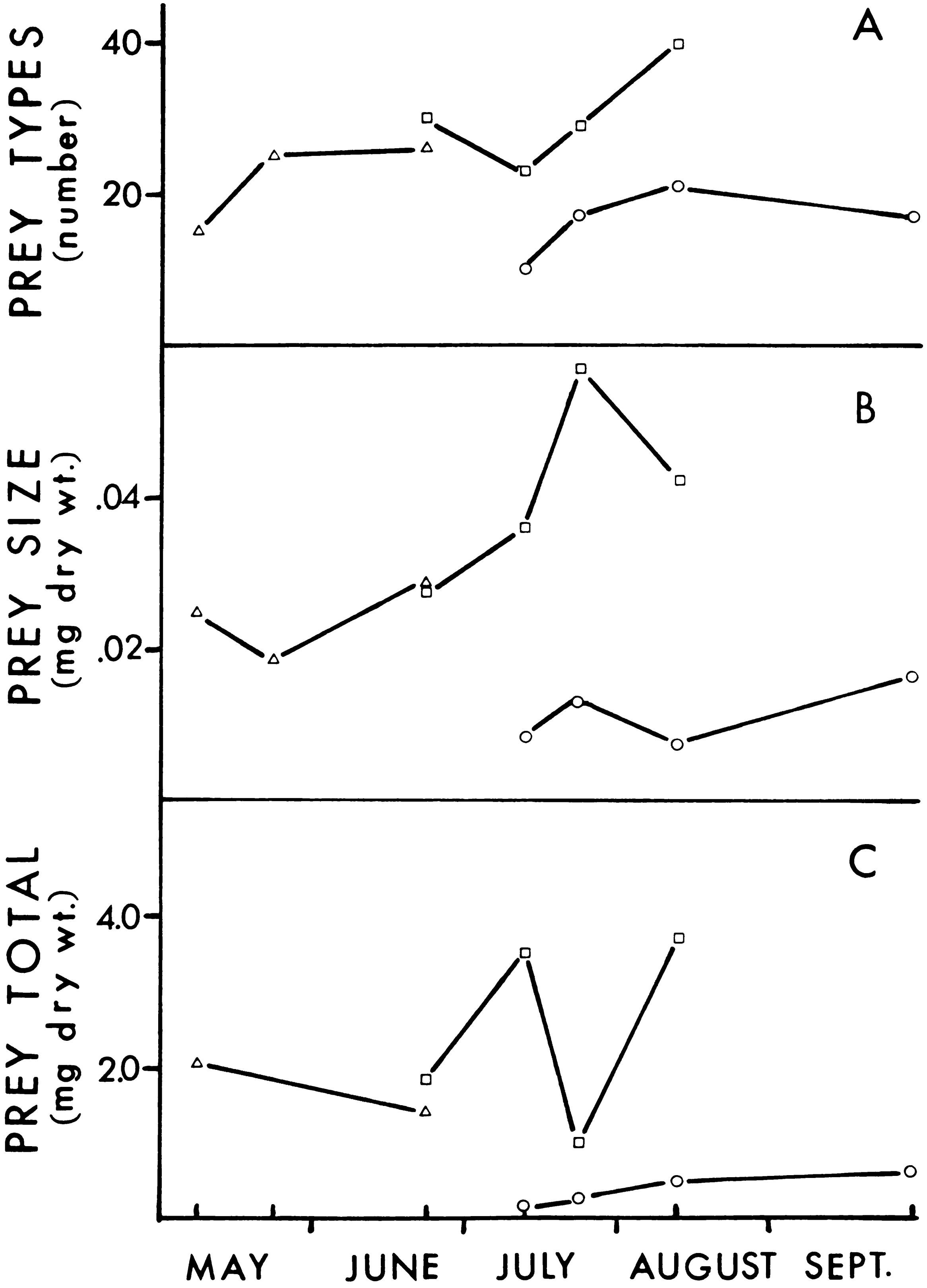
Mean amount of food in the gut for similar size classes of different shiner species was not significantly different either at the beginning or end of the growing season. In the case of size class 4 fish this result appears to be an artifact of small sample sizes since there is a two-fold difference in total prey dry weight.

Mean Prey Size. Mean prey size (mg dry weight) varied considerably between species, but within each species of shiner, size class variations tended to parallel each other across the summer. Mean prey size of the blacknose gradually declined across the summer (Figure 18B), paralleling the decline in total prey intake. In all three blacknose size classes, mean prey weight was significantly greater (1-tailed t-test, $P < 0.05$) on the first sample date than on the last. Although mean prey size of Blacknose 4 was greater than in Blacknose 3 at the beginning of the season, there was no significant difference in prey size among the three classes in September.

The seasonal pattern of mean prey weight of the blackchin was more complex. Initial prey sizes were significantly lower than final sizes, but only in size class 2 was the prey size at the end of September greater than those on intermediate dates. In contrast to the blacknose, mean prey sizes of blackchin size classes were significantly different in September ($P < 0.05$ in all cases).

Prey size of Bluegill 1 is greater in September than in August

Figure 19. Bluegill Seasonal Diet Patterns. A. Number of prey types, B. Mean prey weight, and C. Total amount of food in the gut for fish by size class from Lawrence Lake, 1977. Statistical comparisons are discussed in the text. See page 25 for explanation of size classes. □ Bluegill 3, △ Bluegill 2, and ○ Bluegill 1.


A
PREY TYPES
(number)
40
20
B
PREY SIZE
(mg dry wt.)
.04
.02
C
PREY TOTAL
(mg dry wt.)
4.0
2.0
MAY
JUNE
JULY
AUGUST
SEPT.

($P < 0.05$). This is similar to the trend in Blackchin 2 and in contrast to that in Blacknose 2.

The midsummer depression in prey size of Blackchin 3 and 4 was caused by a combination of many small *Daphnia* and invertebrate eggs in the diet. On the three days of small prey size in these two blackchin groups, *Daphnia* comprised a high percentage of the food (cf. Appendix 3).

Interspecific comparisons of mean prey size yield patterns generally consistent with mouth morphology measurements (Figure 2) of the three species. Except for the first sampling date, mean prey size of blacknose was less than that of the blackchin (2-tailed t-test, $P < 0.05$). By September, Blackchin 2, 3, and 4 all contained on average significantly larger prey than blacknose. Even young-of-the-year bluegills (Bluegill 1) had a significantly ($P < 0.05$) larger mean prey weight than Blacknose 3, which was the blacknose size class containing the largest prey.

Prey Type. Types of prey consumed by the fish varied throughout the growing season (Figures 17A, 18A, 19A; Tables A5, A6, A7) and clearly demonstrated all three species to be opportunistic in feeding patterns, as are other temperate zone freshwater fish (Keast, 1965; Werner and Hall, 1976, 1977). *Daphnia pulex* and *galeata* were a major food resource in early spring and late fall, but occurred in the diets to some extent over the summer. Diptera adults, pupae, and larvae (Chironominae, Tanypodinae, and Ceratopogonidae) comprised the other major resource, the components of which were consumed in varying quantities from spring to fall. Littoral Cladocera, such as *Sida*, *Latona*, and *Ophryoxus* made significant contributions to the fish diets at various times, as did *Hyalella* and the larger benthic invertebrates.

The percent similarity of diets of selected size classes of blackchin,

blacknose and bluegills are presented in Table 6. Percent similarity was computed by the formula

$$\% \; S = \left[1 - \tfrac{1}{2}\sum_{i=1}^{n} |p_{ij} - p_{ik}|\right] \times 100$$

where p_{ij} and p_{ik} are proportions of prey type i in the diet of species j and k, respectively (Schoener, 1970). Proportions presented in Appendix 3 were used in the calculations but standardized to a total of 100% in each size class (see Appendix 3).

