THE UNIVERSITY OF MANITOBA

COMPARATIVE ECOLOGY OF FOUR SPECIES OF DARTERS (ETHEOSTOMINAE) IN LAKE DAUPHIN AND ITS TRIBUTARY, THE VALLEY RIVER

by

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A THESIS

PRESENTED TO THE FACULTY OF GRADUATE STUDIES

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF MASTER OF SCIENCE

DEPARTMENT OF ZOOLOGY

WINNIPEG, MANITOBA

May, 1971

ABSTRACT

The johnny darter Etheostoma nigrum, Iowa darter Etheostoma exile, river darter Percina shumardi, and logperch Percina caprodes occur in Lake Dauphin and its largest tributary, the Valley River. Density and relative abundance of the four species in defined river and onshore lake environments were determined by seining throughout most of the ice-free period. In spring river darter and logperch moved into the lower reaches of the river and spawned; but after the reproductive season johnny darter were virtually the only darters remaining in the river. That species was more abundant in non-current than in current. In the lake unbroken sand or mud bottom (non-cover) was avoided by all darters. Beds of aquatic vegetation were inhabited by Iowa darter, with high densities of young-of-the-year occurring in late summer. Rubble beaches exposed to wave action were inhabited chiefly by river darter. Pebble-rubble beaches protected from wave action contained the greatest overlap of the four species, with johnny darter and Iowa darter prominent following the reproductive season. Preference experiments in the laboratory confirmed the avoidance of non-cover areas in the field, but failed to demonstrate preferences for particular types of cover.

The smallest Iowa darter, river darter and logperch caught in the lake shared a diet consisting mainly of copepods and cladocerans, while small johnny darter in the river ate chiefly midge larvae. Larger fish took a variety of benthic foods. Two or more species of darters occurring together in the same environment at the same time usually ate the same range of foods but concentrated on different items.

Differences in environment inhabited and food eaten indicate that the ways of life of the four species are sufficiently dissimilar to account for their coexistence in the same watershed.

ACKNOWLEDGEMENTS

This study was supported by grants-in-aid of research from the National Research Council of Canada, and the Fisheries Research Board of Canada.

Dr. J. H. Gee provided invaluable advice and encouragement throughout the research and preparation of the thesis. I am also grateful to Dr. R. H. Green, Department of Zoology, and Dr. A. L. Hamilton, Freshwater Institute, Fisheries Research Board of Canada, who lent their expertise to constructive criticism of the manuscript. Field work was carried out with the conscientious assistance of R. Smith, R. Moshenko, K. Machniak and D. Bernard.

Special thanks must go to my wife, Sharron, who typed the manuscript and greatly enhanced the climate in which the study was carried out.

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I. INTRODUCTION

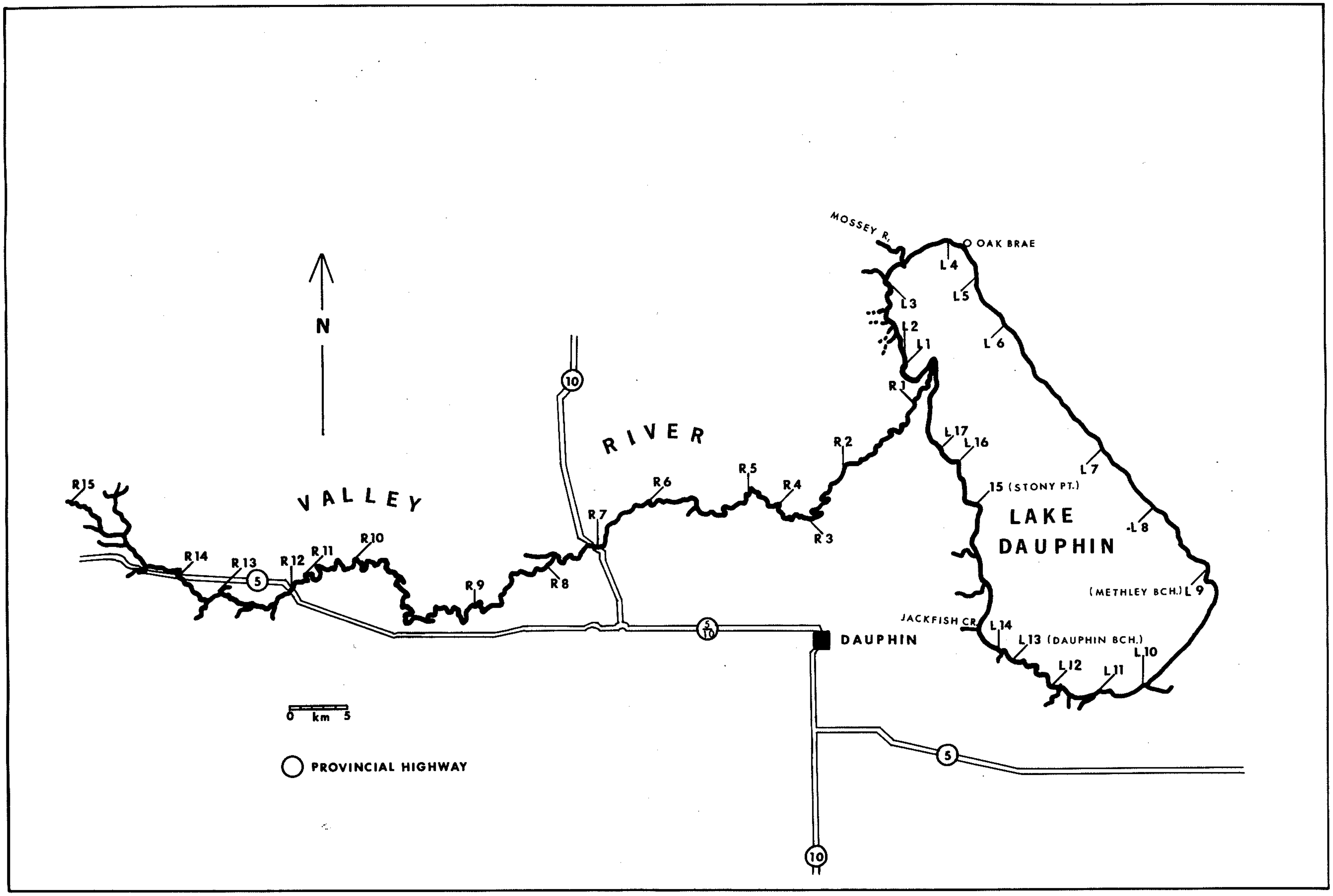
Darters are members of the sub-family Etheostominae within the Percidae. They are small, commonly bottom-dwelling fishes confined to fresh waters in North America east of the Rocky Mountains (Winn, 1958b). The American Fisheries Society (1970) lists 109 species, the majority of which occur only in the Mississippi River Drainage (Winn, 1958a). Moving northward, the group becomes less speciose. Only fifteen species have been reported from Minnesota (Carlander, 1941), and the number occurring in Manitoba is further reduced to five (Fedoruk, 1969). Four of these occur in Lake Dauphin and its tributary, the Valley River. They are: the central johnny darter, Etheostoma nigrum nigrum Rafinesque; the Iowa darter, Etheostoma exile (Girard); the river darter, Percina shumardi (Girard); and the northern logperch, Percina caprodes semifasciata (De Kay).

Knowledge of the life histories of johnny darter, Iowa darter, and logperch is incomplete, dealing mainly with reproduction. The life history of the river darter is virtually undescribed. Winn (1958a,b) examined intensively the reproduction of johnny darter, Iowa darter and logperch. Although emphasizing behaviour, he gave detailed accounts of the environment selected for spawning and the seasonal variation in abundance of darters in the spawning areas. Trautman (1957) gave brief descriptions of the environments in which all four species were collected. Information on the distribution of larval darters in lakes was obtained by Fish (1932) for johnny darter and logperch and by Faber (1967 and pers. comm.) for logperch only. Raney and Lachner (1943) and Speare (1960) worked on the age and growth of the johnny darter. Turner (1921) examined the food of johnny darter and logperch in lakes and streams, while Dobie (1959), Keast and Webb (1966) and Mullan, Applegate and Rainwater (1968) all examined the food of logperch.

This study was undertaken to describe the distribution, relative and absolute abundance and diet of the four species in the different kinds of environment available in Lake Dauphin and the Valley River. Although information was gathered through most of the ice-free period, emphasis was placed on late summer following reproduction, when most young-of-the-year were vulnerable to seining. It was hoped that the knowledge thus obtained would account for the coexistence of the four species of darters in the Lake Dauphin Watershed.

II. STUDY AREA

Lake Dauphin, shown in Fig. 1, is a large shallow lake. The shoreline eastward from the lake's only outlet, Mossey R., is a bench sloping gently into the water from a low ridge which runs parallel to the lake. The bench consists of sand and gravel, and is usually overgrown by grasses and willows to the water's edge. Stands of Scirpus commonly grow for a distance of 50 m or more offshore, as do beds of submerged plants, most often Potamogeton. From four kilometers beyond Oak Brae for 23 km southward, the bench ends sharply and drops to the beach at a 40-50° angle. The beach, 2-4 m wide, consists of granitic boulders interspersed with smaller stones, chiefly of limestone. In the water, the bottom consists of a belt of similar composition, 2 m or more in width, beyond which is sand or mud. The ridge parallelling the lake along this beach is higher and unbroken, so that no river flows into the eastern border of the lake. At the end of this stretch of boulder-beach just before Methley Beach the land again slopes gently into the water. The beach may consist of sand and gravel or of mud-flats, and the shoreline is often masked by dense stands of Phragmites, Scirpus and Carex, which grow out into the water. This continues to the middle of the southern border of the lake, where the land again rises slightly to produce a shoreline similar to that on the east side. However, here the bays usually have sand and gravel or sand beaches, as at Dauphin beach. Northward from Jackfish Creek the shoreline again resembles that in the southeast corner of the lake, but after 8 km the terrain of predominately boulder-beach is resumed. Northward along the western border of the lake extensive stands of Scirpus and Phragmites,



N
VALLEY
RIVER
LAKE DAUPHIN
MOSSEY R.
OAK BRAE
DAUPHIN
JACKFISH CR.
R15
R14
R13
R12
R11
R10
R9
R8
R7
R6
R5
R4
R3
R2
R1
L1
L2
L3
L4
L5
L6
L7
L8
(METHLEY BCH.) L9
L10
L11
L12
L13 (DAUPHIN BCH.)
L14
15 (STONY PT.)
L16
L17
5
10
0 km 5
PROVINCIAL HIGHWAY

particularly at the mouths of streams, interrupt the beaches, while the shores become less stony and gradually assume the features of shores found at the north end of the lake.

Most of the lake is 2-3 m in depth, the deepest sounding being only 3.4 m (Stewart-Hay, MS 1951). Except for the shoreline, the bottom of the lake consists solely of mud. Transparency is usually limited to 15-20 cm, making observation of fishes virtually impossible. Water level at the shores can fluctuate considerably, both seasonably and by the action of seiches.

Although only 10-15 m wide near its mouth, the Valley R. is the largest stream entering L. Dauphin. It originates primarily in the Duck Mountains to the west, but one major tributary drains the Riding Mountain area to the southwest. From the mouth to the station furthest upstream the river extends approximately 170 km. All but the lowest 10-12 km consist of a series of riffles and pools, although areas of riffles become less frequent in the lower reaches. Water level is high during spring runoff, but by late summer most riffles are dry or contain only narrow channels of flowing water. At that time the water level in the last 10-12 km varies like that in the proximal portion of the lake, depending on the direction and strength of wind. (In the case of a strong southerly wind the water may visibly flow upstream.) Except after a heavy rain, the water is clear to the bottom in all but the deepest pools.

In addition to the four species of darters, a number of other species of fishes, the majority of them cyprinids, are also found in the study area. These species are listed below according to whether they were more commonly caught in the river or the lake.

River	Lake
Hybognathus hankinsoni	*Coregonus artedii*
Notropis cornutus	*Esox lucius*
Rhinichthys atratulus	*Notropis atherinoides*
Rhinichthys cateractae	*Notropis hudsonius*
Semotilus atromaculatus	*Pimephales promelas*
Semotilus margarita	*Ictiobus cyprinellus*
Hypentelium nigricans	*Moxostoma* sp.
Catostomus commersoni	*Percopsis omiscomaycus*
Culaea inconstans	*Perca flavescens*
	Stizostedion vitreum vitreum

III. DISTRIBUTION AND ABUNDANCE OF DARTERS IN DIFFERENT ENVIRONMENTS

Part A: MATERIALS AND METHODS

i) COLLECTION OF FISHES

The distribution and abundance of darters in all lake and river environments was determined by seining. To maintain uniformity, only one kind of seine was used. This was a two-man seine with a sown-in bag (1.8 m x 1. 2 m - mesh diam. 0.32 mm). In strong current the seine was spread by one man below the area to be sampled. The second then drove fishes downstream into the seine by vigorously and systematically disturbing the substrate as he moved through the area. Then both men lifted the seine with a forward-sweeping motion. In areas of little or no current the seine was pulled from deep to shallow water, or in water of uniform depth. When this involved seining through plants or over large stones the seine was pulled in a jerky manner to avoid fouling the leadline.

Where estimates of the densities of darters were desired, a barrier-net was used to enclose small areas to be sampled, thereby preventing the escape of fishes during seining. In shallow areas of strong current enclosing was accomplished with the barrier-net or a combination of net and large stones, but the upstream end was usually left open. Blocking of the upstream end was often impractical, and escape against the current was thought to be minimal. In areas of slight or no current the barrier-net was set up to form a rectangle, one side of which was usually the river bank or lake shore. (See Plate 1.)

Repeated seine hauls, each covering most of the enclosed area,

Plate 1: Barrier-net set in typical fashion in Lake Dauphin.

were made until virtually all the darters were captured. If fewer than ten darters were caught in the first haul, seining was stopped when three consecutive hauls yielded no darters. If ten or more were caught on the first haul, seining was stopped after three consecutive hauls produced one or none.

When barrier-nets were used, only 20-50% of the darters caught were taken in the first seine haul, so that this method was considered at least twice as effective as seining without a barrier in capturing darters. Thus only samples of darters taken within barriers were used in estimates of density. Those samples are here called <u>complete samples</u>. Darters taken by sampling without the use of barrier-nets formed <u>incomplete samples</u>, which were nevertheless useful in determining the relative abundance of species in given environments (assuming that such seining was equally efficient in taking all four species).

Extensive attempts to capture darters smaller than 12 mm using a plankton net and stationary surber sampler proved unsuccessful.

ii) MEASUREMENT OF ENVIRONMENTAL VARIABLES

So that abundance of darters could be correlated with particular features of the environment, the following variables were measured immediately after each sample of fish was taken: area sampled, depth, aquatic plants, substrate, surface velocity (in the river) or height of waves (in the lake), and the time of day. Where vegetation was present it was identified, its density noted, and the percent of substrate covered by it estimated. The categories of particle size given by Longwell and Flint (1955) formed the basis for the following categories used to describe substrate: rubble (stones greater than 64 mm diam), pebble (2-64 mm diam), and fine substrate (particles less than 2 mm diam). For every sample the percent of bottom covered by each category of substrate was estimated. Mean surface water velocity was determined by timing the progress of a floating object for a distance of 0.45-1.5 m in both the slowest and fastest portions of the area sampled.

The following additional environmental variables, which tended not to vary within a station, were also measured: water temperature, transparency (taken by secchi disk), and weather conditions.

iii) SAMPLING IN 1968, AND THE DEFINITION OF BASIC ENVIRONMENTS TO BE SAMPLED IN 1969

In 1968, sampling was of an exploratory nature. That is, an attempt was made to determine what kinds of environment were available and to what extend they were populated by the four species of darters. All sampling was of the incomplete type. The pattern of sampling and the results obtained are given in Appendix 1. On the basis of those results, environmental variables which had the greatest observable effect on the numbers of darters were selected, and a potentially large number of combinations of environmental variables was reduced to a few 'basic' environments. These provided a guide for sampling in 1969, and were defined as follows for the lake:

a) Non-cover: An area lacking any type of cover (either plants or stones) over at least 75% of the bottom.

b) Plant-cover: An area having plants growing over at least 75% of the bottom. Included were beds of aquatic plants at depths of 0.15-0.9 m. growing in fine substrate sometimes interspersed with pebble or rubble, and with the substrate often partially or totally covered with plant debris. Areas containing the stout-stemmed emergent plants Scirpus and Phragmites were sampled only in May and June, when there was new growth and beds of non-emergent plants were scarce. The latter, including beds of Ranunculus and Potamogeton, were sampled after June. A broad-leaved species of Potamogeton was most frequently encountered. Often the plant beds were protected on the offshore side by extensive stands of Scirpus. Plate 2 shows an example of this environment.

c) Protected pebble-rubble: An area of shoreline which is protected from wave action by stands of emergent plants or by a point of land, and in which at least 75% of the bottom is covered by a mixture of pebble and rubble. In this environment, the bottom was usually gently sloping, and the seine was usually pulled onshore from a depth of 0.3-0.75 m. The ratio of pebble to rubble varied roughly in the range 4:1-1:4. Most stones were usually limestone fragments, and in most cases there was proportionately more pebble towards shore. From July on, the substrate was often covered with heavy growths of filamentous algae. Plate 3 shows an example of protected pebble-rubble environment.

d) Exposed rubble: An area of shoreline exposed to wave action, in which at least 75% of the bottom is covered by rubble. In this environment, the bottom sloped sharply, and the seine was usually pulled onshore from a depth of 0.6-1 m. The stones were largely granitic. From July on, the substrate at some stations was covered by heavy growths of filamentous algae. An example of this environment is shown in Plate 4.

'Basic' environments in the river were defined as follows:

a) Current: An area within which surface velocity reaches at

Plate 2: A submerged bed of Potamogeton, comprising plant-cover environment. Note extensive offshore stands of Scirpus, which protect this area from wave action.

Plate 3: Protected pebble-rubble environment, sheltered by a dense stand of Scirpus and Phragmites (in background).

3

2

Plate 4: Exposed rubble environment.

Plate 5: A complex of current and non-current environments in the river. Indicated by arrows are:

i) A stretch of current with a bottom of rubble.

ii) A uniform stretch of current with a bottom of fine pebble.

iii) An area of deep non-current with a bottom of rubble.