Size classes within species were more similar to each other in food utilization than they were to other species. Smaller blackchin and blacknose were somewhat more alike in prey types taken than were the larger fish. and interspecific similarities tended to decrease across the summer. Incidents of high interspecific similarity could usually be attributed to intensive co-utilization of one or two prey types, e.g. cyclopoids on 23 April and Daphnia on 6 May. Blackchin 2 and Blacknose 2 and 3 were the predominant size classes of young-of-the-year present at the end of the summer. Diet similarities among these size classes in 1977 were approximately the same for all interspecific comparisons.

When prey utilization was analyzed from the standpoint of the habitat in which the prey were found (Table 7 and Appendix 4), the most striking difference between blackchin and blacknose shiners was their differential use of prey occurring at the air-water interface ("Surface Prey"). Surface prey comprised more than 50% of the blackchin diet at times yet were virtually never consumed by blacknose. Open water prey also contributed a large proportion to the blackchin diet but contributed very little to that of the blacknose. In contrast, blackchin consumed relatively few benthic prey, especially Ceratopogonidae larvae which contributed 60% or

Table 6. Diet Similarity of Shiners and Bluegills. Percent similarity of selected size classes (see page 25 for size class explanation) of shiners and bluegills. Explanation of computation is presented in text. Calculations are based on data presented in Appendix 3.

	LAWRENCE LAKE 1977								
	23 IV	6 V	21 V	24 VI	11 VII	23 VII	11 VIII	28 IX	$\bar{X} \pm$ S.E.
BC4 v. BC2	30.7	87.0	43.4	42.1				82.8	57.2 ± 11.5
BC4 v. BN4	20.8	46.8	21.6	28.9	11.4			7.3	22.8 ± 5.7
BC4 v. BN2	13.6				12.4			6.1	10.7 ± 2.3
BC4 v. BG3				42.8	21.6	30.6			31.7 ± 6.1
BC3 v. BN3	58.8	45.6	24.8	17.9			34.6	3.7	30.9 ± 8.1
BC3 v. BN2	42.5				26.8		38.1	2.9	27.6 ± 8.9
BC2 v. BN4	46.9	51.0	21.6	59.1			23.0	13.7	35.9 ± 7.6
BC2 v. BN3	60.4	70.1	25.9	48.9			28.5	10.1	40.7 ± 9.4
BC2 v. BN2	50.3						31.5	11.2	31.0 ± 11.3
BC2 v. BG1							35.6	21.1	28.4 ± 7.3
BN4 v. BN2	42.7				68.0		73.9	60.6	61.3 ± 6.8
BN4 v. BG3				50.0	29.1		19.7		32.9 ± 9.0
BN2 v. BG1					53.6		39.6	24.8	39.3 ± 8.3

Table 7. Seasonal Mean Percent Contribution of Prey From Four Habitats to the Diets of Shiners and Bluegills. Mean percent ± 1 S.E. of prey by weight in the diet assigned to each habitat for various size classes of fish (see page 25 for explanation of size classes). Data are from Lawrence Lake, 1977. Raw data are presented in Appendices 3 and 4. N = number of dates included in the calculations.

	S.C.	VEGETATION	BENTHOS	OPEN WATER	SURFACE	OTHER	N
BLACKCHIN	4	3.3 ± 1.9	13.8 ± 5.2	48.4 ± 16.6	23.2 ± 9.6	8.7 ± 4.5	7
	3	13.9 ± 5.4	13.3 ± 4.8	48.8 ± 12.8	10.9 ± 3.9	12.2 ± 5.8	7
	2	17.9 ± 9.5	22.0 ± 11.6	40.8 ± 14.9	5.3 ± 2.7	12.2 ± 3.7	6
BLACKNOSE	4	18.6 ± 6.4	59.5 ± 8.8	12.1 ± 6.5	0	6.5 ± 1.5	7
	3	30.3 ± 7.7	48.6 ± 7.5	11.3 ± 8.8	0	6.9 ± 1.9	7
	2	55.5 ± 20.9	29.3 ± 16.1	4.9 ± 2.1	0	9.9 ± 5.9	3
BLUEGILL	5	7.5 ± 1.6	49.4 ± 7.8	30.0 ± 16.3	7.4 ± 5.9	2.5 ± 2.5	2
	3	10.2 ± 1.8	29.3 ± 6.5	16.0 ± 1.3	8.2 ± 3.5	32.1 ± 5.8[1]	4
	2	22.5 ± 18.6	19.3 ± 3.1	44.1 ± 21.5	0	10.0 ± 2.6	3
	1	44.9 ± 3.5	27.3 ± 9.9	22.8 ± 13.4	0	5.9 ± 3.4	4

[1] Primarily amphipods which are found both in the Vegetation and Benthos.

more to the blacknose diet at times. Bluegills utilized relatively little surface prey but the proportions of prey taken from other habitats were more evenly divided than in either shiner species.

Individual variation in prey type diversity was examined by means of two simple diversity indices, H' (Pielou, 1969) and S (Table 8). H', as a measure of diversity, represents not only the total number of prey types but also the evenness of utilization among them. The formula is

$$H' = -\sum_{i=1}^{n} p_i \ln p_i$$

where p_i is the proportion of prey type i in the diet. S is simply the number of prey types comprising the gut contents. $\overline{H}'$ and $\overline{S}$ are means for all individuals in the size class and H'_c and S_c are cummulative indices computed as if the contents of all fish in each size class came from a single fish. Thus, comparison of $\overline{H}'$ to H'_c is a measure of the relative heterogeneity of the diet of an individual, on average, compared to that of the size class as a whole, and similarly for $\overline{S}$ and S_c.

Mean individual prey diversity as computed by both indices was higher for blacknose than blackchin in May and September. Individual blackchin, on average, showed very little difference in either index between the two dates. In contrast, prey type diversity was much higher in the blacknose in September than May. However, in both species there was relatively little difference between the dates in individual specialization relative to the performance of each size class as a whole. That is, the relative overlap of individuals within each size class was approximately the same at both times of the year.

Table 8. Prey Type Diversity of Blackchin and Blacknose Shiners. Two measures of prey type diversity, H' and S are presented for fish from Lawrence Lake, 1977. Both measures are presented as mean individual diversities and as means relative to cummulative population diversities. See text for explanation of computations. Size classes (S.C.) are explained on page 25. N = number of fish included in the calculations.

	S.C.	$\bar{H}' \pm$ S.E.	H'_c	$\bar{H}'/H'_c$	$\bar{S} \pm$ S.E.	S_c	$\bar{S}/S_c$	N
				6 MAY 1977				
BLACKCHIN	4	0.618 ± 0.080	0.740	0.835	6.2 ± 0.6	10	0.62	5
	3	0.837 ± 0.137	0.946	0.884	6.2 ± 1.0	14	0.44	5
	2	1.132 ± 0.214	1.306	0.867	6.4 ± 0.7	11	0.58	5
BLACKNOSE	4	1.147 ± 0.260	1.510	0.760	11.0 ± 1.1	21	0.52	5
	3	1.064 ± 0.335	1.522	0.699	9.4 ± 2.0	20	0.47	5
				28 SEPTEMBER 1977				
BLACKCHIN	4	0.701 ± 0.260	0.604	1.159	6.8 ± 1.3	14	0.49	5
	3	0.595 ± 0.139	0.840	0.708	4.2 ± 0.6	11	0.38	5
	2	0.730 ± 0.189	0.931	0.785	4.4 ± 1.0	9	0.49	5
BLACKNOSE	4	2.333 ± 0.049	2.608	0.895	18.8 ± 0.6	31	0.61	5
	3	1.695 ± 0.194	2.211	0.767	15.7 ± 1.5	26	0.60	6
	2	1.811 ± 0.125	2.354	0.769	11.3 ± 0.9	20	0.56	4

Diet Changes With Ontogeny

All three species exhibited marked changes in prey types consumed as they grew (Table 7, Appendices 3, 4). Vegetation prey were more important to small than to large size classes in all cases, but they were of lesser importance to small blackchin than to blacknose or bluegills. At larger sizes the shiners became more specialized in habitats utilized in foraging. The blacknose consumed predominately benthic prey and the blackchin predominately open water forms, although mean percent similarity among corresponding size classes was still 20 - 30% (Table 6) in spite of differences in primary habitat types. The bluegill remained rather generalized in habitat use across several size classes although smaller fish consumed more open water prey and larger fish took more benthic organisms. This shift to benthic organisms by bluegills at about 50 mm has been reported by others (Hall, et al, 1970).

DISCUSSION

Mechanisms of resource partitioning within and among species should be subject to intense selection pressure in a finite environment because of their direct bearing on both reproduction and survival. In order to understand the mechanisms by which species coexist we must know what factors are important in molding the system through natural selection. These factors, both biotic and and abiotic, may act as constraints on the system and augment competitive effects directly or indirectly, or they may have a moderating influence and ameliorate potential competitive interactions.

Environmental and Evolutionary Constraints on Resource Partitioning

Several factors and their possible effects on resource partitioning can be identified for the blackchin-blacknose shiner system. Most prey populations generally decline across the shiner growing season with relative abundances of the various species varying through time (Anderson and Hooper, 1956; Ball and Hayne, 1952; Gerking, 1962; Hall, 1964; Keast and Harker, 1977; Keen, 1976, 1970; Threlkeld, 1977). This phenomenon presents littoral zone fish with the lowest resource levels during the period of their most active individual growth and population recruitment. The overall decline in total amount of food consumed by the shiners across the growing season in 1977 is strong evidence that indeed resources did decline over that time and were no doubt limiting to individual growth. The sporadic peaks in total food consumed by Blackchin 4 and Bluegill 3 offer some evidence that resources may be variable within the general seasonal decline.

The seasonality of the aquatic environment in the north temperate zone limits most growth to the warmer months of the year for poikilothermic animals. Temperature-dependent metabolic rate restricts the time in which major life history events of potential competitors can occur.

Evolutionary constraints, particularly phylogenetic restrictions on morphology, set limits on the range of adaptations available to a species. Some morphological complexes may be more labile than others and therefore more subject to change through selection. For instance, trophic structures and their positioning appear to be more evolutionarily flexible than overall body plan (e.g. generalized centrarchid vs. cyprinid body shape) (see Fryer and Iles, 1972 and Myers, 1960 for examples).

Predation pressure could act as a constraint or an ameliorating factor in this system. Differential predation on the superior competitor or intensive overall predation maintaining populations below a competitive threshold would reduce competition. Alternatively, restriction of habitat and/or prey types available to competitors because of predation pressure would augment competition.

Although predation was not studied directly in this investigation, several lines of indirect evidence suggest its importance to restricting resource partitioning, hence increasing effects of competition, among the shiners and bluegills. All small fish were confined to the vegetation during daylight hours, but entered more open habitats at dusk. This migration in conjunction with increased feeding of the shiners in evening habitats indicates that the vegetation serves as a refuge during the day. Schooling behavior of shiners and the smallest bluegills during the day also indicates that protection from predation is important. Predation was rarely witnessed in the field but bass hve been observed to hunt in small groups at dusk, presumably to more effectively forage among the schools as they begin to disperse. Also, bass were observed to take a heavy toll of schooled young-of-the-year perch when the school became disoriented by initial attacks. And shiners have been found in the stomachs of bass as small as 30 mm TL (J. Gilliam, personal communication). This indicates that even schooling behavior is not completely effective against predation. Finally, the decline in Age I shiners from early July to mid-August 1978 in Lawrence Lake (848,5 to 112.0 individuals) suggests that predation risk is considerable. It is unlikely that disease or senescence could account for the high loss rate because fish collected in seine hauls over the same period of time did not appear to be in poor condition.

In summary, coexistence among shiners and bluegills is constrained by a resource base which declines across the growing season, apparently limiting resources, at least for the shiners. Further, indirect evidence suggests predation severely limits the range of habitats available to all three species and inflicts heavy mortality on the shiners. Seasonality of the environment and phylogenetic constraints, although of less proximal importance to resource partitioning, nevertheless set ultimate limits to coexistence mechanisms.

Mechanisms of Resource Partitioning

Resource partitioning among blackchin and blacknose shiners is permitted by morphological differences which affect not only the size of prey that can be eaten but the habitats which can be effectively foraged as well. Life history differences also contribute to shiner coexistence.

Relative differences in habitats foraged and prey sizes captured between the shiners are in accord with morphological differences of the two species. Basic differences in shiner morphology are that the blackchin has a larger and more terminally positioned mouth than the blacknose, which has a subterminal mouth. With a smaller, more specialized mouth, the blacknose would be expected to take smaller prey from a narrower range of habitats, and indeed this is the case.

Mean prey size is usually smaller in the blacknose than the blackchin although the upper limit on the range of prey sizes taken is approximately the same. Mouth width has been determined by Lawrence (1957) and Werner (1974) to be a better indicator than jaw length of the maximum prey size a fish can handle. This appears to be the case with the two shiners, although the overall larger mouth of the blackchin, in conjunction with the pharyngeal teeth, may make it differentially more efficient at handling prey than the blacknose as prey approach the upper limit. If this were the case, the blackchin would be expected to efficiently incorporate more large prey than blacknose and therefore have a larger mean prey size.

During the day, shiners do not exhibit habitat segregation either by species or by size class within species; all size classes of both species are found over dense vegetation on the bench where feeding activity is minimal. Conversely, there are differences in twilight habitat utilization as reflected in prey differences among size classes and between species. Similarly, bluegill size classes segregate by habitat while feeding, with young-of-the-year found in deeper water than Age I fish.

The range of habitats foraged by the blacknose is more restricted than the range of the blackchin. Of the four habitats recognized in this study, the blacknose utilizes primarily the vegetation and the benthos; very little food is taken from the open water column and virtually none is taken at the surface. The blackchin, on the other hand, forages all four habitats. Thus for these shiners, which do not demonstrate habitat segregation during the day, differences in habitat use in the evening are due to different apparent foraging capabilities in those habitats. The almost complete absence of blacknose on the transect in Three Lakes may be due to the lack of exposed benthos on the bench. In the evening in Three Lakes, blackchin were observed in the overstory at Position 6 where they presumably can forage on Daphnia.

Laboratory observations of the blacknose support inferences from the field concerning its foraging capabilities. This species would not take food from the water surface and was rather inefficient at capturing Daphnia in the water column, frequently missing the intended prey.

Not only are there differences between species in habitats foraged, and therefore types of prey consumed, but within each species there is an ontogenetic progression through different foraging habitats (Table 7). These differences serve to minimize food use overlap both within and among species. All size classes of blackchin shiners consume predominantly open water prey with the remainder of the diet coming from the vegetation and benthos (small fish) or the benthos and the surface (large fish). Blacknose shiners exhibit a more distinctive diet shift, switching from predominantly vegetation prey (small fish) to predominantly benthic organisms (large fish). Thus the primary prey of the two shiner species are found in different habitats. The less distinct diet segregation among size classes of the blackchin as compared to the blacknose may be because the open water habitat, extensively utilized by all blackchin, is

volumetrically the largest habitat in the littoral zone with the shortest mean generation time, and therefore should support a larger prey community with a faster turnover rate than other habitats. The open water should then support heavier grazing than the other habitats.

The bluegill diet is more evenly distributed across habitat types than that of either of the shiners. Still, an ontogenetic shift from vegetation to open water then to benthos as primary prey source is apparent. Habitat segregation of bluegill size classes no doubt reduces competition for food within the species. Separation of feeding in time and space of bluegills and shiners should also reduce interspecific competition for food up to the point where prey captured by bluegills in the vegetation during the day are not available to shiners in the evening.

Both food and habitat utilization data of this study are in close accord with studies of other investigators. Keast (1965) reports the food of the blackchin shiner is primarily Cladocera and Diptera adults. Sheppard (1965) reports that blacknose consume primarily Cladocera (*Chydorus* and *Daphnia* with some *Bosmina* and *Polyphemus*) and dipteran larvae and pupae. Flying insects were found in the gut contents on only 1 day and they amounted to only 2% of the total volume of food present. Results from another study (Keast, 1978) indicate prey of Bluegill 0 and I are primarily Cladocera, chironomids, other insect larvae and amphipods. These results are all very similar to the findings of this study.