4

5

least 0.45 m/sec, and does not fall below 0.15 m/sec. The current environment was always part of a complex in which shallow, turbulent stretches of current alternated with quieter, deeper pools and channels. (See Plate 5.) Depths and surface velocities up to 0.4 m and 1.2 m/sec respectively were sampled in May, although rapids with greater flow were present. After May depth and surface velocity in all areas of current fell below those values. In some cases, the bottom was covered by pebble less than 2 cm diam, and the current quite uniform. More often the bottom was covered by rubble, so that flow was very irregular (sometimes ranging from 0.2 to 0.9 m/sec in a single sample). In the latter case, the substrate was sometimes covered with filamentous algae or moss. Many areas of current environment sampled were intermediate between the two types described above.

b) Shallow non-current: An area of which at least 75% is no more than 0.3 m in depth, and in which surface velocity does not exceed 0.15 m/sec. This environment was usually adjacent to a bank or sandbar. In many cases the bottom was covered by fine substrate, or pebble, or a mixture of both. Often the substrate was heavily silted and interspersed with sticks, other debris, or patches of aquatic plants.

c) Deep non-current: An area of which at least 75% exceeds 0.3 m in depth, and in which surface velocity does not exceed 0.15 m/sec. This environment included a wide range of situations in the river. The maximum depth sampled was 1 m, while substrate ranged from all fine substrate to mostly rubble. As in shallow non-current environment, the substrate was often heavily silted and interspersed with debris and patches of plants. (Dense plant-beds, which were seen in deep and shallow non-current environments, were not sampled in 1969.)

iv) SAMPLING PLAN FOR 1969

In 1969, sampling was designed primarily to produce: (a) estimates of densities of darters (based on complete sampling) in the basic environments during the late summer, following reproduction, which was thought to be the time of greatest probable demand on food resources, (b) estimates of the relative numbers of the four species (based on both complete and incomplete sampling) in basic environments throughout the year, and (c) distribution of river darter and logperch in the river at various times of the year.

Since very few darters of any species were caught in non-cover environment in the lake during 1968, this environment was not sampled in 1969.

There were six sampling periods. The first five, beginning with early May, were at three week intervals, the fifth period lasting from July 27 to August 4 and representing late summer, following reproduction. The final sampling period was in September.

In early August complete sampling to obtain estimates of density was carried out at three stations for each basic environment. When it appeared desirable to confirm the absence of a particular species, and/or collect additional specimens, a large incomplete sample was taken as well. In addition, incomplete samples were taken at three other stations for each environment, so that samples from a total of six stations were available for study of relative numbers of the four species. During the remaining collection periods, where possible, each lake environment was sampled at three or more stations. Sampling was complete at one or more of these stations, and incomplete at the rest. During the first three periods, proportionately more sampling was done in the river than later on. The purpose of this was to find the upstream limits of river darter and logperch while they were relatively abundant in the river.

Details concerning dates, stations visited, and environments sampled at each station are given in Appendix 2.

v) AGE DETERMINATION

It was considered possible that darters of the same species, but belonging to different age classes,might be found in different environments. Therefore, darters caught during each collection period were aged by construction of length-frequency histograms. Separation of age classes was usually limited to defining, where possible, the youngest class present. Length-frequency distributions, with details concerning age class separation, are given in Appendix 3.

Fishes in their first summer of growth (young-of-the-year) are called age 0. Lumping of all older fish with an age class is indicated by a + sign.

Part B: RESULTS

i) DENSITIES OF DARTERS IN THE BASIC ENVIRONMENTS DURING THE LATE SUMMER, FOLLOWING REPRODUCTION (1969)

The first stated purpose for sampling in 1969 was to provide estimates of density for the four species in basic environments during the period of probable maximum demand on food resources. During early August mean densities were obtained by complete sampling for the basic river and lake environments. In examining these densities, lake and river environments will be considered separately, as will age 0 and age 1+ fishes.

Fig. 2 A shows mean densities of age 0 darters in lake environments. It is evident that:

i) In all three environments sampled, density of age 0 Iowa darter was far greater than that of age 0 individuals of the other species.

ii) In plant-cover age 0 Iowa darter reached their highest density.

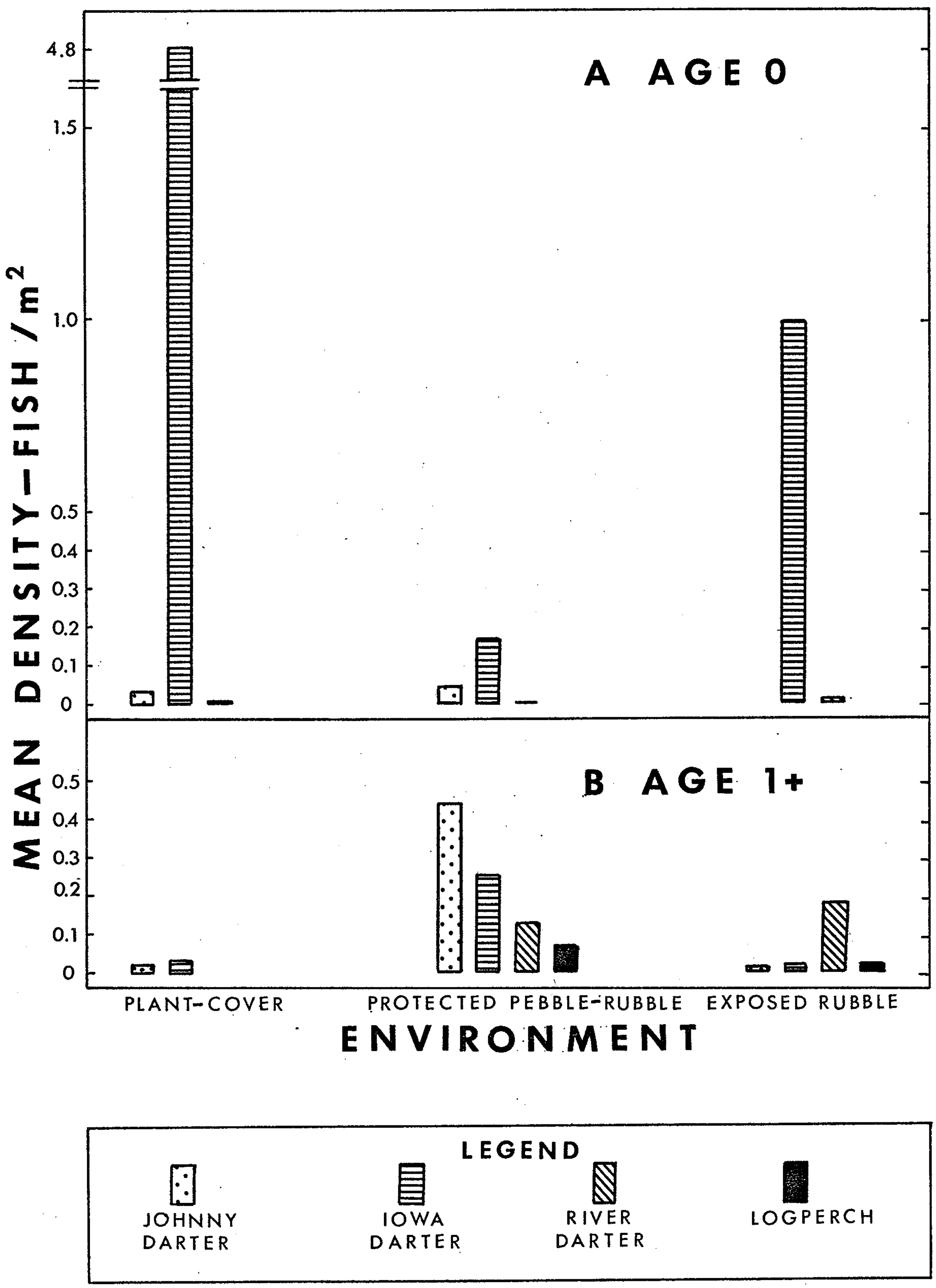
iii) In protected pebble-rubble age 0 Iowa darter attained their lowest density, while age 0 individuals of the other species combined reached their greatest density.

Mean densities of age 1+ darters in lake environments appear in Fig. 2 B. Considering each environment in turn, one can see that:

i) In plant-cover densities of age 1+ individuals of all four species were either very low or nil. The greatest density was obtained for Iowa darter, but this was insignificant when compared to that of age 0 fish of the same species.

ii) In protected pebble-rubble considerable overlap among age 1+ individuals of all four species occurred. The greatest density was that of johnny darter, with Iowa darter next in abundance.

iii) In exposed rubble age 1+ individuals of all four species were present, but river darter reached a far greater density than the others.



A AGE 0
B AGE 1+
MEAN DENSITY—FISH / m²
4.8
1.5
1.0
0.5
0.4
0.3
0.2
0.1
0
PLANT-COVER
PROTECTED PEBBLE-RUBBLE
EXPOSED RUBBLE
ENVIRONMENT
LEGEND
JOHNNY DARTER
IOWA DARTER
RIVER DARTER
LOGPERCH

Fig. 3 shows the mean densities of age 0 darters in river environments. Johnny darter were the only age 0 darters taken in complete sampling. Their density was lowest in current, and greater in shallow than in deep non-current.

The mean densities of age 1+ darters in river environments are given in Fig. 3 B. Except for a single logperch taken in deep non-current, johnny darter were also the only age 1+ darters taken in complete sampling. Their density was lowest in current, and, unlike that of age 0 individuals, was greater in deep than in shallow non-current.

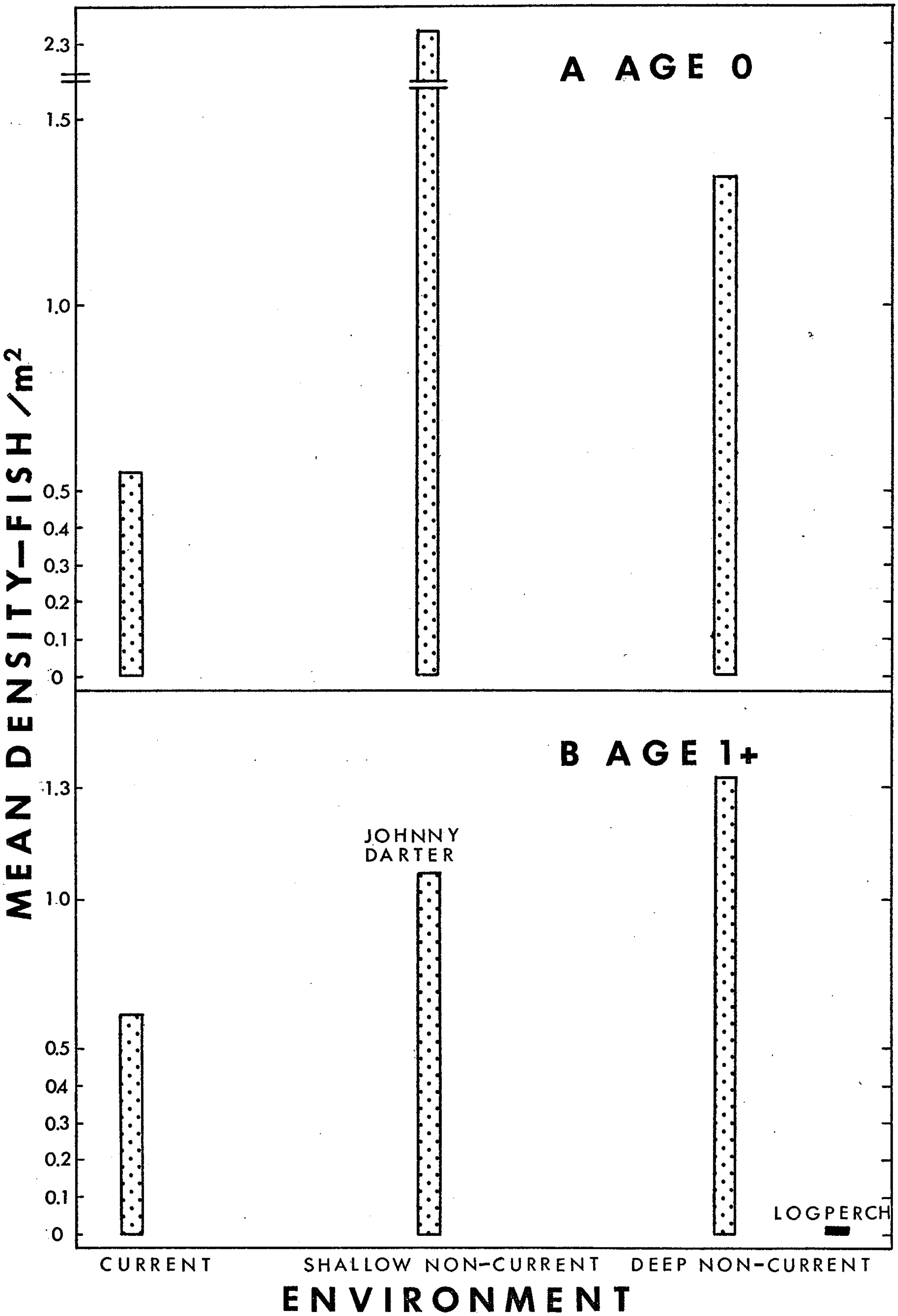
In general, the variation in densities obtained for the same environment at different stations was high. But this does not negate differences among environments. Details concerning variation in density are given in Appendix 4.

In summary, density estimates show that during early August:
(i) In each lake environment the highest density of age 1+ darters was attained by a different species, (ii) The greatest overlap of the four species occurred in protected pebble-rubble, and (iii) in the river virtually all darters were johnny darter.

ii) THE RELATIVE NUMBERS TAKEN OF THE FOUR SPECIES OF DARTERS IN BASIC LAKE ENVIRONMENTS THROUGHOUT 1969

The second stated purpose of sampling in 1969 was to determine the relative abundance of the four species in the basic environments throughout the year, using numbers obtained in both complete and incomplete sampling. The inclusion of incomplete samples for early August will also reinforce the picture of species-composition available from density estimates for that important period. However, it would be of little

Figure 3: Mean densities of darters in three river environments during early August, 1969. These means were obtained in the same way as those for lake environments.


A AGE 0
B AGE 1+
MEAN DENSITY—FISH /m²
2.3
1.5
1.0
0.5
0.4
0.3
0.2
0.1
0
1.3
JOHNNY DARTER
LOGPERCH
CURRENT
SHALLOW NON-CURRENT
DEEP NON-CURRENT
ENVIRONMENT

value to consider relative numbers of darters in river environments because of the preponderance of johnny darter throughout the year. But the relative numbers of darters caught in the three lake environments sampled throughout 1969 are shown in Fig. 4. (The ratios of actual numbers caught are given in Appendix 5.) The species-composition in different environments during the same period may be compared visually with reference to Fig. 4.

As shown in Figs. 4 A and B, during early and late May plant-cover and protected pebble-rubble were represented only by single stations. Also, during early May very few darters of any species were caught in exposed rubble, despite intensive sampling in that environment. Nevertheless, it appears that:

i) In plant-cover only Iowa darter were present.

ii) In protected pebble-rubble environment Iowa darter were the predominant species.

iii) In exposed rubble the species composition changed from slight predominance of Iowa darter over river darter in early May to heavy predominance of river darter in late May.

For June and early July, it is evident that:

i) In plant-cover johnny darter were present, although Iowa darter continued to be the dominant species.

ii) In protected pebble-rubble there was considerable overlap in the distribution of all four species, but river darter were predominant.

iii) In exposed rubble river darter were quite predominant. The change in predominant species in protected pebble-rubble since May was not due to a decreased emphasis on the single station at which this environment

Figure 4: Relative numbers of darters caught in three lake environments through 1969. In each environment, the number caught of the predominant species, given over the corresponding bar, is converted to 100, and the numbers caught of the other species are accordingly transformed.

A: Early May

B: Late May

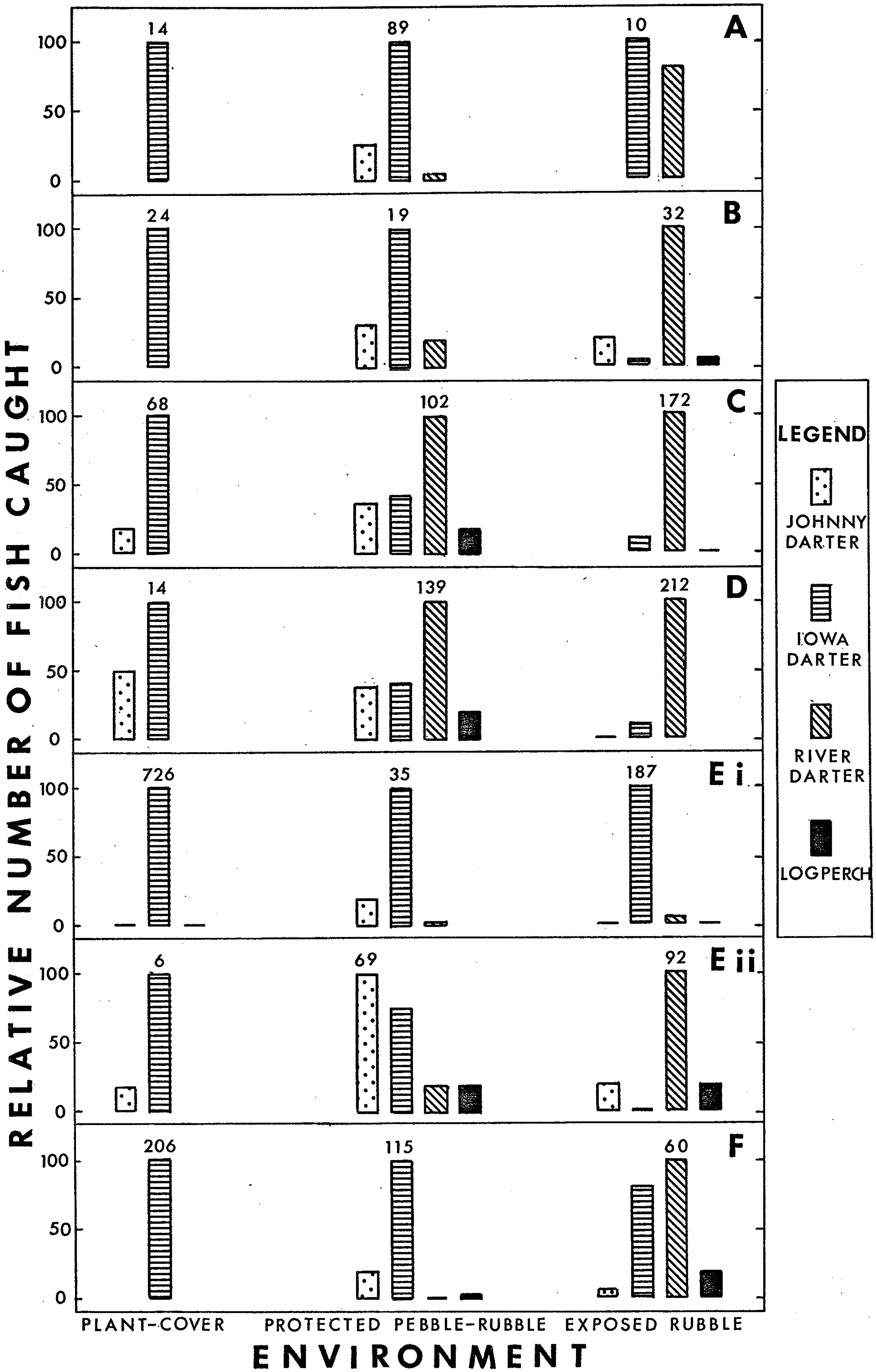
C: June

D: Early July

E: i: Early August, age 0

E: ii. Early August, age 1+

F: September



RELATIVE NUMBER OF FISH CAUGHT
ENVIRONMENT
PLANT-COVER
PROTECTED PEBBLE-RUBBLE
EXPOSED RUBBLE
A
B
C
D
E i
E ii
F
14
89
10
24
19
32
68
102
172
14
139
212
726
35
187
6
69
92
206
115
60
100
50
0
LEGEND
JOHNNY DARTER
IOWA DARTER
RIVER DARTER
LOGPERCH

was sampled during May. Since the ratio of numbers caught at that station alone during June was J.D. 28 : I.D. 12 : R.D. 55 : L. 1, the decrease in abundance of Iowa darter and increase in abundance of river darter at that station was even more marked than Fig. 4 C indicates.