The pattern of declining food intake and prey similarity across the summer in blackchin and blacknose shiners is similar to that found in centrarchids by Seaburg and Moyle (1964). A similar decline in feeding rate was noted by Keast (1970) for several species, but Moyle (1973) reports only a change in prey types taken by cyprinids in his study.

Although his data do not lend themselves to the appropriate analysis for determining changes in ration weight, the reported (Moyle, 1969) increase in algae and detritus imply a decline in food quality across the summer.

Habitat utilization by blackchin shiners has been previously studied by Keast, et al (1978). Their daytime censuses of 11 habitats ranging from "weedy shallow" to "exposed clay" found blackchin almost exclusively in the weedy shallow habitat. A similar distribution was found in night-time censuses (2200 - 2400h) but evening migrations were not mentioned. This is not too surprising, however, since 1400 m of transect (11 habitats) were traversed in 2 hours, mostly after dark, so day - night habitat differences could have been missed if timing were not just right. The same study reported bluegill $<$80 mm (total length) confined to weedbeds; young-of-the-year were found in dense stands of Potamogeton when they returned from the limnetic zone in late July (Keast, 1978).

Foraging theory predicts that as resources and return rates decline, species should drop less profitable habitats from their foraging itinerary while at the same time increasing or holding constant diet breadth (MacArthur and Pianka, 1966). Of the four foraging habitats recognized in this study, the blacknose utilizes only three, virtually never capturing prey at the surface. Of the remaining three habitats, the open water is foraged only in early spring when prey densities are high and contributes very little to the blacknose diet later in the season. Laboratory observations indicate blacknose are relatively inefficient foragers in the open water so return rate would be expected to decline rapidly with decreasing prey abundances. As most resources decline through the summer, blacknose restrict their feeding to primarily the vegetation and benthos but compensate for low resource levels by

incorporating a larger array of prey from these habitats into the diet. Blackchin, on the other hand, utilize all habitats until midsummer when the vegetation is dropped. Diet breadth reaches a peak at this time and declines across the remainder of the summer. The blackchin, then, not only utilizes a broader range of habitats than the blacknose, but also consumes a narrower range of prey types, thus apparently able to choose only the most abundant or profitable prey in each habitat. The blacknose is left in the position that its niche is included (Miller, 1964) within that of the blackchin without a clear foraging habitat refuge. Only benthic Ceratopogonidae are an exclusive blacknose resource.

The greater success of the blackchin as compared to the blacknose shiner in Lawrence Lake appears to be due to its more generalized mouth structure conferring the ability to opportunistically forage in the most profitable habitats. The blacknose, then, is expected to be generally less abundant and more variable in abundance and frequency of occurrence. Data presented in Table 2 indicate the blacknose is somewhat more restricted in local distribution than the blackchin, and it is less abundant than the blackchin in Three Lakes and Pine Lake (Table 3) as well as in Bassett Lake (personal observation). Sufficient relative abundance data are not available from the other lakes to permit comparison.

The bluegill, like the blackchin, is quite generalized in its diet. Unlike either of the shiners, though, it has the tremendous added advantage of foraging in the vegetation (with access to the bottom) during the day. Thus, the bluegill need not rely on only the short crepuscular periods for foraging time.

Why shiners do not utilize the vegetation during the day is impossible to answer based on this study, but several reasons may be hypothesized.

Although shiners appear to be obligate schoolers to the extent that several must be kept together when in captivity or they do not settle down, it seems unlikely that such a behavioral trait would be so rigidly maintained without a constant selection pressure for it, at the cost of not foraging during the day. Two possible counterbalancing costs are predation by ambush within the vegetation and high metabolic cost of foraging in a structured environment. Small bluegills are subject to less predation than are shiners because of their greater body depth, but most of the bass and perch would still be able to capture the small centrarchids. Yet, the bluegills are in the vegetation which would indicate that shiners should be there too if predation were the only factor.

The body plan of shiners is markedly different from that of bluegills. Shiners are relatively long and fusiform whereas bluegills are relatively short-bodied, gibbose and narrow in cross-section. The bluegill body plan permits precise turns and well modulated movement with the use of pelvic and pectoral fins which would facilitate foraging in a structured environment. Shiners are designed for sustained motion and fin development does not permit the precision in movement of which bluegills are capable (Alexander, 1974). Thus, shiners could find maneuvering through the vegetation to be metabolically very costly for minimal returns. Also, awkward movement by many fish could cause resource depression (Charnov, et al, 1976), further limiting returns. The relative foraging efficiency of shiners in various habitats could be investigated in the laboratory, supplying much needed information for the interpretation of shiner habitat distributions.

The apparent habitat segregation of shiners and bluegills may be due to bluegill avoidance of shiner schools or simply bluegills positioning themselves where they can capture open water prey during the day. The structure of young-of-the-year bluegill schools differs considerably from that of shiner schools. Bluegill schools and individuals within the schools are rather sedentary as compared to shiner schools which are very mobile. It seems likely that an intermingling of the two species would disrupt both school types, but especially the bluegill schools, enough to invite predation. Bluegills that do overlap with shiners are frequently found within rather than over the vegetation, but these fish are beyond the schooling stage. Remaining in the vegetation offers them predator protection and access to prey.

That Age 0 bluegills on the slope are in a position to feed on open water prey during the day seems more likely for Three Lakes than for Lawrence Lake. Young-of-the-year in Three Lakes are in deeper water than in Lawrence so they may have access to some prey during the day. Prevailing winds could bring more prey to fish on Transect 2 in Lawrence Lake than on other transects, but this seems insignificant if the prey are deep.

Interspecific resource partitioning, then, between blackchin and blacknose shiners occurs primarily through selection of food from different habitats and microhabitats during crepuscular feeding periods. Relative foraging specialization of the two species is determined by trophic structure differences which make the blackchin a relative generalist compared to the blacknose. In an environment of variable resources, the ability to be opportunistic makes the blackchin more successful at garnering resources than the blacknose. The bluegill

exhibits habitat complementarity with the shiners but the reasons for it are unclear. The greater efficiency of bluegills foraging within *Scirpus* beds during the day, as compared to the shiners, may be due to smaller energetic demands and greater precision of an individual with the gibbose centrarchid body plan as compared to the fusiform cyprinid body. The significance of the crepuscular shift in habitat use by the shiners may be two-fold. Moving into more open habitats not only allows shiners to forage in habitats not utilized during the day, but also allows them to forage in less structured habitats where their body design should function more efficiently.

Migration

Diel migration from daytime refuge habitats to nighttime foraging areas is a phenomenon common to many fish communities. Perhaps the best known examples are those of marine and reef fishes which migrate a few meters to several kilometers after dusk to forage in the open water column or open benthic regions (Collette and Talbot, 1972; Davis and Birdsong, 1973; Gladfelter, 1979; Hobson, 1968, 1972, 1973; Hobson and Chess, 1976, 1978; Pearcy, et al, 1977; Starck and Davis, 1966). Daily migration both vertically and horizontally in the water column have been observed in freshwater fishes, for example golden shiners (Hall, et al, 1979; Suffern, 1973), sockeye salmon (Eggers, 1978; Narver, 1970), northern mimic shiners (Black, 1945; Moyle, 1973) and bluegill sunfish fry (Werner, 1969).

Several characteristics are common to all these examples. Departure from refuge habitats is cued by light level, schools usually disperse at the foraging grounds and fish which undergo these movements are subject to

intense predation pressure. Another adaptation common to many fish exhibiting diel migration and twilight feeding peaks is correspondence of λ_{max} of scotopic visual pigments to λ_{min} of the surrounding water at dusk (Lythgoe, 1966; McFarland and Munz, 1975). That is, the wavelength at which night vision (rod) pigments are most active corresponds to the wavelength of maximum transmittance of water at dusk. This relationship is reported not only for marine planktivores (McFarland and Munz, 1975; Munz and McFarland, 1973) but for freshwater cyprinids and centrarchids as well (McFarland and Munz, 1975). More work needs to be done on the relative visual capabilities of piscivores and their planktivorous prey and on seasonal and intrapopulation variability in pigment absorption maxima before the full significance of the role of visual pigments in ecological interactions can be ascertained.