For the important early August collection period, relative abundance of age 0 and age 1+ darters were examined separately. For age 0 darters it is evident that:

i) In plant-cover Iowa darter were virtually the only age 0 darters present.

ii) In both stony shore environments Iowa darter were also quite predominant.

For age 1+ darters, it is evident that a different species was predominant in each environment. This is described as follows:

i) In plant-cover Iowa darter were predominant, although present in insignificant numbers, compared to age 0 fish of the same species.

ii) In protected pebble-rubble johnny darter and Iowa darter were the most abundant species, the first being slightly predominant. River darter and logperch were also present, so that overlap in distribution of all four species occurred.

iii) In exposed rubble river darter were quite predominant.

Fig. 4 F shows the relative abundance of the four species in September. It can be seen that:

i) In plant-cover Iowa darter were the only species present.

ii) In protected pebble-rubble Iowa darter were also predominant, although all four species were present.

iii) In exposed rubble river darter were slightly predominant over Iowa darter, while the other species were also present.

The ratios of numbers of darters caught in different lake environments during the same period may also be compared statistically. The ratios in two environments at a time were compared by computing chi-square for 2 x n contingency tables. (Where only one species was present in either environment, no comparison was made.) According to total chi-square values obtained, all pairs of ratios differed by more than chance. The accuracy of about half of these total chi-square values was reduced by low expected values (where more than 20% of expected values were less than 5). But, with one exception, all total chi-square values were far greater than critical, leaving no doubt that the ratios compared actually differed. In other words, during any collection period the species-composition of darters in the three lake environments was quite different. (Both individual and total chi-square values are listed in Appendix 5.)

iii) DISTRIBUTION OF DARTERS IN THE RIVER

The distribution of johnny darter and Iowa darter in the river can be described simply. Johnny darter, both in 1968 and 1969, were present throughout the year at all stations visited, while Iowa darter were rare, with only seven caught in 1969.

By contrast, river darter and logperch varied seasonally in abundance and were limited in their upstream distribution. The third stated purpose of sampling in 1969 was to determine the distribution of river darter and logperch in the river at various times of the year. However, presumably due to less favourable climatic conditions, catches of these species in the river in 1969 were poorer than those in 1968. Thus results from both years are included here.

Table 1 shows the distribution of river darter and logperch caught in the river in June, 1968 and throughout 1969. The following points are evident:

i) Both species were restricted in their upstream distribution. In both years logperch were found to penetrate 94 km from the stream mouth, despite the inclusion of additional stations in 1969. River darter in June, 1968 and in 1969 penetrated only 38 km from the stream mouth, although a single fish was caught 70 km upstream in August, 1968.

ii) The greatest numbers of both species in 1969 were caught in late May. After that period their numbers in the river declined sharply, until none were caught in September.

iii) Almost all fish caught during late May, 1969 and June 1968 were sexually mature, of age 2+. Most of these were ripe, the remainder partially or totally spent.

iv. Aggregations of river darter occurred only in the two stations closest to the stream mouth, up to 22 km, while aggregations of logperch occurred up to 70 km from the stream mouth.

In addition, it should be noted that, except for river darter at station R 1, both species were usually caught in current environment. Most of the large numbers caught at stations R 2 and R 4 in June, 1968 were taken from relatively small areas of current with a bottom of fine pebble.

From the preceeding observations, it can be concluded that the presence of river darter and logperch in the river was primarily restricted to the spring spawning activity of mature adults, of which logperch

Table 1: Distribution of river darter and logperch caught in the river in June, 1968 and throughout 1969. In the case of complete sampling, only fishes caught in the first seine haul are counted. Most logperch caught in late May, 1969 were released after their number was recorded. The left-to-right decrease in distance from the lake is equivalent to the west-to-east flow of the river. The names of the four species in this and succeeding tables are abbreviated as follows:

J. D.	johnny darter
I. D.	Iowa darter
R. D.	river darter
L.	logperch

Station (R)	15-10	9-5	4	3	2	1	% mature
km from lake	170-125	94-44	38	34	20	8	
	Area sampled and no. darters caught						
Early May, 1969							
Area-m^2	371	89	32	79	83	93	
No. R.D.	0	0	0	0	0	0	
L.	0	9	0	0	1	0	100
Late May, 1969							
Area-m^2	199	198	132	100	25	167	
No. R.D.	0	0	0	0	0	30	100
L.	0	22	19	0	4	1	91
June, 1968							
Area-m^2	47	142	58	111	47	98	
No. R.D.	0	0	4	0	28	77	98
L.	0	10	41	4	42	17	95
June, 1969							
Area-m^2	126	147	74	101	104	93	
No. R.D.	0	0	0	0	0	2	100
L.	0	2	1	0	6	1	100
Early July, 1969							
Area-m^2	0	68	39	84	61	89	
No. R.D.		0	0	0	0	3	100
L.		1	2	0	2	0	60
Early Aug., 1969							
Area-m^2	154	152	80	56	89	89	
No. R.D.	0	0	1	0	0	0	100
L.	0	1	2	0	2	0	100

September, 1969

Extensive sampling ($506m^2$) yielded no R.D. or L.

penetrated the furthest upstream. It also appears that riffles with a bottom of fine pebble were a preferred spawning environment for both species.

iv) WHEN AND WHERE AGGREGATIONS OF RIPE DARTERS WERE FOUND

The occurrence of aggregations of ripe darters suggests where spawning might occur. Since darter eggs adhere strongly to the substrate (observed in the laboratory), the locale of spawning becomes the place of emergence of larvae. In a discussion of the distribution of young-of-the-year, that would be the logical starting point.

The presence of ripe river darter and logperch in the river in spring has been described above. Also in the river, during May johnny darter were caught in both current and non-current at all stations visited. In the lake ripe darters of all species except logperch were found. Small numbers of ripe johnny darter were caught in protected pebble-rubble from early May until June. Aggregations of ripe Iowa darter were collected from early May until early July in plant cover and protected pebble-rubble, and a few were taken in exposed rubble. Aggregations of ripe river darter were found from late May until early July in protected pebble-rubble and exposed rubble. Particularly high concentrations of ripe adults of that species, with a few immature fish, occurred at Stony Point (station L 15).

v) DIURNAL VARIATION IN ABUNDANCE OF DARTERS IN LAKE ENVIRONMENTS

It was considered possible that one or more species of darters might be involved in a diurnal pattern of onshore-offshore migration in the lake. This would affect the interpretation of data on distribution and abundance obtained only in daytime (as was all data used in preceeding parts of this presentation). To examine this possibility, two sets of day-night complete samples were made during the important early August period in 1969. Protected pebble-rubble environment was sampled at station L 2, and exposed pebble-rubble (not a basic environment) was sampled at station L 9.

A paired t test was used to examine the differences between day and night abundance of johnny darter at station L 2 and or river darter at stations L 2 and L 9 combined. The numbers of age 1+ darters caught in corresponding day and night samples are listed in Table 2. At night there were mean increases of ten johnny darter and 4.5 river darter per sample. These increases were significant at 5% and 1% levels respectively. Because of insufficient numbers, it was not possible to test for day-night differences in abundance for age 0 darters, or for age 1+ Iowa darter and logperch.

The nighttime increases thus obtained should not have been the result of increased vulnerability to capture, as might be expected under conditions of reduced visibility. Presumably the barrier-net method of sampling ensures that, regardless of vulnerability to capture, ultimately most darters are caught. This assumption is supported by the observation that larger catches of johnny darter were usually obtained in the river (high transparency) than in the lake (low transparency), while the proportion of fish caught in the first seine haul was generally lower in the river than in the lake.

These results suggest that, during early August, johnny darter and river darter were more numerous in protected pebble-rubble than was indicated by daytime sampling. However, this does not alter the main

Table 2: Numbers of age 1+ darters caught in corresponding day and night samples at two lake stations during early August, 1969. Three complete samples of approximately 15 m^2 were taken in daytime at each station, and then duplicated at night, their exact location having been marked. Environments sampled were protected pebble-rubble at station L 2 and exposed pebble-rubble at station L 9.

d day n night

Station	Sample Location	No. of darters caught							
		J.D.		I.D.		R.D.		L	
		d	n	d	n	d	n	d	n
L 2	(a)	15	29	0	1	0	4	1	0
	(b)	12	22	0	0	0	2	1	0
	(c)	12	18	0	0	0	6	0	0
L 9	(a)	0	0	0	0	4	5	0	1
	(b)	0	0	0	0	3	9	0	1
	(c)	0	0	0	0	6	14	1	2

points for this period and in this environment, which are that (i) johnny darter were the most abundant darters in protected pebble-rubble, and (ii) the greatest amount of distributional overlap among species of darters occurred here.

IV. LABORATORY EXPERIMENTS

1. ENVIRONMENT PREFERENCE

In the field the abundance of darters was correlated with certain environmental variables. These were: (a) the presence or absence of cover, and (b) exposure to turbulence, caused by wave action, in the lake and current in the river. To provide a choice between current (or turbulence) and quiet water in the laboratory was thought to be too difficult to be practicable for this study. The experiment described here was thus designed to test the hypothesis that darters preferred environments with or without cover, and with a particular kind of cover.

Part A: MATERIALS AND METHODS

i) SOURCE OF EXPERIMENTAL FISHES

Fishes were obtained during August 17 and 18, and September 20, 1969. Johnny darter were taken from the Valley R., and the others from L. Dauphin. On each date, approximately 20 individuals of age 0 and 20 of age 1+ were collected for each species.

ii) HOLDING CONDITIONS

Separate areas were provided for holding and testing of experimental fishes. When not being tested, members of each group were kept in separate, bare 22 and 45 l aquaria equipped with air-stones and filters. Water temperature remained at 21°C, except for brief periods every second day when it was lowered to 10°C by changing the water. Twelve hours of daylight were provided. All fishes were fed frozen brine shrimp and small euchitraed worms twice daily.

iii) EXPERIMENTAL PLAN

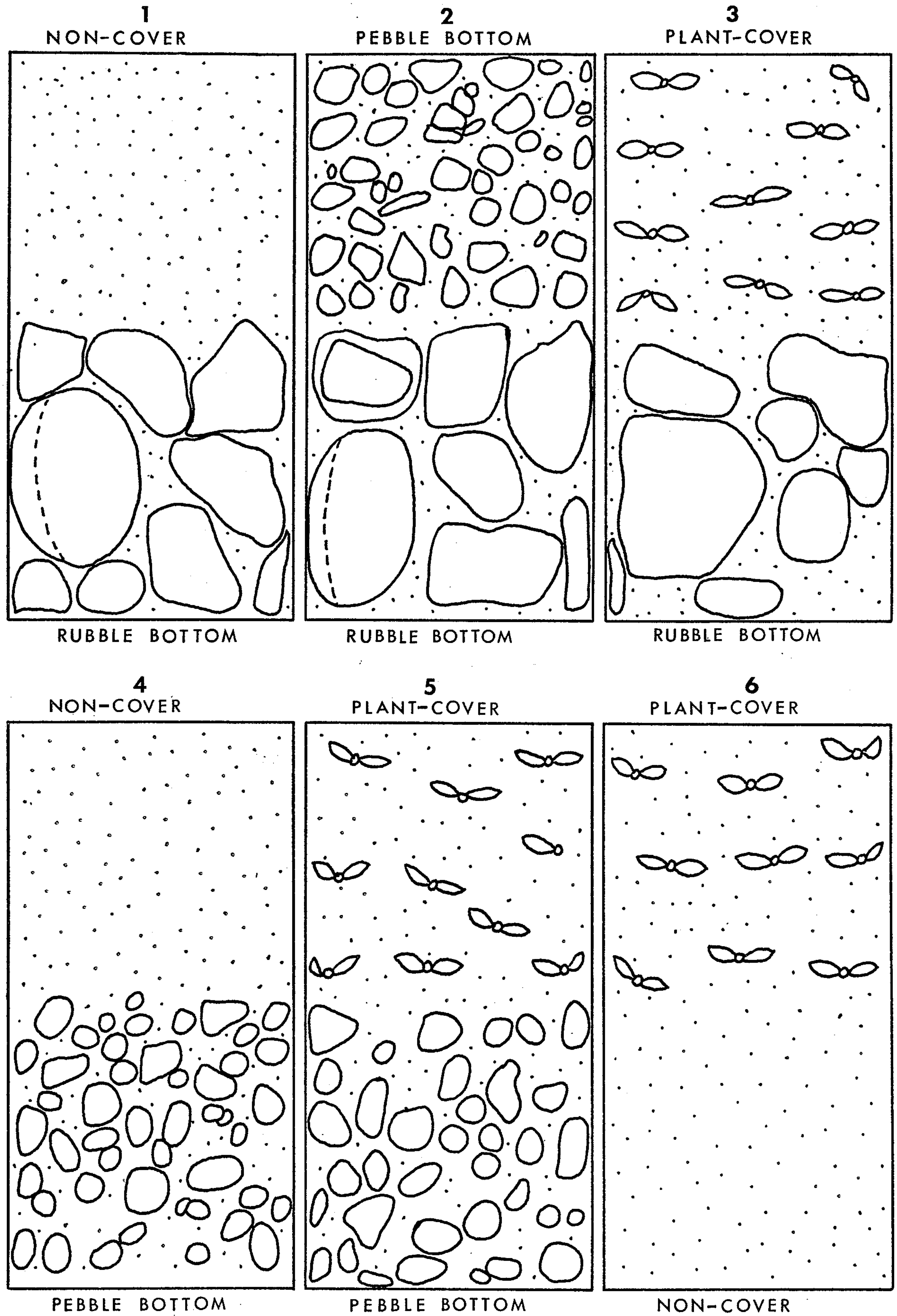
Age 0 and age 1+ darters of each species were offered a choice of four distinct, simulated environments. These were: (i) non-cover (sand bottom only), (ii) plant-cover, (iii) pebble bottom, and (iv) rubble bottom. Individual fish were allowed to choose between two of these environments at a time. Statistical analysis of a sufficient number of individual choices would then provide inferences about preference, or lack of preference, by the age class and species tested. Since two age classes of each species were tested for six combinations of environments, a total of 48 separate tests were carried out.

(iv) APPARATUS FOR ALLOWING A CHOICE

One environment was simulated in each half of a 45 l aquarium 51 cm x 27 cm x 31 cm. The entire bottom was covered with washed, coarse silica-sand to a depth of 2 cm, and other material was then added to each half, depending on the environment simulated. Plants used were of a broad-leaved species of Potamogeton taken from L. Dauphin and L. Manitoba. The actual layout for all six combinations of environments is reproduced in Fig. 5.

The testing locale was a small, black-curtained space in a controlled environment room, held at 17°C, adjoining the holding area. Six aquaria, each containing a different pair of environments, were set in a row 20 cm off the floor within this space. Uniformly strong illumination was provided by two 150 w floodlamps set above and on either side of the row of aquaria, while the remainder of the room was darkened. Three observation slits were cut in the front curtain and

Figure 5: Combinations of simulated environments used in the environment preference experiment (top view, 1/5 actual size). Spaces under the largest stones are indicated by broken lines.


1
NON-COVER
RUBBLE BOTTOM
2
PEBBLE BOTTOM
RUBBLE BOTTOM
3
PLANT-COVER
RUBBLE BOTTOM
4
NON-COVER
PEBBLE BOTTOM
5
PLANT-COVER
PEBBLE BOTTOM
6
PLANT-COVER
NON-COVER

duplicate dummy slits were cut in the back curtain. From these observation slits the fish were watched through the water surface and front wall of each aquarium. The sides of each aquarium were covered with black cloth, so that its contents were isolated from those of adjoining aquaria. Flaps were also cut below each observation slit to allow introduction of fish through the curtain.

v) PROCEDURE

Before testing fish in simulated environments, a control experiment was carried out, in which the bottoms of the six aquaria were left bare. This was to determine if the fish were biased toward the front or back portions of the aquaria.

For each of the six aquaria, a fish was selected randomly from among the eight experimental groups. At 60 second intervals, these fish were introduced through the flaps in the front curtain and released approximately in the middle of the aquaria. The position of each fish was then noted at exact 6 min. intervals for 1 hr. If the fish was on the midline, the position of its anterior end was noted; also, any crossing of the midline 15 sec. before or after the instant of observation was noted. After the last observation was completed, the front curtain was moved aside and the fish removed to the holding aquaria.

In the control portion of the experiment, this procedure was repeated for a total of eight runs. Every second run was preceded by several minutes' aeration of the six aquaria.

Chi-square tests showed that, when all observations in the control runs were lumped, the darters were found significantly more often (5%

level of significance) in the far end of the aquaria. However, when observations for the first and second half hour were examined separately, the fishes were found significantly more often in the far end only during the first half hour. Since the fishes appeared to require the first half hour to adjust to their new conditions, the one hour observation period was retained, and the determination of choice was based on the last half hour.