Predation

Heterotypic schooling is one type of interspecific interaction among the shiners that selects for similarities rather than differences between the two species. Mixed-species schooling over vegetation during daylight hours appears to be a coevolved defense mechanism against predation (Ehrlich and Ehrlich, 1973; Ogden and Ehrlich, 1977). Such species are usually very similar in morphology and pigmentation (Davis and Birdsong, 1973), as are the shiners, thus maintaining the unified appearance of the school and maximizing the number of school members. Other species such as young-of-the-year largemouth bass and young-of-the-year lake chubsuckers which occassionally join shiner schools resemble shiners in general body shape and both species have distinct black lateral stripes when young. Similarity of appearance and behavior are particularly important in schooling fish; predators tend to attack unusual fish (Hobson, 1968; Neill and Cullen, 1974), presumably because it is possible for the predator to track one outstanding fish without losing it among many other similar individuals. Therefore, integrity of the school is particularly important during the intensive predation that occurs during early twilight in many communities (Hobson, 1968, 1972; Majors, 1976; McKaye, in press b).

Laboratory studies (Neill and Cullen, 1974; Radakov, 1973) have demonstrated the decreasing effectiveness of predator attacks as school size increases and one field study (McKaye, in press a) has shown there is a reduced predation rate, per individual prey, on eleotrid fry in schools as compared to individual fish over the same time period. Thus twilight accumulation of fish at the middle bench position in Lawrence may be an adaptation to increase school size during critical periods. Schools disperse at the feeding grounds, though, in response to low light levels presumably because schooling is no longer necessary for predator protection and because solitary foraging (especially for zooplankton) is more efficient than group foraging (Eggers, 1976).

Predation as an important selection pressure has been variously demonstrated or hypothesized in other fish communities as well. Sex ratio (Seghers, 1973), social behavior (Farr, 1975; Seghers, 1974), and body color pattern (Endler, 1979) of the guppy, <u>Poecilia</u> <u>reticulata</u>, have been shown to be influenced by predation. McPhail (1969) suggests predation by <u>Novumbra</u> on young of male sticklebacks (<u>Gasterosteus</u>) was the selective force responsible for the evolution of the black genotype of the stickleback. In a laboratory study, Milinski and Heller (1978) found a change in the foraging behavior of sticklebacks in the presence of a predator such that they were able to forage and be attentive to the

predator at the same time. And, in a very controversial paper, Jackson (1961) suggests that predation by the large, "voracious" fish Hydrocyon vittatus in the Great Lakes of Africa not only restricts other fish less than 40% of its total length to vegetation at the periphery of the lakes, but also has been a major factor in encouraging andromesis of potential prey and in restricting speciation. Although, Fryer (1965) and others have refuted Jackson's hypothesis of the effects of Hydrocyon on speciation.

Whether predation is currently or could potentially facilitate coexistence of species that could not otherwise coexist in these systems remains unclear. Roughgarden and Feldman (1975) and Vance (1978) have demonstrated that it is theoretically possible, and predator mediated coexistence of competitors has been documented repeatedly in field studies (Harper, 1969; Paine, 1966; see Connell, 1975, for a review, and Keough and Butler, 1979, and Harper, 1969 for exceptions). Declining food intake across the growing season, even in size classes of fish whose numbers were diminishing at the same time, indicates that in the year studied, predation did not maintain prey numbers low enough to preclude resource limitation. This does not tell us, however, what the competitive situation would have been without predation.

Life History Patterns

The blacknose shiner breeds before the blackchin shiner in early summer, although there is some overlap. This difference in breeding times cannot be attributed directly as a result of competition, but selection pressure could maintain this difference in order to minimize overlap in food use of young-of-the-year fish. Small size classes utilize relatively more vegetation prey than other size classes within both species. By staggering peak fry periods the first cohort could be growing away from vegetation prey and becoming more specialized as the second cohort hatched. The first few weeks of life are known to be a critical time for fish (Hempel, 1963; Kramer and Smith, 1962), such that reduced competition could be very important to year class success, especially in years of low resources.

Age I fish of both shiner species exhibit very poor survivorship over their second winter, but this pattern is particularly marked in the blacknose. This may be the result of the relatively poorer foraging success of large blacknose in the fall causing low overwinter survival. Survival of adults to breed in a second summer would reduce the chances of species extinction due to year class failure and reduces year to year fluctuations in the size of the breeding population due to poor recruitment. So, to the extent that more adult blackchin than blacknose survive the winter, the differential foraging capabilities of the blackchin again contribute to that species greater success in Lawrence Lake relative to the blacknose.

The Cyprinid Community

The cyprinid community in local warmwater lakes is dominated by the blackchin shiner, a food and habitat generalist. The blackchin has the highest frequency of occurrence of the five species listed in Table 2, and in lakes where quantitative estimates have been made, it is the most abundant species (Table 3, and personal observation). The blacknose shiner and bluntnose minnow (Pimephales notatus) are more specialized than the blackchin, but less so than the pugnose, and are intermediate in frequency of occurrence and population density. The pugnose shiner (Notropis

anogenus), a very small fish with a tiny, upturned mouth, is the least common of the smaller cyprinids. The golden shiner, a specialized zooplankton forager, which attains a larger size than the other four species, is fairly widely distributed but population densities vary greatly among lakes. The golden shiner escapes competition with most other littoral zone fish after its first year through diel migrations to the limnetic zone to feed on plankton (Hall, et al, 1979); very little is known about its first year.

The bluntnose minnow has been studied by Keast, et al (1978) and Moyle (1973). Both studies found it primarily associated with vegetation at a depth of 2 - 4 m, although it was observed in low numbers in more open habitats also. In Pine Lake, small bluntnose are occassionally seen in schools in very shallow, open habitats, but most fish are associated with vegetation. Casual observation showed them to range into deeper water than the blackchin or blacknose. Both Moyle (1973) and Keast (1965) found the bluntnose to be a versatile feeder, consuming Cladocera, chironomids, algae and some flying insects. Observations of bluntnose in aquaria showed them to be much more aggressive foragers than blacknose which they resemble in trophic morphology. The bluntnose readily took food from the surface of the water whereas the blacknose would not (personal observation). The reason for the bluntnose's more limited distribution compared to that of the blacknose in local lakes is unknown and somewhat puzzling in view of its apparently greater foraging versatility and wider range of habitat utilization.

Dominance of the cyprinid community by a generalist species, the blackchin shiner, is similar to the dominance of the bluegill in the centrarchid community. One major difference between the community structure of the two families is that almost all local centrarchids are regularly represented in every warmwater lake; inter-lake variation is usually due to differences in population densities. In the cyprinid community, however, species are frequently absent. If the results from Lawrence Lake can be extrapolated to other lakes it appears that shiners may be particularly sensitive to resource levels and habitat types. That is, with only a very limited time to forage each day, shiners must experience relatively high resource levels in order to obtain sufficient food. The more specialized (less opportunistic) species would be the most sensitive to resource limitations and might require a higher threshold level of resources in order to survive in the system. Centrarchids are not subject to such severe time limits on foraging. Also, with a broader range of sizes between young-of-the-year and adults there is a broader range of prey sizes and types over which a species spreads its resource demands. All of these factors would increase the probability that a species would be present in a community, even if only at low numbers.

The reproductive pattern of many cyprinids may also be important in determining the presence or absence of many species. Since many shiners breed only once, their recruitment would be expected to vary considerably from year to year with resource levels. Again, the more specialized, rarer species would be the most susceptible to local extinctions. Here again, the iteroparous centrarchids would be buffered against complete extinction in the event of the failure of one year class in recruitment.