However, a separate examination of the response of each species showed that, even in the last half hour, river darter consistently chose the far end of the aquaria (11 of 12). Although this species was tested in the experimental runs, similar responses were again obtained (See Appendix 6). Thus river darter will not be considered in the section on experimental results.

Modifications in procedure for the experimental runs involved only the way in which fishes to be tested were selected. For each of the six aquaria, different individuals of the same group were used in consecutive runs, until a sufficient number of choices had been made to produce a result. Then a fish of another group not being tested was introduced. This procedure was repeated until a result was achieved for all of the 48 individual tests required.

If a result was not reached by the time sampling without replacement had exhausted the supply of fish in a group, then the testing was continued by sampling with replacement.

vi) DETERMINATION OF CHOICE AND RESULT

Since each fish was observed at 6 min. intervals for 1 hr., its position was recorded five times in the last half hour. A fish made a choice for one half of the aquarium if: (a) it was in the same half for at least four of the last five observations, or (b) it was in the same half for the last two observations, provided it had not crossed the mid-line within 15 sec.of either of those observations. If neither condition was met, the fish made no choice.

The procedure was based on a closed sequential design constructed by Cole (1962). This type of test, in which testing with individuals is continued until a result is reached, seemed more advantageous than tests with a fixed sample size. Since as few as 12 fish were available for some groups at the beginning of the experiment, the minimum path length of seven individual tests to reach a result was very attractive. In addition, Cole's design was constructed to provide more than customary protection against type I error (in this case, finding a preference where there was none). If a fish made no choice, this was the same as a tie in Cole's experiment and was not counted. The result indicated that the group (species and age class) tested preferred one environment (5% level of significance), or showed no preference.

PART B: RESULTS

It became necessary to switch to sampling with replacement, in order to reach a result, in 35 of the 48 tests. However, in these cases, the ratios of choices made before the start of sampling with replacement did not contradict the eventual ratios and results. (Both ratios are given in Appendix 6.)

For age 0 darters, the results, together with the percentage of choices made for each environment, are shown in Fig. 6. An overall view of results for johnny darter, Iowa darter, and logperch indicates that the combinations of environments offered can be split into two groups of three: those in which non-cover was one of the environments, and those in which both environments contained some form of cover.

In combinations involving non-cover, age 0 darters generally showed preference for the other environment. Iowa darter provided the single exception by displaying no preference between non-cover and rubble bottom. Where some form of cover was available in both environments, the majority of tests indicated no preference. Exceptions were preference by logperch of rubble bottom over pebble bottom and plant-cover, and preference by johnny darter of pebble bottom over plant-cover environment.

As shown in Fig. 7., age 1+ darters generally behaved in the same manner as did age 0 individuals. Where one of the environments offered was non-cover, they usually preferred the other environment. The only exception occurred when Iowa darter showed no preference between non-cover and pebble-bottom. Where both environments contained cover, there was usually no preference. Iowa darter and logperch provided the exceptions by displaying preference for plant-cover over pebble-bottom.

The first part of the hypothesis, that darters prefer environments either with or without cover, is confirmed for johnny darter, Iowa darter and logperch, since environments with cover were almost always preferred over environments without cover. However, there appears to be little support for the hypothesis that darters prefer particular kinds of cover.

Figure 6: Test results, and percentage of <u>choices</u> made in each environment, for age 0 johnny darter, Iowa darter and Logperch in environment preference experiments. Each bar represents the total number of <u>choices</u> made in a test (individual experiment), and its position indicates the percentage of <u>choices</u> made for environments in each end of the aquarium. A line at one end of the bar indicates preference for the environment in that end (5% level of significance).

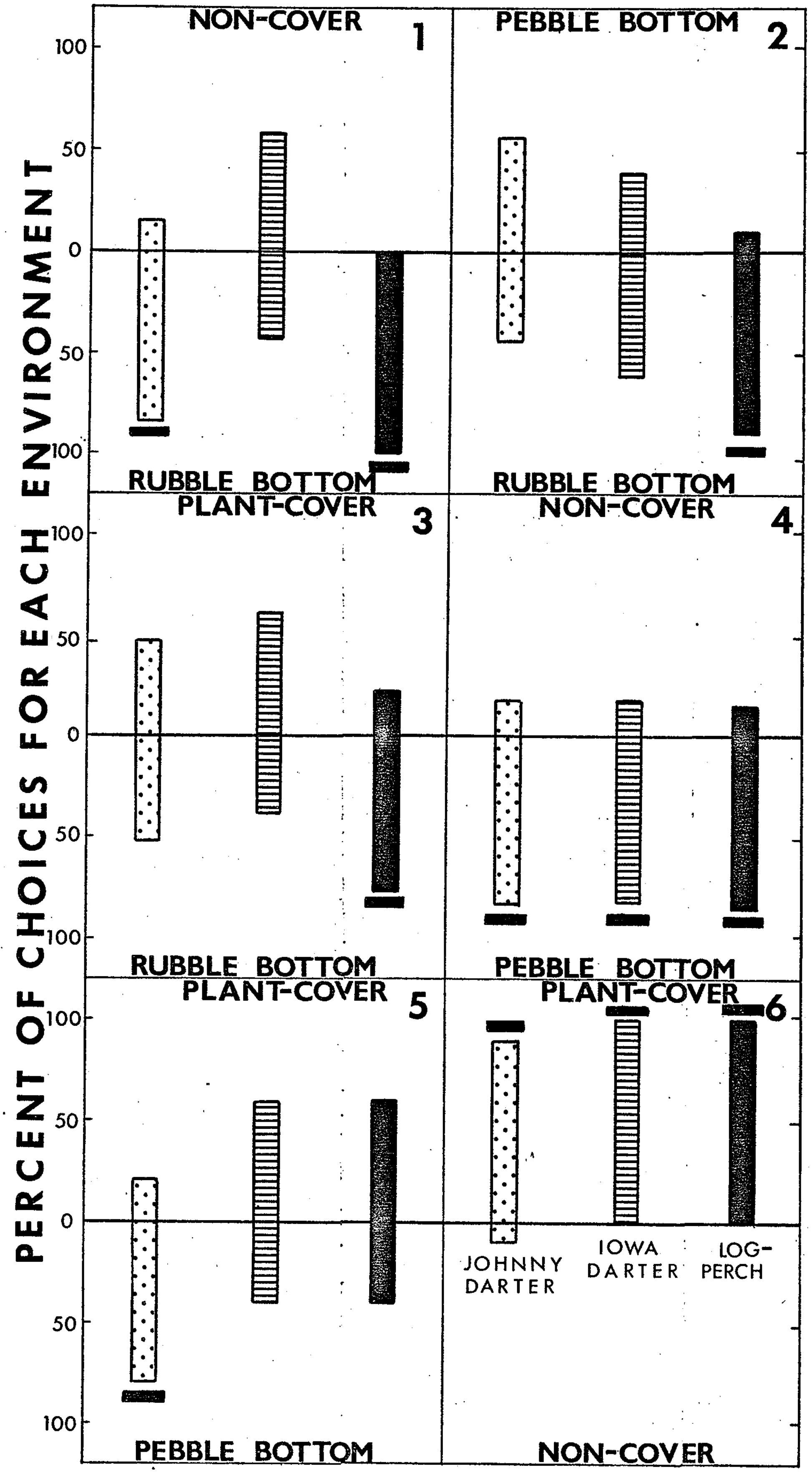
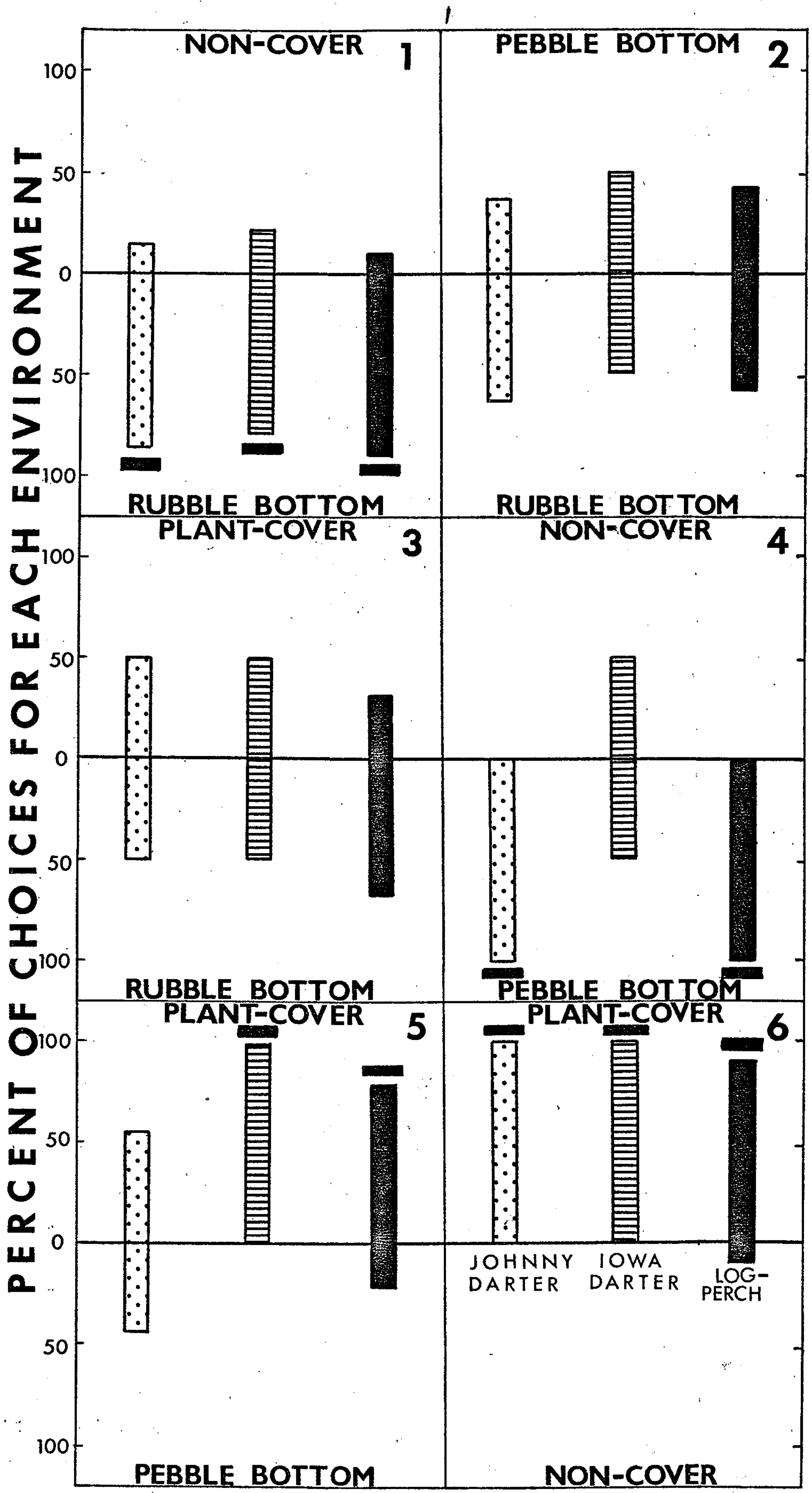

PERCENT OF CHOICES FOR EACH ENVIRONMENT
NON-COVER
1
RUBBLE BOTTOM
PEBBLE BOTTOM
2
RUBBLE BOTTOM
PLANT-COVER
3
RUBBLE BOTTOM
NON-COVER
4
PEBBLE BOTTOM
PLANT-COVER
5
PEBBLE BOTTOM
PLANT-COVER
6
NON-COVER
JOHNNY DARTER
IOWA DARTER
LOG-PERCH
100
50
0
50
100

Figure 7: Test results, and percentage of choices made in each environment, for age 1+ darters in environment preference experiments. Each bar represents the total number of choices made in a test (individual experiment), and its position indicates the percentage of choices made for environments in each end of the aquarium. A line at one end of the bar indicates preference for the environment in that end (5% level of significance).


PERCENT OF CHOICES FOR EACH ENVIRONMENT
NON-COVER
1
RUBBLE BOTTOM
PEBBLE BOTTOM
2
RUBBLE BOTTOM
PLANT-COVER
3
RUBBLE BOTTOM
NON-COVER
4
PEBBLE BOTTOM
PLANT-COVER
5
PEBBLE BOTTOM
PLANT-COVER
6
NON-COVER
JOHNNY DARTER
IOWA DARTER
LOG-PERCH
100
50
0
50
100

2. LABORATORY REARING OF LARVAL DARTERS

The swimming behaviour of the larvae of the four species was observed in order to gain some insight into their probable distribution in the field.

Part A: MATERIALS AND METHODS

i) SOURCE OF EGGS AND HATCHING SUCCESS

Fertilized eggs were obtained in two ways. Approximately 200 eggs were taken from a large nest of johnny darter in the Valley R. on May 25, 1969. On May 28, mature Iowa darter and river darter were taken from L. Dauphin, and mature logperch from the Valley R. In the laboratory, on May 29, eggs were stripped from these fish and artificially fertilized. On June 27 eggs were again obtained from Iowa darter and river darter. In each case, from 70 to 150 eggs per species were obtained.

More than 100 johnny darter emerged on May 31. River darter and logperch emerged on June 6, nine days after fertilization, and Iowa darter emerged two days later. Sixty to 100 larvae were obtained for the last three species. In the second group approximately 50 river darter emerged July 5, and as many Iowa darter emerged the next day.

ii) HOLDING CONDITIONS FOR EGGS AND LARVAE

Eggs were held in small baskets suspended in large, strongly aerated tanks. Water temperatures ranged from 19 to 21°C. Dead and fungus-covered eggs were removed daily.

Within several hours after hatching, larvae of each species were removed to separate, gently aerated, 22 l aquaria in a controlled environment room. This room was kept at 17°C, with 12 hr. of daylight. All larvae were fed approximately three times daily, but the food offered depended on the response of the larvae. Johnny darter readily took powdered Tetramin flakes, and were fed only that. Iowa darter were fed powdered Tetramin flakes and Longlife liquid fry food with some success. These foods, and washed Longlife live brine shrimp nauplii, were offered to river darter and logperch with very little success. Excess food was siphoned off the bottom regularly. Except for replacement of water lost through this, the water was not changed.

iii) OBSERVATIONAL PROCEDURE

To keep track of their activity, the larvae were observed daily from emergence until the last died or no further changes were expected. Up to ten larvae of each species were kept in four well-lighted observation aquaria. During the daily observation periods, the larvae of each species were watched for several minutes, and notes made on their swimming behaviour and position in the aquaria.

Part B: RESULTS

The observations on swimming behaviour of larvae can be summarized for each species in turn.

Newly-hatched johnny darter lay still, or moved about slightly, on the bottom. After a few hours they became fairly active. When disturbed they usually swam upwards with a jerky motion, but quickly settled back to the bottom. Undisturbed movement was confined to occasional short darts along the bottom. This behaviour continued without change until June 17, when the fish were killed, the largest having reached 13 mm in total length.

The swimming behaviour of larval Iowa darter was more complex. Immediately after hatching they lay motionless on the bottom, unless disturbed. After two or three hours they became intermittently active, swimming at all levels. After two days, by the time the yolk sac had been lost, they swam about almost constantly by day.

These larvae made two kinds of swimming movements. Occasional caudal thrusts of large amplitude produce rapid forward motion which was similar to, although smoother than, that of johnny darter. Continuous, rapid, small amplitude caudal oscillations kept the larvae off the bottom and provided comparatively slow forward motion. While swimming continuously in this way, the larval Iowa darter maintained a horizontal attitude during the first few days. This gradually changed to an acute, head-up position until, by August 2, the single surviving fish (12 mm) swam mainly at a close-to-vertical angle. At the same time, swimming became increasingly confined to the bottom half of the aquarium, and periods of swimming were interrupted with increasing frequency by resting on the bottom. Finally on August 16, the fish moved off the bottom only when disturbed, and did not initiate the continuous swimming movement. No further changes in behaviour were seen by August 21, when it had reached 19 mm in total length, so that the observations were terminated.

Apparently due to feeding difficulty, river darter did not survive more than a few days past absorption of the yolk sac; all died before they reached 8 mm in length. Like the Iowa darter, these larvae began to swim within several hours of hatching. Although the methods of swimming were the same as described for Iowa darter, river darter were proportionally more active, and were found most often just beneath the surface. This behaviour had not changed by the time they died.

Similar feeding difficulties were encountered with larval logperch, although two survived until reaching a length of 9 mm. Observations of this species produced essentially the same result as those of river darter.

On several occasions an attempt was made to determine the behaviour of the larvae at night. By turning on a floodlamp suddenly, I caught them in the positions they had held in total darkness. Johnny darter were on the bottom, as by day. River darter and logperch were again usually swimming near the surface. Iowa darter were usually on the bottom, which was unlike their daytime behaviour.

V. FOOD OF DARTERS IN DIFFERENT ENVIRONMENTS

Here an attempt is made to determine what kinds of food were taken by the four species in various environments. This might expose differences in food habits that could help to explain simultaneous occurrence of two or more species in the same environment.

Part A: MATERIALS AND METHODS

i) SAMPLING PATTERN AND METHOD OF DETERMINING MOUTH-SIZE

Darters taken in daytime collections through 1969 from three basic lake environments and three basic river environments were used. (The environments are defined in Section III.)

Since it was assumed that the size of darters would influence the size and kind of food organisms eaten, breakdown into groups seemed advisable. Mouth-size was chosen over age or total size (length or weight). Age was sometimes difficult to determine, and fish of the same age, particularly young-of-the year, often varied greatly in size. The available literature suggest that mouth-size is more directly important than total size. For example, differences in food habits between two species of sculpins, at similar length, have been related to differences in mouth-size (Northcote, 1954).

To obtain mouth-size, a calibrated steel probe with a 30° taper was pushed into the mouth until tissue at the corners was just at the breaking point. This measured the maximum diameter of the rounded mouth in increments of 0.33 mm. Mouth-size of up to ten darters of each mm total length encountered was measured for each species. Six classes of mouth-size were then defined. The ranges of total length corresponding to these classes were determined for each species (Appendix 7), and are shown in Table 3.

Table 3: Ranges in diameter of mouth for the six classes of mouth-size, and ranges in total length corresponding to the classes of mouth-size.

Mouth Diam. -mm	Class of Mouth Size	Total Length -mm J.D.	I.D.	R.D.	L.
0-1.17	(1)	< 23	< 18	---	---
1.18-1.83	(2)	23-35	18-29	< 30	< 31
1.84-2.49	(3)	36-44	30-39	30-41	32-42
2.50-3.15	(4)	45-54	40-52	42-50	43-56
3.16-3.81	(5)	> 54	> 52	51-61	57-74
3.81	(6)	---	---	> 61	> 74

ii) EXAMINATION OF STOMACH CONTENTS

The stomach of darters is well-defined, and most food organisms found in it are relatively intact, so that indentification and sorting of contents can yield valuable qualitative and quantitative information on the kinds of food eaten.

The following procedure was used:

1. For each species taken from a given environment, at the same station and date, a sample of up to ten fish was selected from each available class of mouth-size.
2. The total length of each fish within the sample was measured, and the stomach removed by cutting the alimentary tract just behind the gill arches, and then again through the pyloric sphincter

(located by sliding the scissors under the forward-pointing pyloric cecae).

3. The first stomach in the sample was placed in a water-filled petrie dish, and all its contents removed. These were then sorted into different categories of organisms, and, for each category, the percent-contribution to total volume of identifiable food was estimated.

4. Step three was repeated with the other stomachs in the sample. In each case the organisms in a category were then added to the pile accumulated for that category from previous stomachs.

5. After blotting for 10-15 seconds (a sufficient time to remove surface moisture), the accumulated material for each category (obtained from all fish in the sample) was weighed to the nearest 0.5 mg on a Sartorius electrical balance. Weights of less than 0.5 mg were approximated by estimating volume and calculating the equivalent weight (having previously determined the weight of a larger volume of material).

Part B: RESULTS

i) THE CATEGORIES OF FOOD ORGANISMS FOUND IN THE STOMACHS OF DARTERS

Organisms were usually identified only as far as the categories defined for this study. The taxonomic level at which the categories were separated was not uniform. It depended on possible discrimination between organisms by fishes, and known differences in preferred environment of the organisms. The 26 categories defined for food found in stomachs from 1969 lake and river collections, together with their classification, are listed in Table 4.

Table 4: The categories of food, and their classification (according to Pennak, 1953). Whether a category was found in the river, in the lake, or both is also indicated.

r river
l lake
N. nymphs
L. larvae
P. pupae

*Note that the category 'Mayfly nymphs' includes families other than the Ephemeriidae, and not the entire order of mayflies.

Phylum	Class	Order	Family	Category	Source
Coelenterata	Hydroza			HYDRAS	r
Rotatoria				ROTIFERS	r
Annelida	Oligochaeta			OLIGOCHAETES	r, 1
Arthropoda	Crustacea	Anostraca		ANOSTRACANS	1
		Cladodera		CLADOCERNAS	r, 1
		Copepoda		COPEPODS	r, 1
		Ostracoda		OSTRACODS	r, 1
		Amphipoda		AMPHIPODS	r, 1
		Decapoda	Cambridae	CRAYFISH	1
	Arachnoidea	Hydracarina		WATER MITES	r, 1
	Insecta (all non-aquatic forms)			TERRESTRIAL INSECTS	r, 1
		Plectoptera		STONEFLY N.	r, 1
		Ephemeroptera	Epheme-riidae	EPHEMERIID N.	r, 1
		all other fam.		MAYFLY N.	r, 1
		Hemiptera	Corixidae	CORIXIDS	r, 1
		Trichoptera		CADDIS L.	r, 1
		Coleoptera		BEETLE L.	r
		Diptera	Tipulidae	CRANEFLY L.	r
			Simulidae	SIMULID L.	r
				SIMULID P.	r
			Tendipedidae and Ceratopogonidae	MIDGE L.	r, 1
				MIDGE P.	r, 1
			Tabanidae	TABANID L.	r, 1
Mollusca				MOLLUSCS	r, 1
(Sub-phylum)	Vertebrata	Pisces		FISH	r, 1
				FISH EGGS	r, 1

ii) CONTRIBUTION OF VARIOUS CATEGORIES OF ORGANISMS TO THE FOOD OF THE FOUR SPECIES

The contribution of each category of organisms to the food of darters in a given environment and collection period was assessed by two complementary methods: In (a), the percent-contribution of each category to the total weight of identifiable food was calculated. Weights obtained in the same environment and collection period, but at different stations, from samples of the same species and mouth-size, were combined. Here large organisms taken by a minority of fish can appear to dominate the diet. This weakness is countered by the second method, (b), in which the percentage of fish whose food was dominated by each category (on the basis of estimated contribution by volume) was calculated.

Relying on these methods of assessment, food habits in various environments will be examined for each species in turn. Differences in diet among fish of different classes of mouth-size, but of the same species, will be described only for the late summer, following reproduction (early August), while the diet of the large fish will be described for all collection periods.

JOHNNY DARTER: Figs. 8 (lake) and 9 (river) show the contributions of important categories of organisms in the diet by mouth-size for each environment during early August. Without taking into account differences apparently due to chance, the following points are evident:

i) In the lake, in protected pebble-rubble environment, classes 2 to 4 concentrated on midge larvae.

ii) In the river, in current environment, midge larvae and mayfly

Figure 8: Diet, by mouth-size, of johnny darter caught in lake environments during early August. Large pie charts show percent-contribution by weight of different categories. Those whose contribution is less than 5% are combined with categories not represented by symbols under the heading 'other'. In the small charts the shaded portion represents the percentage of fish whose major category of food was the same as that providing the greatest percent-contribution by weight. The numbers within parentheses refer to the number of fish examined and the number containing identifiable food. Cladocerans, copepods, and ostracods have been combined under the heading 'small crustaceans'.

The legend given here applies to Figs. 8-17.

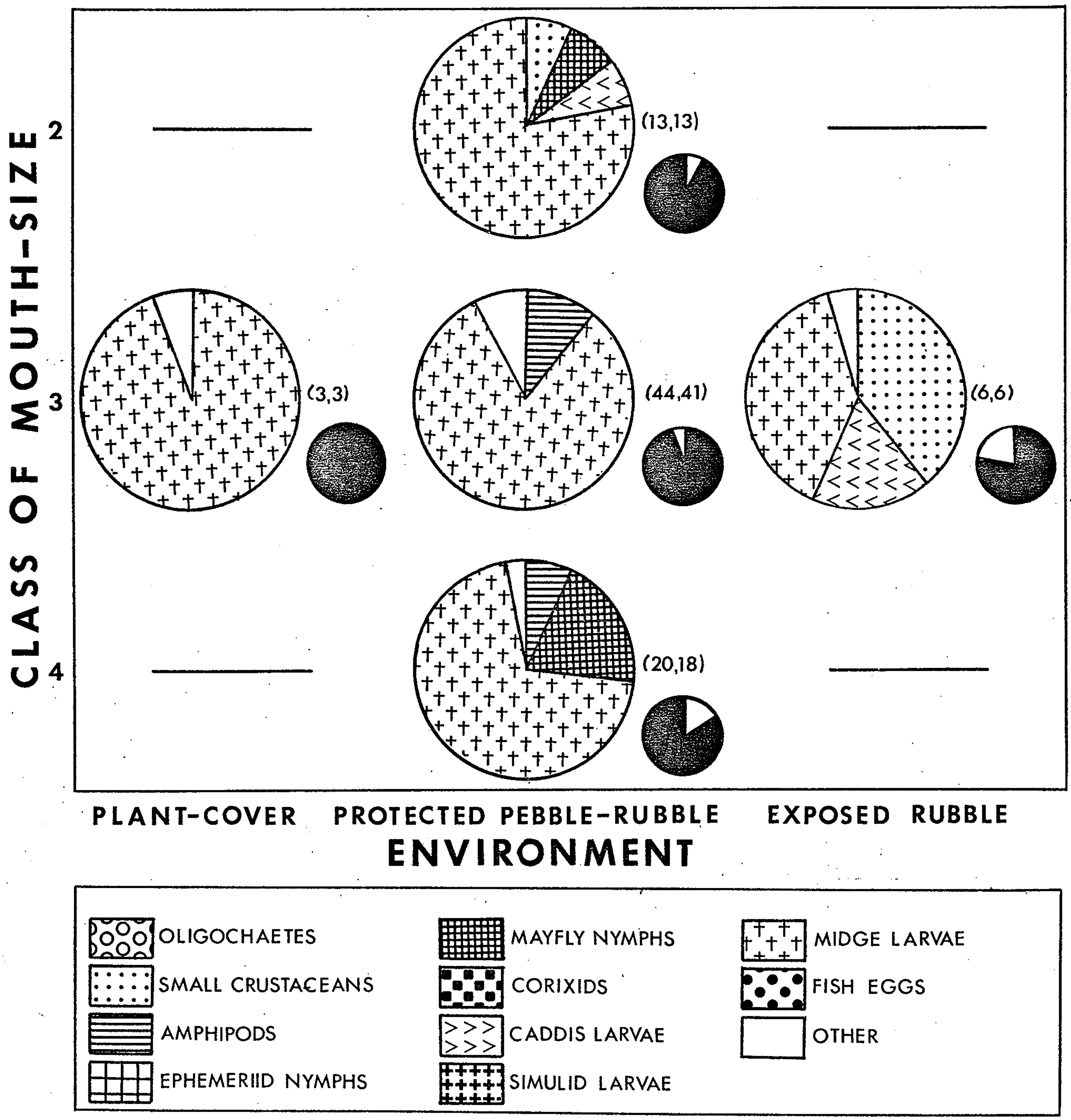
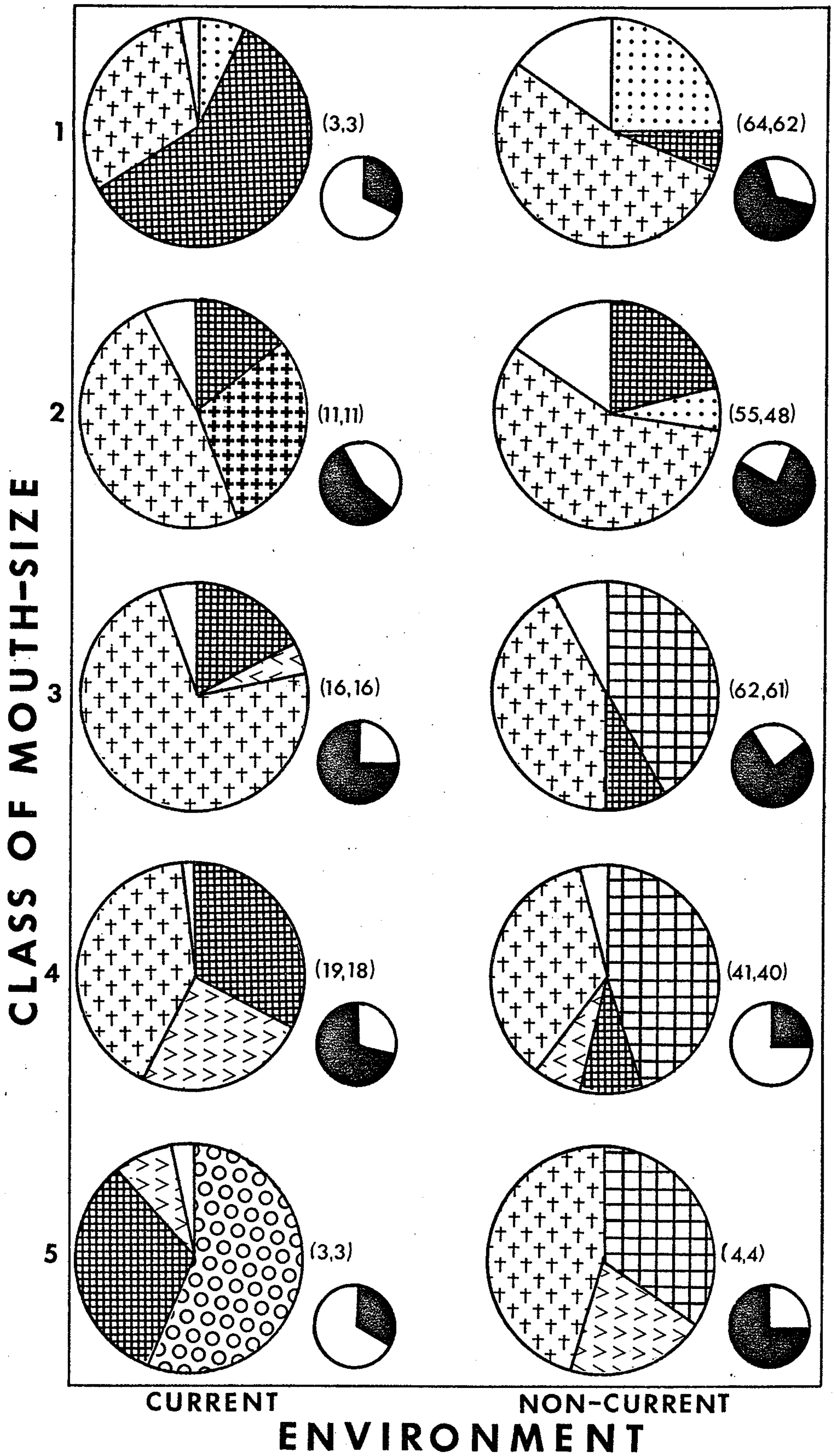

CLASS OF MOUTH-SIZE
2
3
4
(13,13)
(3,3)
(44,41)
(6,6)
(20,18)
PLANT-COVER
PROTECTED PEBBLE-RUBBLE
EXPOSED RUBBLE
ENVIRONMENT
OLIGOCHAETES
SMALL CRUSTACEANS
AMPHIPODS
EPHEMERIID NYMPHS
MAYFLY NYMPHS
CORIXIDS
CADDIS LARVAE
SIMULID LARVAE
MIDGE LARVAE
FISH EGGS
OTHER

Figure 9: Diet, by mouth-size, of johnny darter caught in river environments during early August. Details concerning the pie charts are given with figure 8.



CLASS OF MOUTH-SIZE
1
2
3
4
5
(3,3)
(64,62)
(11,11)
(55,48)
(16,16)
(62,61)
(19,18)
(41,40)
(3,3)
(4,4)
CURRENT
NON-CURRENT
ENVIRONMENT

nymphys* were important to all classes, while caddis larvae were taken only by the larger fish, starting with class 3.

iii) In non-current environment midge larvae were important for all classes. Only class 1 fed heavily on 'small crustaceans' (cladocerans, copepods and ostracods). The larger classes, starting with 3, relied heavily on ephemeriid nymphs.

Seasonal variation in the diet of large johnny darter, of classes 3-5, is shown in Figs. 10 (lake) and 11 (river). The following trends are evident:

i) In the lake, in plant-cover environment, midge larvae dominated the diet from June to early August.

ii) In protected pebble-rubble environment, during early May and June, large johnny darter fed almost exclusively on midge larvae. This organism continued to dominate the diet in succeeding periods, although oligochaetes became important in early July and again in September.

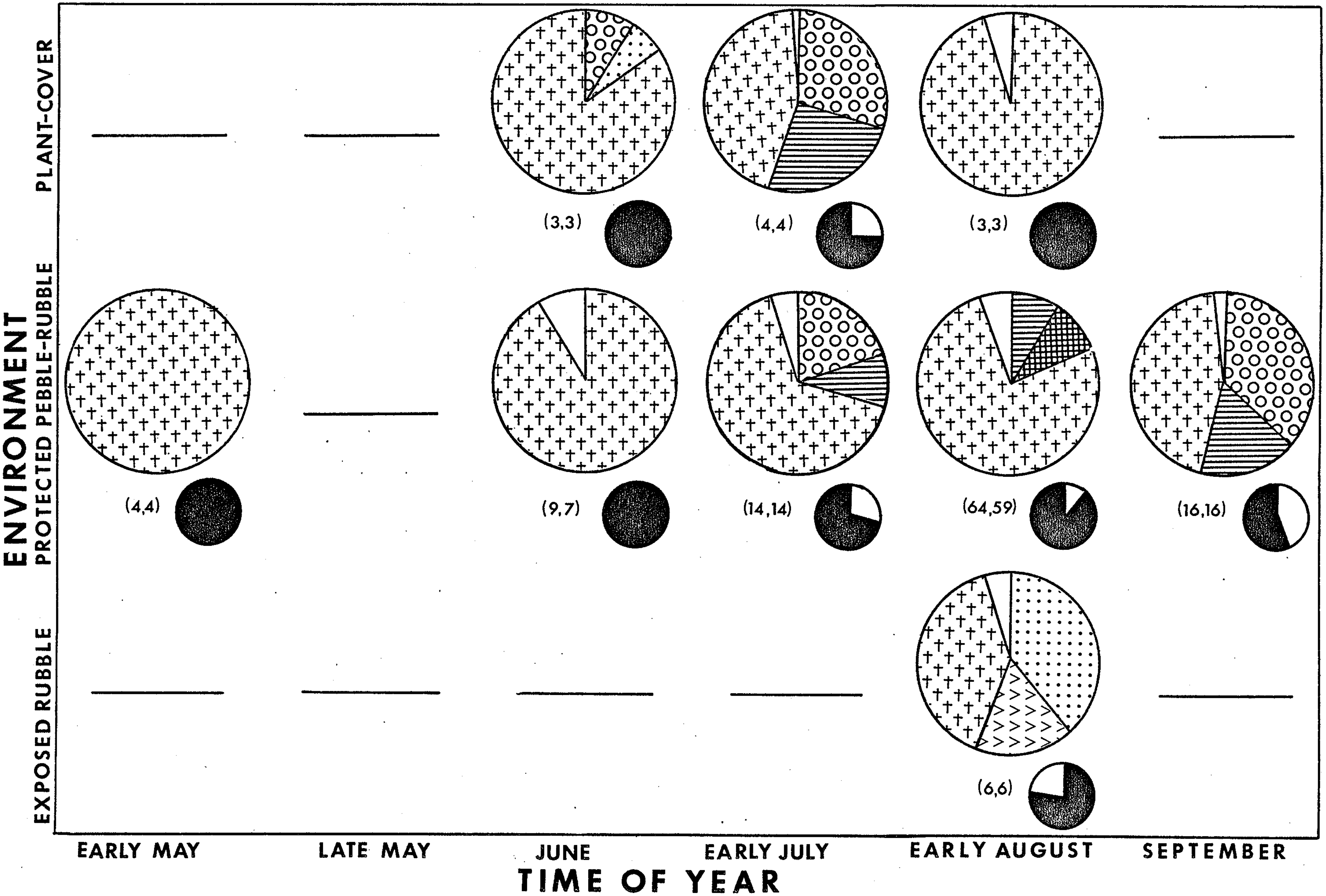
iii) In exposed rubble environment small crustaceans were favoured in early August, although midge larvae were also important in the diet.

iv) In the river, in current environment, midge larvae were important in the diet throughout the year. Simulid larvae dominated the diet in May, and were still important in June. After May, mayfly nymphs contributed heavily to the diet. Caddis larvae first became important in early July and finally dominated the diet in September.

v) In non-current environment midge larvae were dominant or important in the diet throughout the year. During late May, simulid larvae were dominant (although to a lesser extent than in current environment).