CONCLUSION

The results of this study indicate that coexistence of blackchin and blacknose shiners and bluegills depends on several factors, including food and habitat segregation and differences in life history characteristics. Food studies indicate that, for the shiners at least, food is a limiting resource before the end of the summer. This, combined with potential similarities in their diets, suggests the shiners are competing for food, but each species has an exclusive resource, surface prey for the blackchin and benthic ceratopogonids for the blacknose, which may alleviate competitive pressures somewhat. Small bluegills overlap on food type somewhat with shiners but are able to garner increasing amounts of food as summer progresses. Also, bluegills utilize dense vegetation for foraging during the day much more efficiently than do the shiners, which rely almost entirely on foraging at morning and evening twilight periods.

During the day, shiners do not segregate by habitat, but rather appear to be coevolved to school together for predator protection. At the same time, however, young-of-the-year bluegills are found in deeper water than the shiners. Reasons for this segregation my include both intra- and interspecific segregation. Larger bluegills are vertically segregated from the shiners, utilizing the vegetation above which the shiners school.

The observed staggered reproductive peaks of the shiners could potentially reduce competition among young-of-the-year fish.

Predation obviously restricts daytime habitat utilization, apparently augmenting any competitive pressures among species. The role of predation in facilitating coexistence among the species is unclear, but the extensive reduction in adult shiner numbers across the summer, presumably due to predation, suggests that resources would be even more scarce without the loss of those consumers.

One of the purposes of this study was to provide the necessary observations of a natural system from which questions for experimentation could be derived. The three major questions which arise could be explored in an experimental system such as the experimental ponds at W. K. Kellogg Biological Station. First, are blackchin shiners better competitors than blacknose shiners? If so, is the food refuge of the blacknose sufficient for coexistence without involving differential predation on the blackchin? Secondly, is habitat segregation necessary for coexistence of the shiners and young-of-the-year bluegills? And thirdly, does predation facilitate coexistence between the shiners through differential predation on the better competitor (presumably the blackchin)?

Further observations of interest would include long-term monitoring of a lake such as Lawrence Lake to determine the magnitude of temporal variation in population levels of the shiners. Also, comparison of food and habitat utilization patterns from Lawrence Lake with those in other lakes with more diverse habitats and/or cyprinid communities would offer the opportunity to explore niche shifts and community assemblages in these species.

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APPENDICES

APPENDIX 1

HABITAT DESCRIPTIONS OF THE STUDY LAKES

Table A1. Description of Transect Habitats in Lawrence Lake, Michigan, in 1977. All Slopes were covered primarily with *Scirpus subterminalis*. Predominant vegetation at other positions is indicated by: S = *Scirpus subterminalis*; U = *Utricularia* sp.; C = *Chara*. Values presented are mean ± 1 standard error.

	DEPTH (m)	PLANT HT. (m)	% COVER	LENGTH (m)
TRANSECT 1				
LIP	1.25 ± 0.17	0.48 ± 0.05 S	96.3 ± 3.8 S	104
TRANSECT 2				
LIP	0.96 ± 0.06	0.52 ± 0.03 S	100 ± 0 S	94
BENCH				
OPEN	0.78 ± 0.02	0.05 U 0.30 S	42.5 ± 4.8 U	42
SCIRPUS	0.73 ± 0.03	0.40 ± 0.04 S	97.5 ± 2.5 S	38
TRANSECT 3				
LIP	1.00 ± 0.12	0.54 ± 0.06 S	97.5 ± 2.5 S	48
INSHORE	0.52 ± 0.03	0.10 ± 0 C	63.8 ± 12.0 C	48

Table A2. Description of Transect 2 Habitats in Lawrence Lake, Michigan, in 1978. Predominant vegetation is *Scirpus subterminalis* unless otherwise indicated as *Utricularia* sp. (U). Values presented are mean ± 1 standard error.

	DEPTH (m)	PLANT HT. (m)	% COVER	LENGTH (m)
	24 JULY 1978			
BENCH				
HABITAT A				13
POSITION 1	0.60 ± 0	0.08 ± 0.03 U	4.0 ± 2.0 U	
2	0.75 ± 0.02	0.11 ± 0.02 U	17.0 ± 5.5 U	
3	1.02 ± 0.03	0.48 ± 0.04	78.8 ± 3.8	
HABITAT B				44
POSITION 1	0.40 ± 0.04	0.10 ± 0	2.0 ± 1.5	
2	0.76 ± 0.01	0.17 ± 0.02 U	45.0 ± 5.4 U	
3	0.98 ± 0.04	0.61 ± 0.02	72.2 ± 12.6	
HABITAT C				25
POSITION 1	0.51 ± 0.01	0.26 ± 0.09	4.8 ± 1.8	
2	0.70 ± 0	0.33 ± 0.03	77.8 ± 3.5	
3	0.92 ± 0.01	0.66 ± 0.02	98.5 ± 0.5	
SLOPE				83
POSITION 4	2.5 ± 0.12	0.50 ± 0.02	84.3 ± 3.0	
5	3.5 ± 0.18	0.35 ± 0.05	78.1 ± 10.0	
	16 AUGUST 1978			
BENCH				
HABITAT A				13
POSITION 1	0.60 ± 0	0.03 ± 0.01 U	20.2 ± 11.2 U	
2	0.64 ± 0.01	0.09 ± 0.03 U	22.0 ± 10.3 U	
3	0.92 ± 0.05	0.43 ± 0.12	78.8 ± 2.4	

Table A2 (cont'd.).

	DEPTH (m)	PLANT HT. (m)	% COVER	LENGTH (m)
BENCH				
HABITAT B				44
POSITION 1	0.40 ± 0.04	0.03 ± 0.01	20.2 ± 11.2	
2	0.66 ± 0.01	0.12 ± 0.01 U	60.8 ± 5.0 U	
3	0.97 ± 0.06	0.57 ± 0.06	90.0 ± 2.2	
HABITAT C				25
POSITION 1	0.51 ± 0.01	0.03 ± 0.03	10.5 ± 0.5	
2	0.65 ± 0.02	0.32 ± 0.04	83.8 ± 5.5	
3	0.84 ± 0.02	0.69 ± 0.04	98.8 ± 1.3	
SLOPE				83
POSITION 4	2.5 ± 0.12	0.59 ± 0.02	89.3 ± 4.8	
5	3.5 ± 0.18	0.46 ± 0.24	85.4 ± 8.26	

Table A3. Description of Transect Habitats in Three Lakes II, Michigan, in 1978. Predominant vegetation is *Chara* sp. unless otherwise indicated as *Potamogeton* sp. (P). Values presented are mean ± 1 standard error.

	DEPTH (m)	PLANT HT. (m)	% COVER	LENGTH (m)
BENCH				187
POSITION 1	0.59 ± 0.02	0.51 ± 0.02	100 ± 0	
2	0.75 ± 0.02	0.54 ± 0.02	100 ± 0	
3	0.92 ± 0.01	0.55 ± 0.02	100 ± 0	
SLOPE				187
POSITION 4	1.10 ± 0.10	0.52 ± 0.04	96.7 ± 1.2	
5	1.92 ± 0.08	0.45 ± 0.05	90.6 ± 6.0	
6	3.50 ± 0.17	0.87 ± 0.07 P	58.3 ± 9.9 P	

APPENDIX 2

TRANSECT COUNT VARIATION

Table A4. Examples of Transect Count Variation. Fish counts from Transect 1 on 12 and 13 August 1977 and for two replicates on 22 August 1978 are presented as examples of count variation.