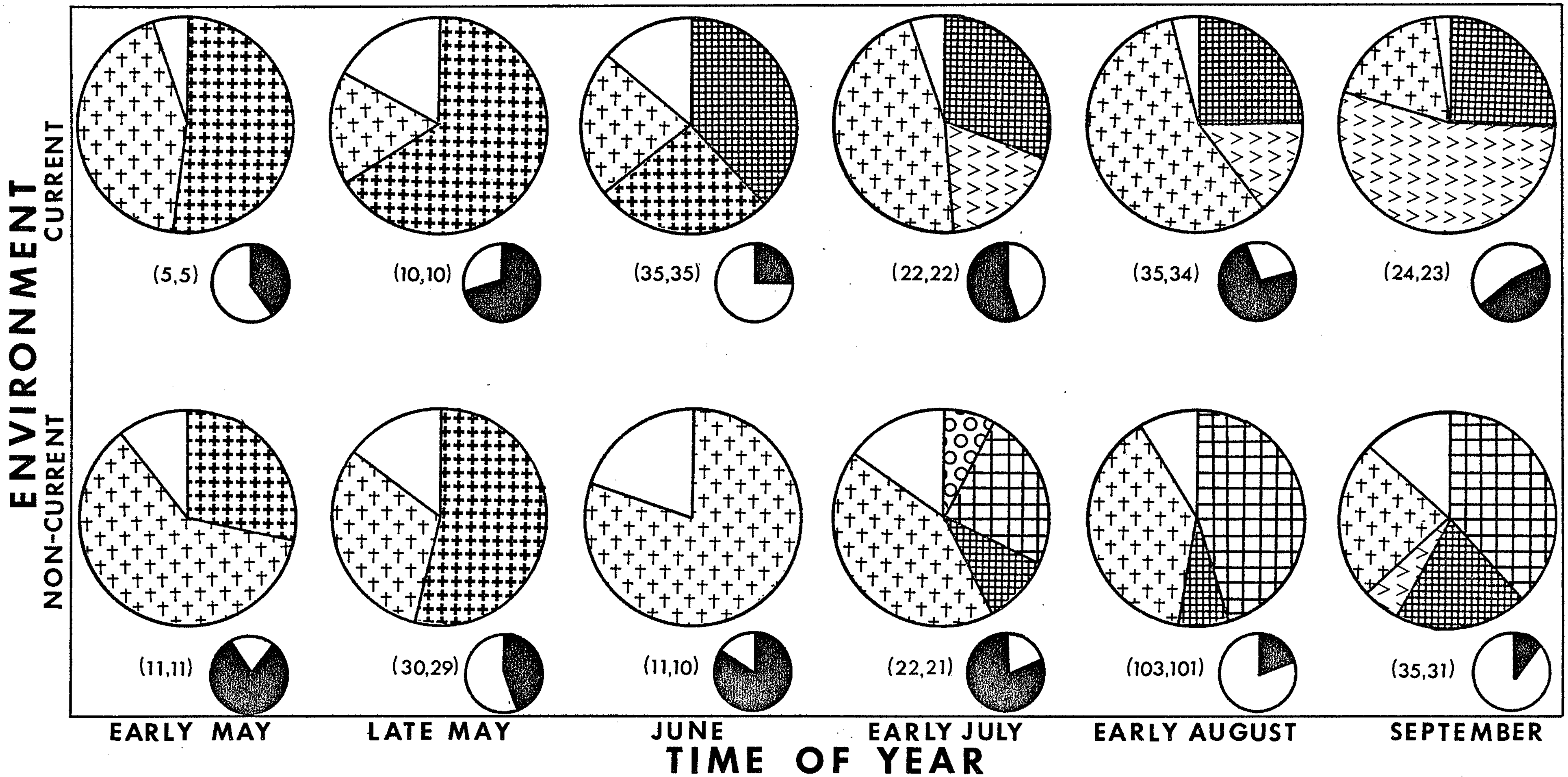
*Excluding the family ephemeriidae, which is placed in a separate category.

Figure 10: Diet of large johnny darter caught in lake environments throughout 1969. Large johnny darter include classes of mouth-size 3-5. For a given date and environment, the diet of the class represented by the most fish is shown. But if two or more classes are represented by ten or more fish, then their percentage figures are averaged to give the diet shown.



ENVIRONMENT
PLANT-COVER
PROTECTED PEBBLE-RUBBLE
EXPOSED RUBBLE
(3,3)
(4,4)
(3,3)
(4,4)
(9,7)
(14,14)
(64,59)
(16,16)
(6,6)
EARLY MAY
LATE MAY
JUNE
EARLY JULY
EARLY AUGUST
SEPTEMBER
TIME OF YEAR

Figure 11: Diet of large johnny darter caught in river environments throughout 1969.



ENVIRONMENT
CURRENT
NON-CURRENT
(5,5)
(10,10)
(35,35)
(22,22)
(35,34)
(24,23)
(11,11)
(30,29)
(11,10)
(22,21)
(103,101)
(35,31)
EARLY MAY
LATE MAY
JUNE
EARLY JULY
EARLY AUGUST
SEPTEMBER
TIME OF YEAR

Ephemeriid nymphs contributed heavily to the diet from early July on.

IOWA DARTER: Since this species was rarely taken in the river, examination of its food is restricted to lake environments. Fig. 12, which shows the diet by mouth-size in the three lake environments during early August, illustrates the following points:

i) In plant-cover environment class 1 fed predominately on small crustaceans, while all larger classes fed predominately on amphipods. Small crustaceans were also important for class 2, while midge larvae were important for classes 1 and 2.

ii) In protected pebble-rubble environment amphipods again dominated the diet of classes 2 - 4. Small crustaceans were also important in class 2, while mayfly nymphs were important in the larger classes.

iii) In exposed rubble environment the only classes represented, 1 and 2, fed predominately on small crustaceans and midge larvae, the smaller class taking proportionately more small crustaceans.

Seasonal variation in the diet of large Iowa darter, of classes of mouth-size 3-5, is shown in Fig. 13. The following trends are evident:

i) In plant-cover environment, in May, both midge larvae and amphipods were important in the diet, but after May amphipods were quite dominant.

ii) In protected pebble-rubble environment, in early May, midge larvae were virtually the only food. They continued to be important until early July. Amphipods contributed heavily to the diet from late May on. In June, early August and September they were quite dominant. In early August mayfly nymphs were also important.

iii) In exposed rubble environment midge larvae dominated the diet in

Figure 12: Diet, by mouth-size, of Iowa darter caught in lake environments during early August.

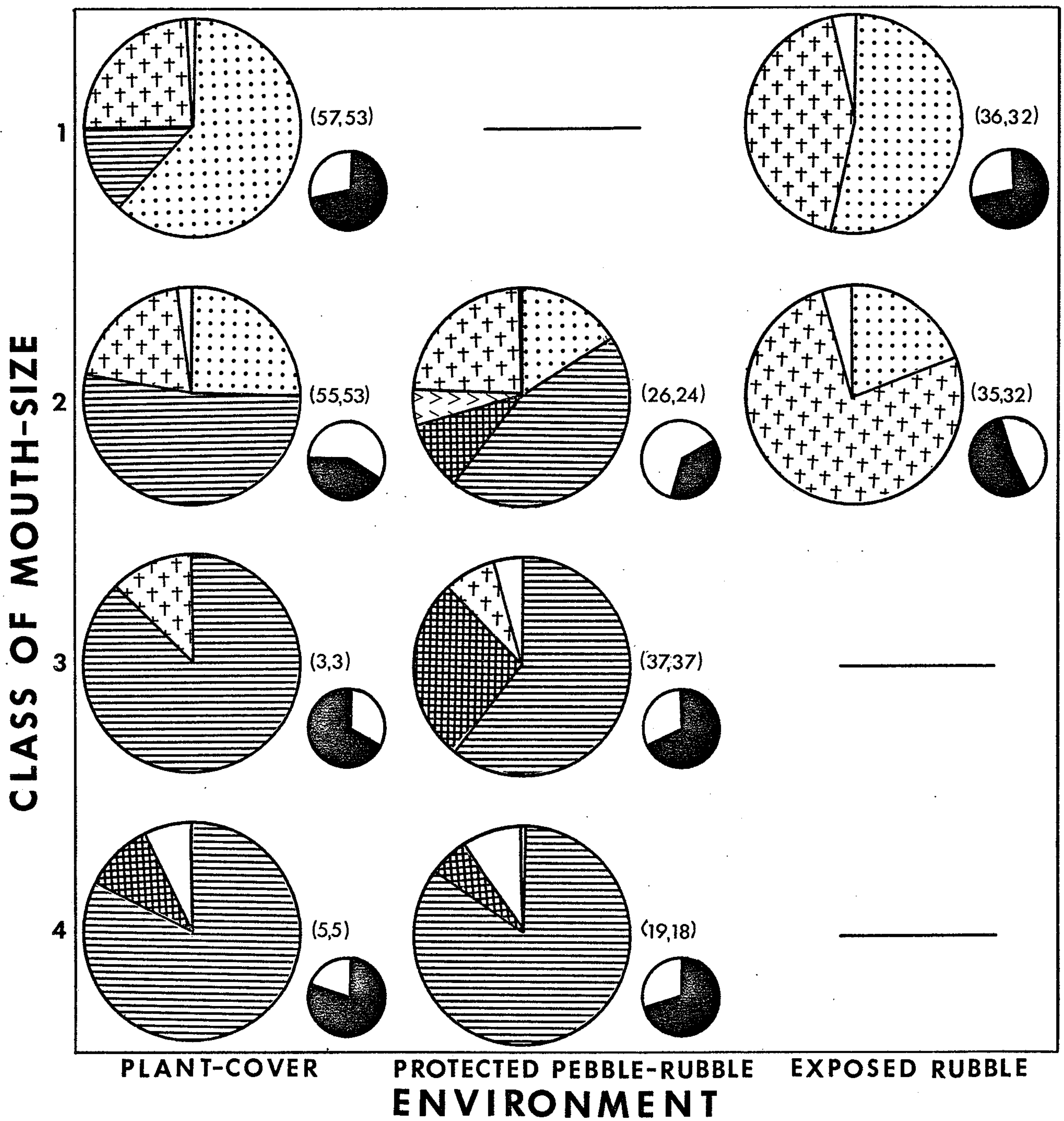
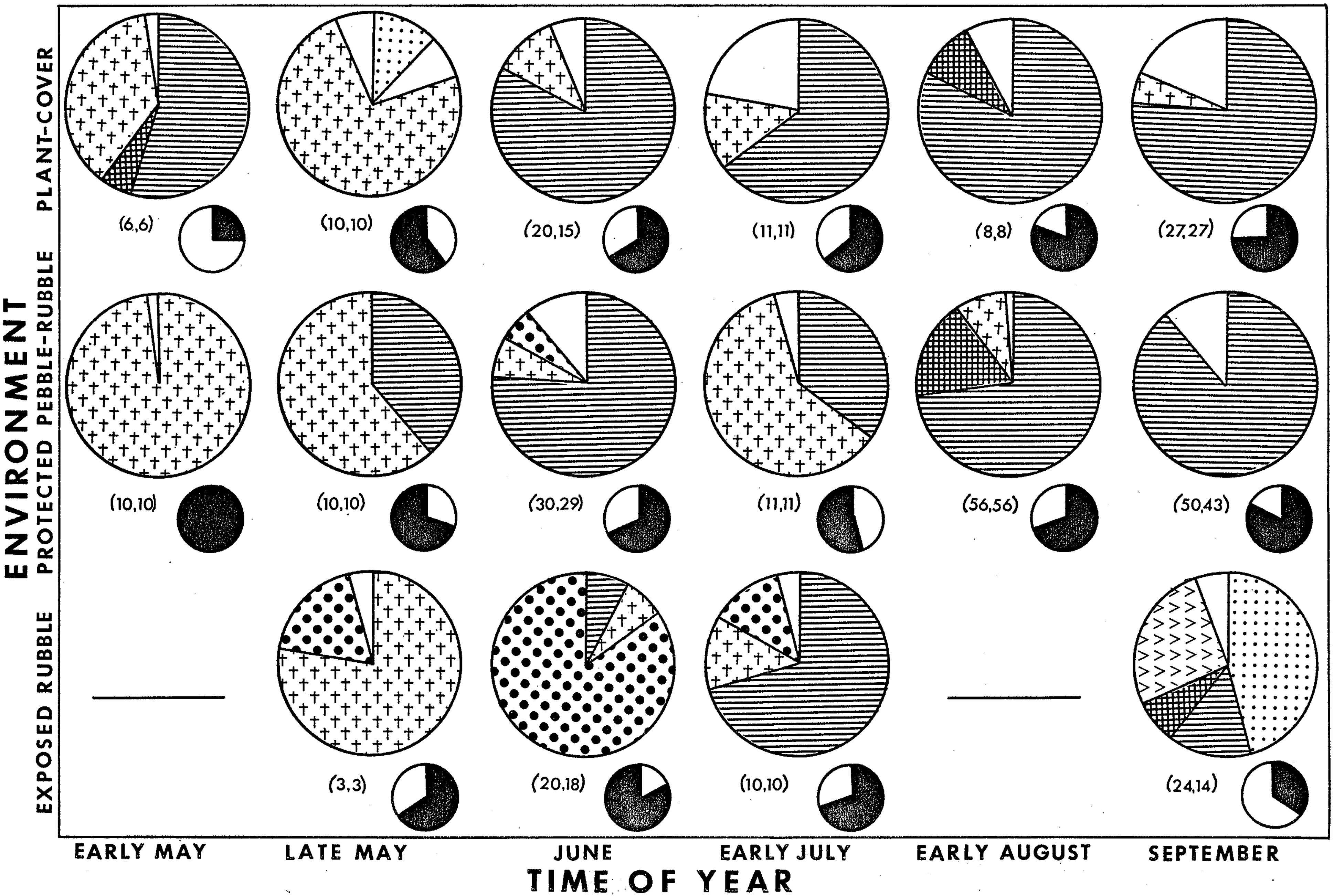

CLASS OF MOUTH-SIZE
1
2
3
4
(57,53)
(36,32)
(55,53)
(26,24)
(35,32)
(3,3)
(37,37)
(5,5)
(19,18)
PLANT-COVER
PROTECTED PEBBLE-RUBBLE
EXPOSED RUBBLE
ENVIRONMENT

Figure 13: Diet of large Iowa darter caught in lake environments throughout 1969. Large Iowa darter include classes of mouth-size 3-5.


ENVIRONMENT
PLANT-COVER
PROTECTED PEBBLE-RUBBLE
EXPOSED RUBBLE
(6,6)
(10,10)
(20,15)
(11,11)
(8,8)
(27,27)
(10,10)
(10,10)
(30,29)
(11,11)
(56,56)
(50,43)
(3,3)
(20,18)
(10,10)
(24,14)
EARLY MAY
LATE MAY
JUNE
EARLY JULY
EARLY AUGUST
SEPTEMBER
TIME OF YEAR

late May, and were again important in early July. Fish eggs were dominant in June, and important in late May and early July. Amphipods became the dominant food item in early July, but amphipods, small crustaceans and caddis larvae all contributed heavily to the diet in September.

RIVER DARTER: Aggregations of this species in the river in 1969 occurred only at the lowest station in late May. In the non-current environment available at that station, this species fed predominantely on midge larvae (as did johnny darter caught in the same place).

Fig. 14 shows the diet by mouth-size in the two lake environments frequented by this species during early August. It illustrates the following points:

i) In protected pebble-rubble environment corixids dominated the diet of classes 4 and 5 (the smallest caught), although fish eggs and mayfly nymphs were also important.

ii) In exposed rubble environment class 2, the smallest caught, fed exclusively on small crustaceans. In all larger classes fish eggs dominated the diet, although caddis larvae and mayfly nymphs were also important.

Seasonal variation in the diet of larger river darter, of classes 4-6, is portrayed in Fig. 15, and the following trends are evident:

1) In protected pebble-rubble environment fish eggs and mayfly nymphs contributed heavily to the diet until early August. Corixids became important in early July, and dominant in early August.

ii) In exposed rubble environment fish eggs dominated the diet from

Figure 14: Diet, by mouth-size, of river darter caught in lake environments during early August.

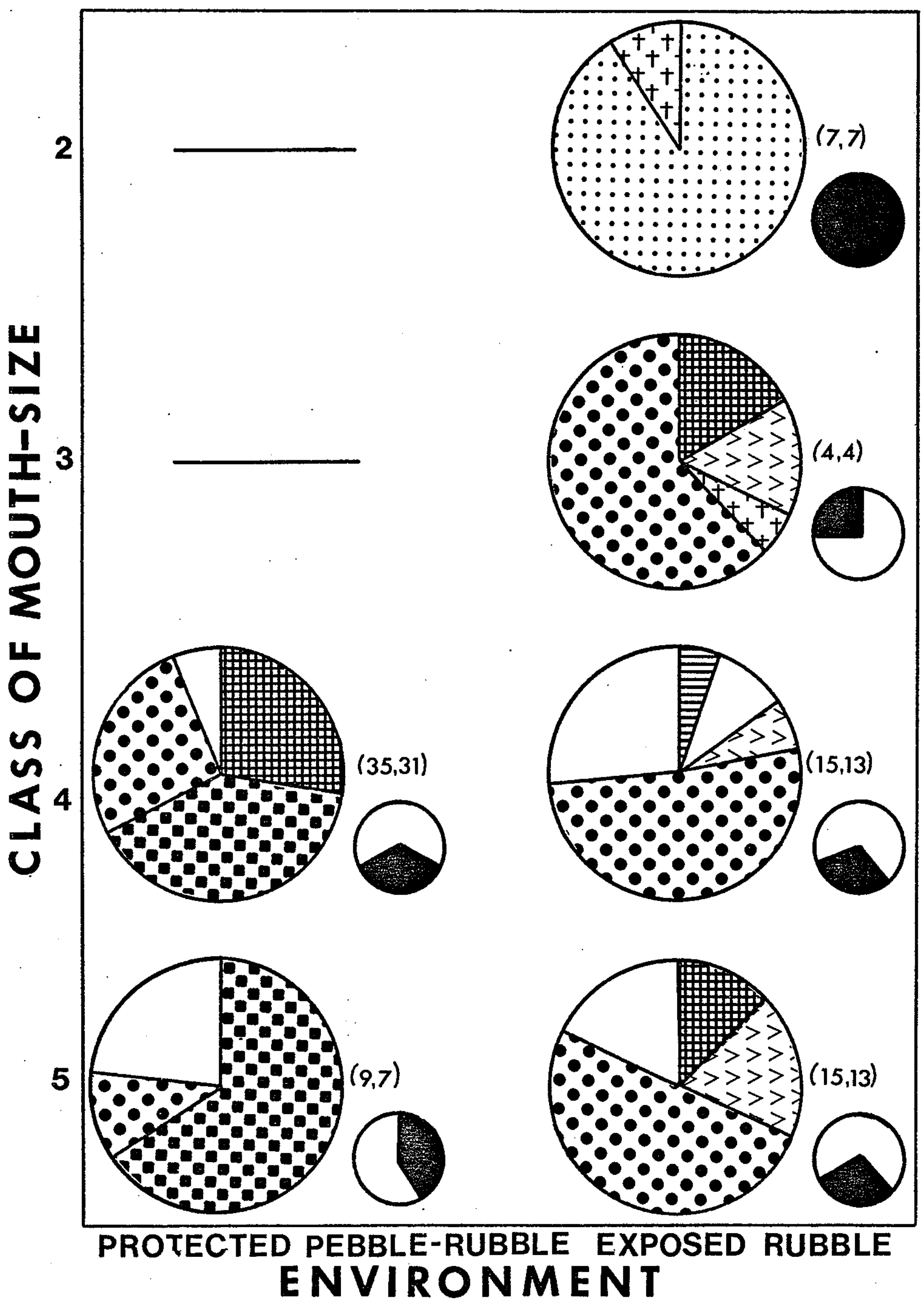
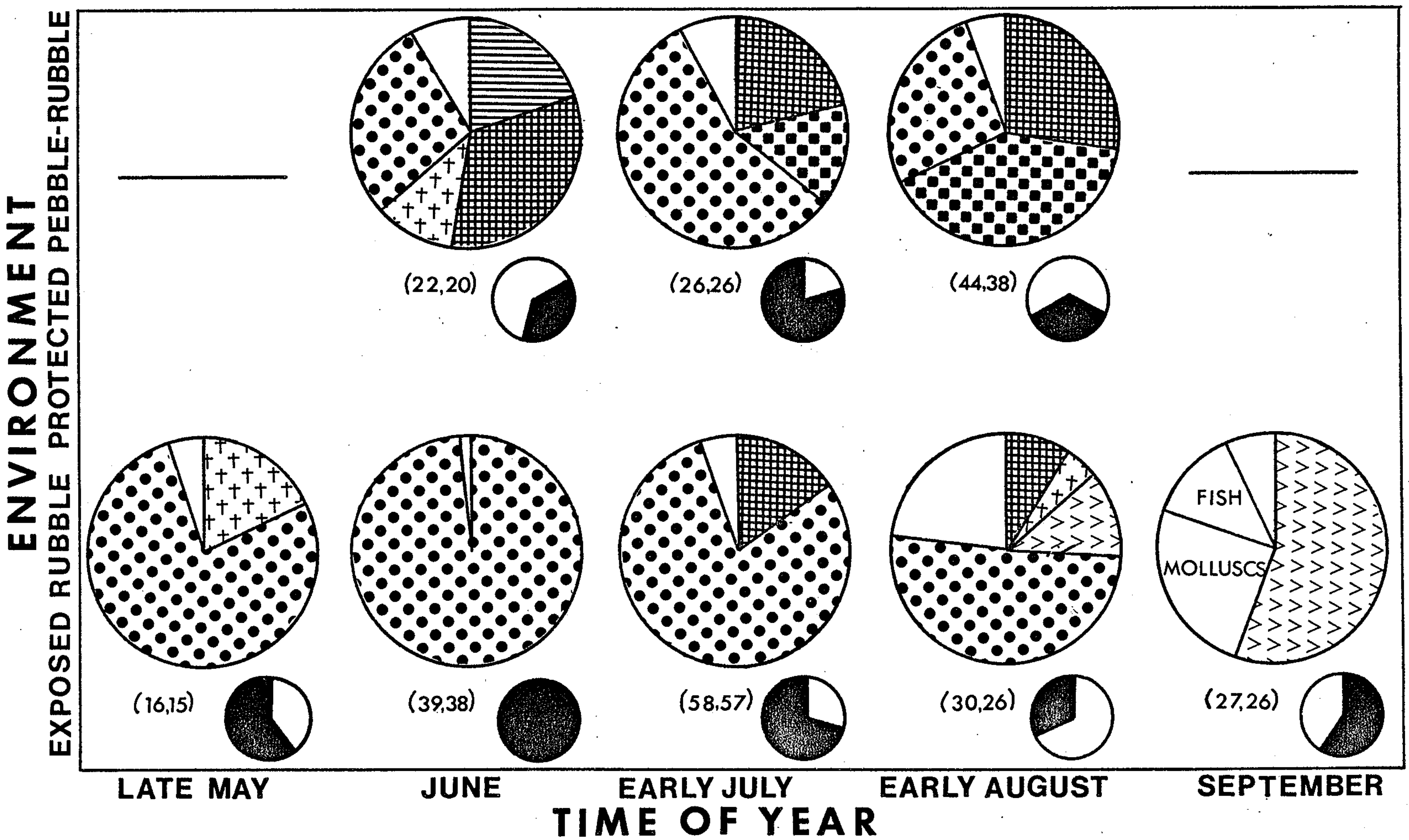

CLASS OF MOUTH-SIZE
2
3
4
5
(7,7)
(4,4)
(35,31)
(15,13)
(9,7)
(15,13)
PROTECTED PEBBLE-RUBBLE
EXPOSED RUBBLE
ENVIRONMENT

Figure 15: Diet of large river darter caught in lake environments throughout 1969. Large river darter include classes of mouth-size 4-6.


ENVIRONMENT
EXPOSED RUBBLE
PROTECTED PEBBLE-RUBBLE
(22,20)
(26,26)
(44,38)
(16,15)
(39,38)
(58,57)
(30,26)
(27,26)
FISH
MOLLUSCS
LATE MAY
JUNE
EARLY JULY
EARLY AUGUST
SEPTEMBER
TIME OF YEAR

late May to early August. In June they were virtually the only food taken by large river darter in this environment. In late May midge larvae were also important, while mayfly nymphs were important in early July and early August. By early August caddis larvae became important in the diet, and they dominated it in September. Fish and, to a lesser extent, molluscs were also important in the diet in September.

LOGPERCH: The occurrence of this species in the river during 1969 was primarily restricted to some aggregations in the lower reaches in late May. They were found in current and non-current environments, but only a sample from non-current at one station was available. The diet of those fish was dominated by fish (small larvae), while ephemeriid nymphs were also important. Unfortunately, information on the diet of logperch in the lake is also limited, because of poor catches of this species throughout 1969.

Fig. 16 shows the diet, by mouth-size, in early August, and illustrates the following points:

i) In both protected pebble-rubble and exposed rubble environments class 3, the smallest caught, fed exclusively on small crustaceans.

ii) In protected pebble-rubble environment larger fish concentrated on mayfly nymphs, but also fed heavily on amphipods and, perhaps, fish eggs.

iii) In exposed rubble environment the diet of larger logperch was dominated by midge larvae, although fish eggs were also important.

Seasonal variation in the diet of large logperch, of classes 4-6, is shown in Fig. 17. The following trends are evident:

i) In protected pebble-rubble environment fish eggs dominated the diet in June and continued to be important in early July. From June to early

Figure 16: Diet, by mouth-size, of logperch caught in lake environments during early August.

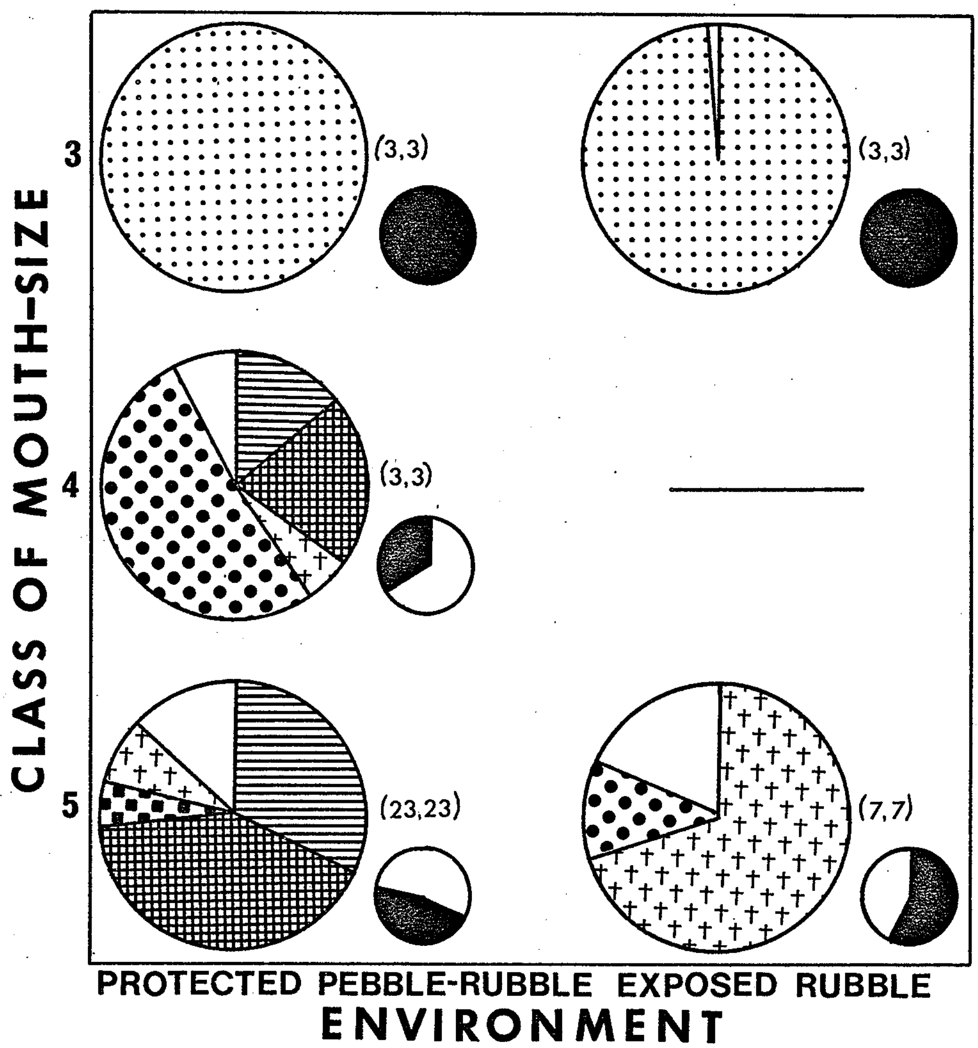
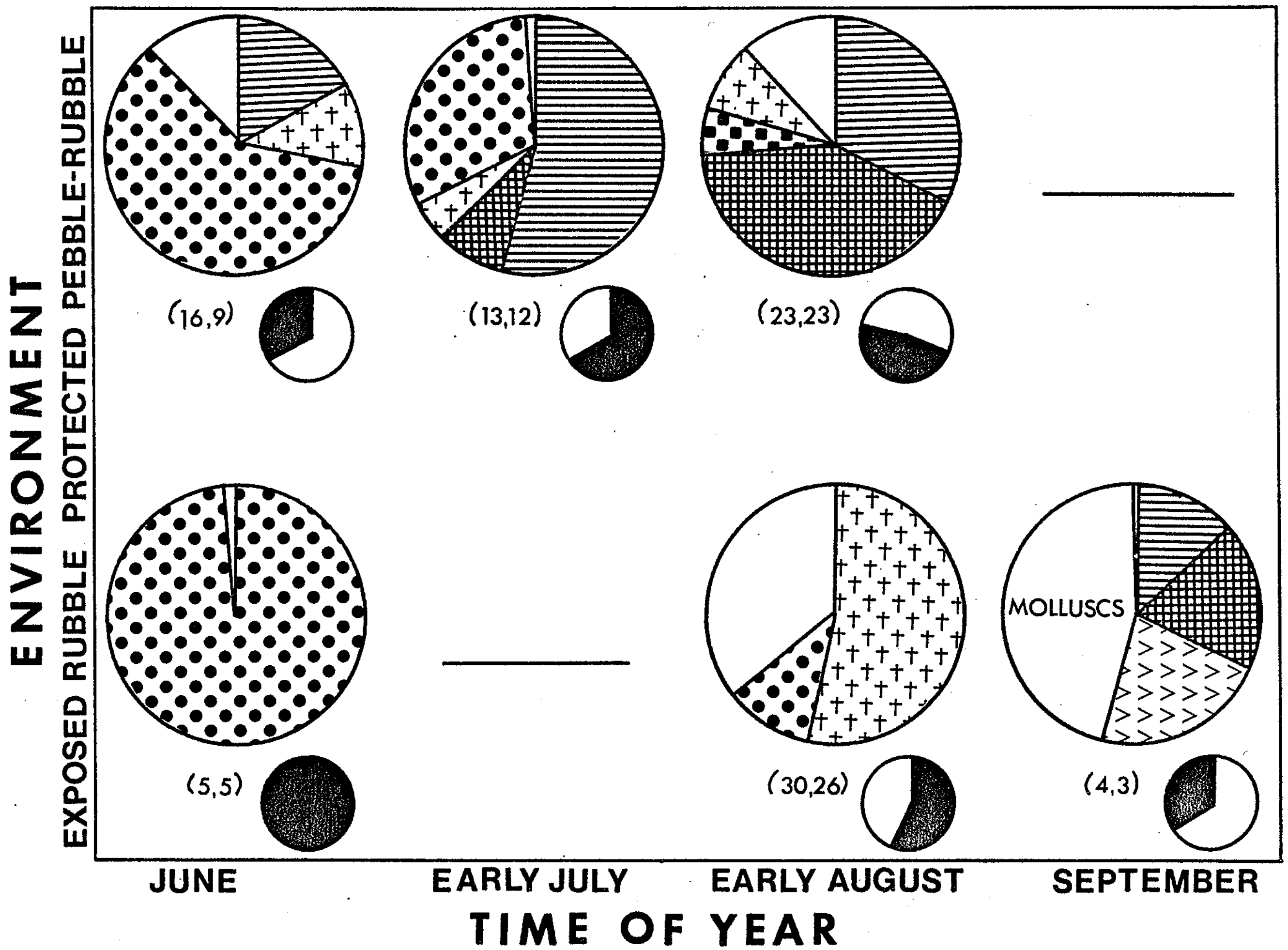

CLASS OF MOUTH-SIZE
3
4
5
(3,3)
(3,3)
(3,3)
(23,23)
(7,7)
PROTECTED PEBBLE-RUBBLE
EXPOSED RUBBLE
ENVIRONMENT

Figure 17: Diet of large logperch caught in lake environments throughout 1969. Large logperch include classes of mouth-size 4-6.


ENVIRONMENT
PROTECTED PEBBLE-RUBBLE
EXPOSED RUBBLE
(16,9)
(13,12)
(23,23)
(5,5)
(30,26)
(4,3)
MOLLUSCS
JUNE
EARLY JULY
EARLY AUGUST
SEPTEMBER
TIME OF YEAR

August, amphipods contributed heavily to the diet, but during the latter period mayfly nymphs became the dominant food item.

ii) In exposed rubble environment fish eggs were virtually the only food in June. By early August midge larvae dominated the diet, although fish eggs continued to be important. In September large logperch ate predominately molluscs, although caddis larvae and mayfly nymphs also contributed heavilty to the diet.

The degree of similarity in the food of different species of darters collected at the same time and in the same environment can now be investigated.

A coefficient of percentage similarity (Whittaker and Fairbanks, 1958) was calculated for the diet of pairs of coexisting species. The coefficient was calculated from the formula: $Cps = 100 - .5\Sigma(a_i - b_i) = \Sigma \min (a_i, b_i)$, where a_i is the percentage of the diet of species a which is made up of category i, and b_i, is the percentage of the diet of species b which is made up of category i. Calculation was based on percent-contribution, by weight, of each category to the diet. It was applied to the diet of (i) the smallest class of mouth size caught (1 for johnny darter and Iowa darter; 2 for river darter; 3 for logperch), and (ii) large fish (as previously defined), where significant numbers of two species were collected in the same environment at the same time. The availability of a sufficiently large sample to allow analysis of diet was considered to be a satisfactory indication that a significant number of fish were present.