		1977		1978	
		12 VIII	13 VIII	1	2
BLACKCHIN	S	108	128	130	174
	M	35	48	180	203
	L	167	204	58	35
	XL	12	14	55	44
	TOTAL	322	394	423	456
	$\bar{X} \pm 1$ S.E.	358.0 ± 36.0		439.5 ± 16.5	
BLACKNOSE	S	3	14	9	0
	M	100	166	77	44
	L	21	30	100	93
	XL	7	15	52	42
	TOTAL	131	225	238	179
	$\bar{X} \pm 1$ S.E.	178.0 ± 47.0		208.5 ± 29.5	
GRAND TOTAL		453	619	661	635
	$\bar{X} \pm 1$ S.E.	536.0 ± 83.0		648.0 ± 13.0	

APPENDIX 3

DIET SUMMARIES

APPENDIX 3

DIET SUMMARIES

Summaries for the 1977 growing season of percent contribution of prey taxa comprising greater than 1% by weight (mg dry weight) of the diet of shiners and bluegills are presented in Tables A5, A6, and A7. Fish were taken from Lawrence Lake usually within one hour after sunrise. The entire intestinal contents from 375 fish were enumerated and representative prey from each taxa were measured. Fish are listed by size class; an explanation of size classes is on page 25. All insects are larvae or nymphs unless otherwise indicated.

Table A5. Blackchin Diet Summary.

	23 APRIL				6 MAY				21 MAY		
SIZE CLASS:	5	4	3	2	4	3	2	1	4	3	2
Tanytarsus				4.8							
Baetis										28.5	
Cyclopoids	1.6	5.2	32.8	40.4	2.3	4.0	8.2	20.4			
Bosmina			2.3	17.5			1.6				
Chydorus								5.3			
Ophryoxus											1.1
Sida	6.6							1.4			
Simocephalus											
VEGETATION TOTAL	8.2	5.2	35.1	62.7	2.3	4.0	9.8	27.1		28.5	1.1
Chironominae	10.4	9.1	16.1	6.2			2.2	58.6	40.8	27.5	77.7
Ceratopogonidae				2.3							
Tanypodinae										2.7	
Ephemeroptera											
BENTHOS TOTAL	10.4	9.1	16.1	8.5			2.2	58.6	40.8	30.2	77.7
Daphnia	77.7	79.5	47.0	17.4	94.0	91.0	81.2	11.4			
Calanoids											
Leptodora											
OPEN WATER TOTAL	77.7	79.5	47.0	17.4	94.0	91.0	81.2	11.4			
Diptera adults					1.8	2.6	2.6		49.8	10.5	
Insect adults		3.1							4.0		
Scapholeberis											
SURFACE TOTAL		3.1			1.8	2.6	2.6		53.8	10.5	
Corixidae											
Diptera pupae	2.5	1.7	1.1	1.3	1.3		1.8		2.0		
Hyalella										6.3	4.7
Invertebrate eggs											1.1
Mites				8.2			2.0	1.6	1.9	22.0	11.9
OTHER TOTAL	2.5	1.7	1.1	9.5	1.3		3.8	1.6	3.9	28.3	17.7

Table A5 (cont'd.).

	24 JUNE			11 JULY		23 JULY	11 AUGUST		28 SEPTEMBER		
SIZE CLASS:	4	3	2	4	3	4	3	2	4	3	2
Tanytarsus			7.7								
Cyclopoids											3.8
Ophryoxus											2.4
Pseudochydorus								3.2			
Sida	18.3	21.4	13.5		7.0	1.3	1.5	1.8			
Simocephalus			1.3								
VEGETATION TOTAL	18.3	21.4	22.5		7.0	1.3	1.5	5.0			2.4
Chironominae	14.1	2.9	23.5	9.8	14.0	13.5	25.6	14.7	2.1		4.0
Ceratopogonidae					1.6						
Tanypodinae					1.2		1.5	1.5			
Ephemeroptera						2.7					
BENTHOS TOTAL	14.1	2.9	23.5	9.8	16.8	16.2	27.1	16.2	2.1		4.0
Daphnia		34.3	12.5	70.8	30.5	5.8	39.0	47.3	85.7	83.9	76.4
Calanoids										11.9	9.0
Chaoborus								1.2	1.0		
Leptodora			3.9		1.7						
OPEN WATER TOTAL		34.3	16.4		32.2	5.8	39.0	48.5	86.7	95.8	85.4
Diptera adults	54.7	26.0	8.3	2.0	3.8	29.8	22.2	6.3	8.9		3.5
Insect adults	5.6		2.4			3.8	2.0	2.3			
Scapholeberis			6.6								
SURFACE TOTAL	59.3	26.0	17.3	2.0	3.8	33.6	24.2	8.6	8.9		3.5
Corixidae	3.1	1.5									
Diptera pupae	1.5	4.2	5.6	5.8	1.1	10.3	1.4			1.9	
Hyalella											
Invertebrate eggs				6.3	24.2	28.8	1.5				
Mites	1.2	3.2	16.0	2.5	13.8	1.4	2.2	19.5			
Ostracods							1.1				
OTHER TOTAL	5.8	8.9	21.6	14.6	39.1	41.5	6.2	19.5		1.9	

Table A6. Blacknose Diet Summary.

	23 APRIL			6 MAY		21 MAY		24 JUNE	
SIZE CLASS:	4	3	2	4	3	4	3	4	3
Tanytarsus								4.1	12.3
Baetis	2.5								
Cyclopoids	33.4	62.7	89.1		3.9		3.6		
Acroperus									
Alona						1.3	1.8	3.5	10.9
Bosmina		1.3	1.5						
Chydorus							4.0		
Latona								2.5	1.6
Ophryoxus	1.5						1.3	3.5	2.1
Sida						1.4	1.4	11.4	9.1
Simocephalus									
VEGETATION TOTAL	37.4	64.0	90.6		3.9	2.7	12.1	25.0	36.0
Chironominae	35.6	20.6	6.9	23.8	13.6	19.3	20.8	25.5	21.1
Ceratopogonidae	7.8	2.3		21.9	3.7	70.3	59.6	2.8	
Tanypodinae				3.7	3.4	2.1		7.9	25.8
Caenis					7.0				
BENTHOS TOTAL	43.4	22.9	6.9	49.4	27.7	91.7	80.4	36.2	46.9
Daphnia	6.1	7.5	1.3	45.6	64.0			25.9	1.3
Calanoids									
Leptodora									
OPEN WATER TOTAL	6.1	7.5	1.3	45.6	64.0			25.9	1.3
Diptera pupae			1.5					1.3	1.4
Hyalella									
Invertebrate eggs									
Mites		1.4		2.5		1.7	4.0	4.5	8.3
Ostracods	10.5				2.1	1.3	1.1	1.6	2.1
Polycentropodidae								1.7	
OTHER TOTAL	10.5	1.4	1.5	2.5	2.1	3.0	5.1	9.1	11.8

Table A6 (cont'd.).

	11 JULY		11 AUGUST			28 SEPTEMBER		
SIZE CLASS:	4	2	4	3	2	4	3	2
Tanytarsus	6.9	4.1	5.2	4.4	6.4			
Baetis		1.1						
Cyclopoids						2.0		
Acroperus		2.0	2.1	9.2	5.1	4.5	4.2	2.4
Alona	5.2	2.6		1.1	1.3	10.0	5.1	24.0
Bosmina								
Eurycercus						1.5		
Latona	1.2	2.3		1.9	1.0	11.6	9.0	4.4
Ophryoxus		1.3		1.1	1.6	9.5	6.6	18.6
Sida		24.1	1.1	1.3	1.5	3.1	15.0	8.4
Simocephalus					1.3	1.1		
VEGETATION TOTAL	13.3	37.5	8.4	19.0	18.2	43.3	39.9	57.8
Chironominae	48.7	48.5	44.9	36.0	39.6	9.7	6.8	7.8
Ceratopogonidae	9.4	4.4	18.8	10.1	6.2	22.4	36.4	4.4
Tanypodinae	20.8	4.0	16.1	12.5	14.7	5.2	1.0	8.3
Caenis				2.4				
BENTHOS TOTAL	78.9	56.9	79.8	61.0	60.5	37.3	44.2	20.5
Daphnia			1.8	2.5	7.3	4.0	3.7	2.9
Calanoid						1.1		1.7
Leptodora					1.4			
OPEN WATER TOTAL			1.8	2.5	8.7	5.1	3.7	4.6
Diptera pupae			1.0					
Hyalella						2.6	3.6	
Invertebrate eggs				3.7				
Mites	1.4	3.0	3.2	8.5	5.3	2.8	2.4	4.4
Ostracods	1.5		1.3	2.7	4.0	6.8	2.8	10.4
Polycentropodidae								
OTHER TOTAL	2.9	3.0	5.5	14.9	9.3	12.2	8.8	14.4

Table A7. Bluegill Diet Summary.

	6 MAY	21 MAY			24 JUNE		
SIZE CLASS:	2	5	4	2	5	3	2
Tanytarsus						1.3	
Baetis		2.8					
Coenagrionidae		6.2					
Leptoceridae							
Cyclopoids				3.4			4.7
Acroperus							
Camptocercus							
Eurycercus							
Latona							1.5
Ophryoxus				1.3			1.9
Pseudochydorus							
Sida				3.4	5.9	10.0	51.2
Simocephalus							
VEGETATION TOTAL		9.0		8.0	5.9	11.3	57.8
Chironominae	14.9		13.5	14.3	28.7	27.3	22.5
Ceratopogonidae					1.8		
Tanypodinae			2.4	3.4	1.1	1.7	2.8
Caenis							
Ephemerella		3.7					
Hexagenia		37.9			25.5		
Oligochaete							
BENTHOS TOTAL	14.9	41.6	15.9	17.7	57.1	29.0	25.3
Daphnia	75.4	45.1	72.8	54.0	7.9	1.8	2.8
Calanoids		1.2			5.8	13.4	
OPEN WATER TOTAL	75.4	46.3	72.8	54.0	13.7	15.2	2.8
Diptera adults		1.5			13.3	14.1	
Insect adults							
Scapholeberis						2.8	
SURFACE TOTAL		1.5			13.3	16.9	
Anisoptera							
Corixidae							
Diptera pupae	1.4		1.0		3.5	5.4	
Hyalella	3.6		3.7	4.5		5.2	4.4
Mites	2.2		3.6	8.5		8.1	3.1
Planorbidae							
Polycentropodidae					1.5	3.3	
Trichoptera				2.2			
OTHER TOTAL	7.2		8.3	15.2	5.0	22.0	7.5

Table A7 (cont'd.).

	11 JULY		23 JULY		11 AUGUST		28 SEPT.
SIZE CLASS:	3	1	3	1	3	1	1
Tanytarsus			1.6	1.8		5.8	
Baetis		1.8	2.5		1.6		
Coenagrionidae					2.0	1.0	
Leptoceridae	7.4						
Cyclopoids	3.6	6.0		6.6	2.9	6.0	6.6
Acroperus		9.9		1.5		20.5	1.5
Camptocercus		1.3					
Eurycercus						1.7	1.2
Latona				2.3		1.5	
Ophryoxus		8.8		3.7			7.0
Pseudochydorus	1.5	1.6				2.1	
Sida	1.4	19.1	1.1	30.7	3.9	9.9	18.4
Simocephalus						1.4	
VEGETATION TOTAL	13.9	48.5	5.2	46.6	10.4	49.9	34.7
Chironominae	13.9	29.8	20.9	18.9	6.2	7.9	3.8
Ceratopogonidae			1.8				
Tanypodinae	12.8		21.1	15.7	5.4	8.7	
Caenis			2.8		3.3		
Ephemerella							
Hexagenia							
Oligochaete		21.4					2.8
BENTHOS TOTAL	26.7	51.2	46.6	34.6	14.9	16.6	6.6
Daphnia	8.9			2.5	7.0	22.2	1.9
Calanoids	10.4		12.9	1.4	9.4	7.4	55.8
OPEN WATER TOTAL	19.3		12.9	3.9	16.4	29.6	57.7
Diptera adults			9.0		5.7		
Insect adults					1.3		
Scapholeberis							
SURFACE TOTAL			9.0		7.0		
Anisoptera	28.3						
Corixidae					1.8		
Diptera pupae					1.1		
Hyalella			13.4		30.7	2.1	
Mites	8.6		6.1	12.6	6.4		
Planorbidae			1.2		2.2		
Polycentropodidae					4.0		
Trichoptera			2.5				
OTHER TOTAL	36.9		23.2	12.6	46.2	2.1	

APPENDIX 4

DIET SUMMARIZED BY PREY HABITAT

Table A8. Mean Percent Contribution of Prey from Each Habitat to the Diet of Shiners and Bluegills. Fish species are listed by size class (see page 25 for explanation). Data, which are from Lawrence Lake, 1977, are derived from Appendix 3.

	23 APRIL				6 MAY				21 MAY				24 JUNE			
SIZE CLASS:	5	4	3	2	4	3	2	1	5	4	3	2	5	4	3	2
BLACKCHIN																
VEGETATION	8.2	5.2	35.1	62.7	2.3	4.0	9.8	27.1		0	28.5	1.1		14.1	21.4	22.5
BENTHOS	10.4	9.1	16.1	8.5	0	0	2.2	58.6		40.8	30.2	77.7		18.3	2.9	23.5
OPEN WATER	77.7	79.5	47.0	17.4	94.0	91.0	81.2	11.4		0	0	0		0	38.2	12.5
SURFACE	0	3.1	0	0	1.8	2.6	2.5	0		53.8	10.5	0		59.3	26.0	17.3
OTHER	2.5	1.7	1.1	9.5	1.3	0	3.8	1.6		3.9	28.3	17.7		5.8	8.9	21.6
BLACKNOSE																
VEGETATION		37.4	64.0	90.6	0	3.9				2.7	11.8			25.0	36.0	
BENTHOS		43.4	22.9	6.9	49.4	27.7				91.7	80.4			36.2	46.9	
OPEN WATER		6.1	7.5	1.3	45.6	64.0				0	0			25.9	1.3	
SURFACE		0	0	0	0	0				0	0			0	0	
OTHER		10.5	2.9	0	2.5	2.1				3.0	5.1			9.1	11.8	
BLUEGILL																
VEGETATION							0		9.0	0		8.1	5.9		11.3	59.3
BENTHOS							14.9		41.6	15.9		17.7	57.1		29.0	25.3
OPEN WATER							75.4		46.3	72.8		54.0	13.7		15.2	2.8
SURFACE							0		1.5	0		0	13.3		16.9	0
OTHER							7.2		0	8.3		15.2	5.0		22.0	7.5

Table A8 (cont'd.).

	11 JULY				23 JULY				11 AUGUST				28 SEPTEMBER			
SIZE CLASS:	4	3	2	1	4	3	2	1	4	3	2	1	4	3	2	1
BLACKCHIN																
VEGETATION	0	7.0			1.3					1.5	5.0		0	0	6.2	
BENTHOS	9.8	16.8			16.2					27.1	16.2		2.1	0	4.0	
OPEN WATER	72.5	30.5			5.8					39.0	48.5		86.7	95.8	85.4	
SURFACE	2.0	3.8			33.6					24.2	8.6		8.9	0	3.5	
OTHER	14.6	39.1			33.3					6.2	20.5		0	1.9	0	
BLACKNOSE																
VEGETATION	13.3	37.5							8.4	19.0	18.2		43.3	39.9	57.8	
BENTHOS	78.9	56.9							79.8	61.0	60.5		37.3	44.2	20.5	
OPEN WATER	0	0							1.8	2.5	8.7		5.1	3.7	4.6	
SURFACE	0	0							0	0	0		0	0	0	
OTHER	2.9	3.0							5.5	14.9	9.3		12.2	8.8	20.5	
BLUEGILL																
VEGETATION		13.9		48.5		5.2		46.6		10.4		49.9				34.7
BENTHOS		26.7		51.2		46.6		34.6		14.9		16.6				6.6
OPEN WATER		19.3		0		12.9		3.9		16.4		29.6				57.7
SURFACE		0		0		9.0		0		7.0		0				0
OTHER		36.9		0		23.2		12.6		46.2		10.8				0