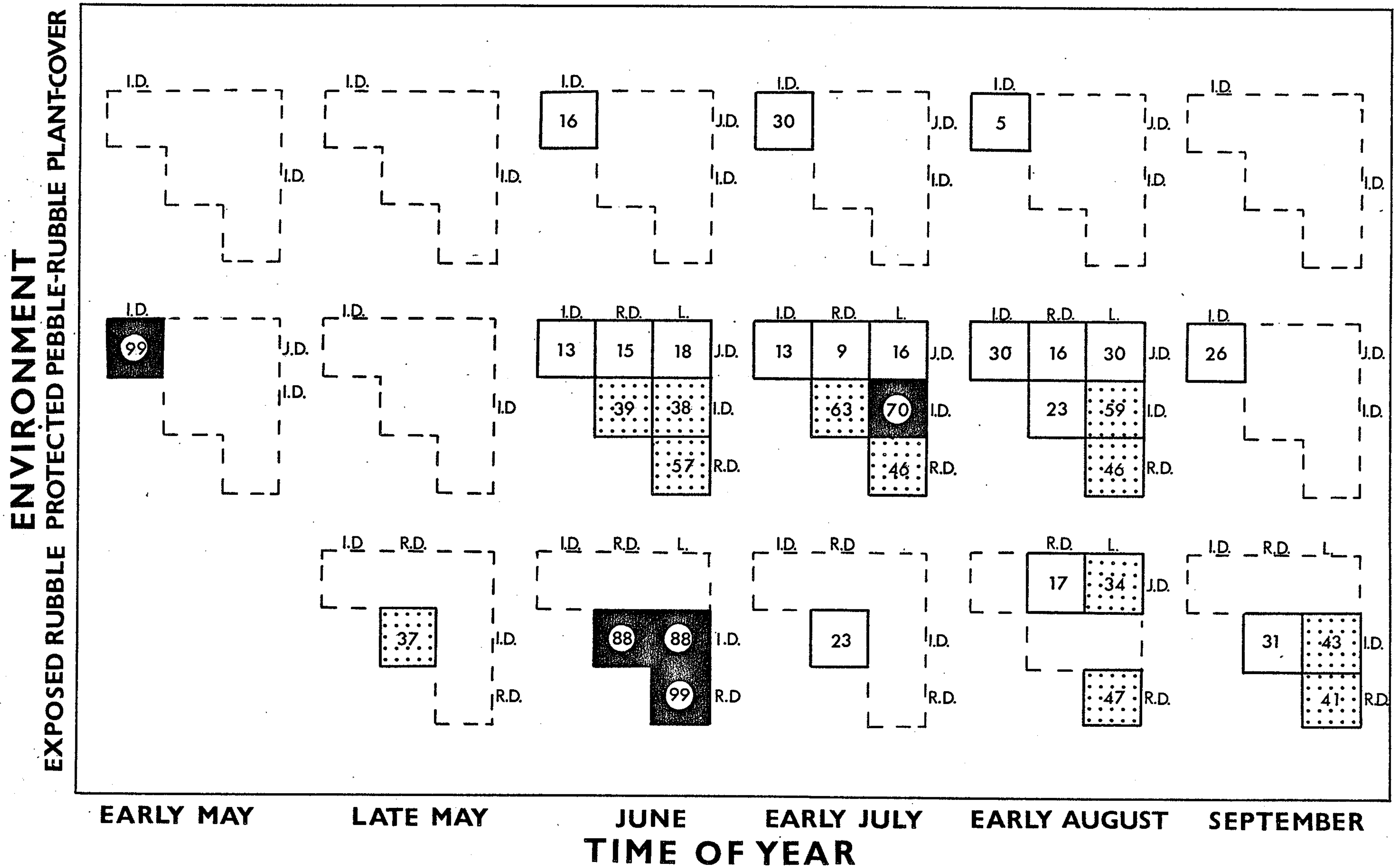
The smallest river darter, Iowa darter and logperch taken in the lake during early August were shown to favour small crustaceans, regardless of environment. In exposed rubble coefficients of percentage similarity were Iowa darter - river darter 62, Iowa darter - logperch 54, and river darter - logperch 91, reflecting the divergence of Iowa darter to midge larvae as a secondary food.

In river environments in 1969, the presence of aggregations of mature logperch in the lower reaches in late May provided the only instance in which johnny darter occurred with significant numbers of another species. The food of large logperch and johnny darter in non-current was only slightly similar (Cps = 23).

In the lake, considerable overlap in the distribution of large darters occurred throughout the year. Fig. 18 shows when and where significant numbers of each species occurred, and gives coefficients of percentage similarity for each pair of coesisting species. Ranking degrees of similarity into slight (Cps = 0-33), moderate (Cps = 34-66) and great (Cps = 67-100), permits the following interpretation. Only five of the 34 coefficients calculated indicated great similarity in the diet of two species occurring together. In early May, in protected pebble-rubble, Iowa darter and johnny darter had diets consisting almost entirely of midge larvae. Sharing of fish eggs produced great similarity in the diet of Iowa darter, river darter and logperch in exposed rubble in June, and of Iowa darter and river darter in protected pebble-rubble in July. In general, the diet of logperch, being the most heterogeneous, showed the greatest amount of similarity to that of the other species. On the other hand, the food of johnny darter, because it was always dominated by midge larvae, was only slightly similar to the food of the other species in most cases.

Figure 18: Similarity in food of different species of darters collected together in the lake throughout 1969. For each period and environment those species are shown of which sufficient numbers of large individuals were collected to allow analysis of food. For each pair of species shown together, the coefficient of percentage similarity of food is given in the appropriate square. Blank squares indicate slight similarity, stippled squares moderate similarity, and shaded squares great similarity.

J.D.	johnny darter
I.D.	Iowa darter
R.D.	river darter
L.	logperch


ENVIRONMENT
EXPOSED RUBBLE
PROTECTED PEBBLE-RUBBLE
PLANT-COVER
I.D.
J.D.
R.D.
L.
16
30
5
99
13
15
18
9
16
30
16
30
26
39
38
57
63
70
46
23
59
46
37
88
88
99
23
17
34
47
31
43
41
EARLY MAY
LATE MAY
JUNE
EARLY JULY
EARLY AUGUST
SEPTEMBER
TIME OF YEAR

VI. DISCUSSION

i) THE DISTRIBUTION AND ABUNDANCE OF THE FOUR SPECIES IN DIFFERENT ENVIRONMENTS

In the broadest sense, the waters of the study area may be divided into the onshore zone of the lake, the offshore zone of the lake, and the river. The onshore zone has been divided into four basic environments with a residue of intermediate situations. The river has been divided into three basic environments, again with a residue of intermediate situations. It must be stressed that the boundaries of both the broad zones and the basic environments are rarely clear. This problem appears to apply to freshwater environments generally. Larkin (1956) noted the "vague demarcation of ecological zones in freshwater environments".

Both the distribution of sexually mature darters during the reproductive season and the initial distribution of the larvae were necessarily related to spawning. Aggregations of sexually mature river darter and logperch in the lower reaches of the river during June, 1968 and late May, 1969 were evidently part of a spawning migration from the lake. The distribution of sexually mature river darter in the lake during that time indicated that stony shores, particularly at Stony Point (station L 15), also constituted important spawning environment for that species. Whereas on stony shores generally the interstices between rubble-sized stones were filled with coarse pebble, at Stony Point they were filled with coarse sand to fine pebble, which was probably ideally suited for egg-deposition. The behaviour of river darter is probably similar to that of logperch, blackside darter *Percina maculata*, and channel darter *P. copelandi*, in which the spawning partners partially bury themselves in sand or gravel, so that the fertilized eggs become covered with the substrate (Winn, 1958b). Reproductive migrations of logperch from lakes to inlet and outlet streams have been described by Fish (1932) and Winn (1958b). Trautman (1957) suggested that river darter caught in streams in spring were upstream migrants.

Winn (1958b) stated that johnny darter spawned in both rivers and lakes, wherever suitable substrate for egg deposition on the undersides of stones was available. However, comparatively few ripe johnny darter were found in the lake in spring, and throughout the year few johnny darter were caught along the eastern shore, which has no tributaries. This suggests that almost all breeding by this species in the study area took place in the rivers.

Winn (1958a) observed Iowa darter spawning in lakes and the lower reaches of inlet streams, almost always on fibrous root material or organic detritus. In the study area a major segment of the population evidently bred in plant-cover in the lake. Some Iowa darter may also move just inside the mouth of the Valley R. or into other streams and spawn.

Because larval darter in the first few weeks after hatching were not vulnerable to seining, and were not caught by other methods, their distribution can only be inferred from: (i) the distribution of the smallest darters caught by seining, (ii) the behaviour of larvae reared in the laboratory, and (iii) the findings of other workers. The newly hatched larvae of all four species were 5-6.5 mm in length, but only johnny darter and Iowa darter were caught by seining in the late larval stage, at a length of 12-15 mm. In the laboratory neither species altered its behaviour before reaching the length at which it was taken by seining, suggesting that the distribution of larvae was similar to that of young-of-the-year caught by seining. It thus appears that in the study area larval johnny darter are bottom-dwellers occurring predominately in non-current environment in the river and, to a lesser extent, in onshore environments in the lake. Fish (1932) caught larval johnny darter down to 5.5 mm in length along the bottom near shore in Lake Erie. Larval Iowa darter probably swim about by day, but remain in onshore environments, often near the hatching site. The smallest logperch caught in 1969 were well-developed post-larvae exceeding 32 mm taken in the lake. Coupled with the behaviour of larvae in the laboratory, where they swam almost continuously near the surface, this supports the findings of Fish (1932) and Faber (pers. comm.) that larval logperch are pelagic in lakes. Literature concerning larval river darter is lacking, but, like the logperch, this species was also captured only in the post-larval stage (exceeding 23 mm) and swam almost continuously near the surface in the laboratory. Larval river darter thus also appear to be pelagic in L. Dauphin. By swimming off the bottom, most river darter and logperch hatched in the Valley R. probably move actively, and/or are carried, to the lake soon after emerging from the substrate. Petravicz (1938) observed larval blackside darter, a stream dwelling species of Percina, swimming at the surface in pools for the first three weeks after hatching and then settling to the bottom.

Faber (1967) believed that the pelagic habit of the larvae of some fishes was a mechanism for dispersal from the spawning areas. Larval river darter and logperch appeared to disperse in this way throughout L. Dauphin from their spawning areas in the lower river and on the more suitable stony shores. Miura (MS 1962) found that larvae of species which remained near a lakeshore nevertheless also migrated along the shoreline. Northcote (1967) stated that some cyprinids disperse to parts of lakes other than the pelagic zone after hatching. It appears that the non-pelagic larvae of johnny darter and Iowa darter also disperse at least to some extent from their areas of hatching in the study area. Specifically, this could account for the abundance of late-larval and post-larval Iowa darter in exposed rubble environment.

The distribution of age 0 and 1+ johnny darter in the Valley R. agrees with the findings of Speare (1960) who also caught johnny darter in all environments of a stream, while taking proportionately fewer in riffles. In addition, this was the only species of darter common in both the river and lake after the reproductive season. Trautman (1957) also remarked on the universal distribution of johnny darter in Ohio, and on its preference for quiet water when in high-gradient streams. The prevalence of Iowa darter in plant-cover is understandable, as Winn (1958a) found this species in winter in "the organic debris and plant zone" of a lake, and Trautman (1957) found it in marshy areas along shore in Lake Erie. The latter suggested that the Iowa darter was confined to "habitually clear waters", but L. Dauphin's turbidity indicates that transparency does not limit its distribution. Trautman (1957) also provided the only reference to the ecology of the river darter, noting that it was caught in the deeper portions of streams. Yet this was the dominant species of age 1+ darter in exposed rubble.

Non-reproductive logperch have been found to occupy a variety of environments. Winn (1958b) suggested that this species moved to deeper water in rivers and lakes following reproduction. Trautman (1957) stated that in Lake Erie logperch inhabited areas with sand and/or gravel bottom, ranging from beaches to bars 30 mm in depth, and was frequently found in aquatic vegetation. Turner (1921) described the logperch as "the most common and widely distributed of the whole group of darters" in Ohio, while Keast and Webb (1966) found it confined to areas of pebbly bottom in a lake. In the study area logperch were found in stony shore environments after the reproductive season, but definitely absent from vegetation. Their presence in offshore areas remains a possibility. They were considerably less abundant than other species of darters.

The general preference for cover over non-cover by johnny darter, Iowa darter and logperch in environment preference experiments was correlated with very poor catches of all species in onshore non-cover areas in the lake in 1968. But at the same time johnny darter in the river were abundant in non-current areas without cover. This may have been caused by crowding of this species in areas of cover. The second inference obtained from these experiments, that the three species did not appear to prefer one kind of cover over another, appeared to contradict their distribution in the lake.

Relatively more johnny darter and Iowa darter were caught in protected than in exposed rubble, but it may be that wave action was more important than substrate (type of cover) in causing the difference. The avoidance of aquatic plant beds by logperch in the field may have been a response to local conditions, since elsewhere this species has been found in vegetation.

ii) FOOD OF THE FOUR SPECIES

Larkin (1956), in reviewing food habits of freshwater fishes, noted that "the young of most species share an early plankton diet". This was substantially true in L. Dauphin for the smallest Iowa darter, river darter and logperch. Turner (1921) also found that young logperch less than 40 mm in length in Lake Erie fed mainly on copepods and cladocerans. By contrast, he found that in streams both young logperch and young johnny darter less than 21 mm in length had a mixed diet of copepods and minute midge larvae. The same was true for small johnny darter in the Valley R.

Larkin (1956) indicated that freshwater fishes, being generally not highly specialized, may when occurring together eat the same foods, but in different proportions. In the study area, larger darters of all species took a wide range of benthic food items. In general the diets of different species taken in the same environment at the same time were qualitatively similar. But distinct differences in the proportion of different items ensured that, as shown by coefficients of percentage similarity, their diets were in most cases quantitatively only slightly or moderately similar. Situations in which diets of coexisting species were greatly similar arose from the sharing of midge larvae or eggs early in the year.

Different species, particularily if unrelated, may become specialized towards taking different foods as they assume adult form and behaviour. Miura (MS 1962) described divergence in food habits of minnows, suckers and sculpins after development from the larval form. Keast and Webb (1966) suggested that the dissimilar morphology of adults of unrelated species predisposed them to taking different foods. The logperch, possessing a bony snout, frequently uses it to push over small stones in search of food. This behaviour has been observed by Winn (1953), Keast and Webb (1966) and myself. But in L. Dauphin the diet of large logperch was generally more heterogeneous than that of the other species. Apparently the stone-turning habit of the logperch does not predispose it to feeding on particular kinds of benthic organisms. Various authors (Dobie, 1959: Keast and Webb, 1966; Mullan, Applegate and Rainwater, 1968; Turner 1921) have examined the diet of adult logperch, and Turner has also described the diet of adult johnny darter. Midge larvae, other insect larvae and amphipods, in varying proportions, were the main foods taken.

iii) HOW THE FOUR SPECIES CAN OCCUR TOGETHER

In ecological literature a competitive exclusion principle has been advanced which states in effect that two species whose way of life is similar cannot survive together. It was well stated by Crombie (1947): "...species with identical needs and habits cannot survive in the same place if they compete for limited resources--at least if their needs and habits remain identical". Darwin (1859) recognized that closely related species are more likely to have similar needs and habits than unrelated species. Thus the sympatric occurrence of closely related, even congeneric species in various taxonomic groups has posed a problem which has been widely investigated (for example, Beauchamp and Ullyott, 1932 for triclads; Lack, 1946 for birds; Bovbjerg, 1952 for crayfish; Dumas, 1956 for salamanders; Damman, 1961 for snakes; Miller 1967 for gophers). Considerable attention has also been focused on coexisting, closely related species of freshwater fishes (for example, Northcote, 1954 for sculpins; Nilsson, 1958 for coregonids; Gee and Northcote, 1963 for dace).

The four species of darters present in the study area showed major differences in their distribution by environment, even though differences related to type of cover would not have been predicted from the results of preference experiments. The diets of species occurring together in the same environment at the same time were usually only slightly or moderately similar. Exceptions which occurred early in the year when two or more species in lake environments concentrated on midge larvae or fish eggs may have been signs of a supply temporarily in excess of demand for those items. Both divergence by diet and by environment inhabited may be an indication of the 'unwillingness' of the four species to enter into competition for food resources. As suggested by Larkin (1956), spatial separation, or separation by environment, achieves the same result as a difference in diet. That author also emphasized the plasticity of fishes in all aspects of their ecology, which allows them to make various adjustments in potentially competitive situations.

In conclusion, these fishes were to a great extent found in different environments, but often occurred together. In such potentially competitive situations they usually favoured different food items. These features are part of diverse and flexible ways of life which have allowed the four species of darters to survive together in the L. Dauphin Watershed.

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Appendix 1: PATTERN OF SAMPLING AND THE ABUNDANCE OF DARTERS IN DIFFERENT ENVIRONMENTS IN 1968

Stations visited and environments sampled during each 1968 collection period are shown in Table 1. All sampling was of the incomplete type.

Station	Time of Year June 10-12	July 8-11	Aug. 10-14	Sept. 15-17
L 2			3, 4, 6	3, 4, 6
L 6			5	5
L 8			5, 7	5, 7
L 9			3, 4	3, 4
L 10			7	7
L 11			2, 4	2, 4, 5
L 12			1, 4	1, 4
L 13	6, 7	6		
L 14		5, 7	5	5, 7
L 15	5	5		5
L 16		1, 3, 4	1, 4	1, 4
L 17	3	3		
R 1	15	15	12, 15	15
R 2	9, 12	9, 12	9	9, 11, 14
R 3	14	14	11, 14	11, 14
R 4	9, 11	9, 14	9, 12, 13	9, 11, 13
R 5	8, 13	8, 13	8, 11, 13	8, 12, 13
R 6	8, 9, 15	8, 14	8, 11, 15, 16	8, 11, 14, 16
R 7	9, 11	9,11, 14, 16	8, 11, 14	8, 11, 14
R 8	9, 12	12		
R 9	8, 9, 15	8, 9, 12		8, 9, 11, 14
R 12			14	13
R 14		8, 16		8, 15, 16
R 15		8, 9, 15		8, 9, 12, 15

Determination of 'basic' environments for 1969 sampling was based on results of collections made in August and September, 1968. During those periods, age 0 and older fishes of all four species were caught in the lake. Certain environmental features appeared to influence the abundance of one or more species. These were:

i) The presence or absence of cover for small fishes. (Cover could be provided by stones or aquatic plants.)

ii) The presence of aquatic plant beds.

iii) Protection from, or exposure to, wave action.

iv) A substrate which is mainly granitic rubble, or a mixture of pebble and rubble, composed mainly of limestone fragments.

The features described in (iii) and (iv) are strongly correlated, as the majority of protected shores have a substrate of limestone fragments, while the majority of exposed shores have a substrate of granitic rubble. Since this correlation is not evident in some areas, stony shores may be separated in either way. It is then found that differences in species-composition between types of stony shore environments are clearest if they are separated according to degree of exposure to wave action, rather than according to type of substrate.

In Table 2, the numbers of age 0 and 1+ fishes of each species caught in four kinds of environment, based on the features described, are given. It is apparent that:

i) Very few darters of any species were taken in areas without cover, despite the very large total area sampled.

ii) Beds of aquatic plants were inhabited almost entirely by age 0 Iowa darter.

Table 2: Numbers of darters caught in four kinds of lake environments in August and September, 1968.

Environment	Total area-m^2	Age:	Johnny d.		Iowa d.		River d.		Logperch	
			0	1+	0	1+	0	1+	0	1+
Without cover	1026		3	5	16	2	26	4	3	2
With aquatic plants	157			4	115	1	5		5	
Protected stony shores	200		13	94	59	39	15	29	4	17
Exposed stoney shores	586		19	27	33	16	104	98	13	25

iii) Johnny darter and Iowa darter were the most abundant species on protected stony shores.

iv) River darter were the most abundant species on exposed stony shores.

v) There was considerable overlap of the four species on stony shores, particularily on protected stony shores.

In the river, johnny darter were caught at all stations during each collection period. In August and September, 1968, they were more prevalent in non-current ($3.18/m^2$--37 incomplete samples) than in current environment ($2.05/m^2$--13 incomplete samples). During the same period, proportionally more age 0 johnny darter were caught in shallow than in deep non-current environments; the ratios of age 0 to age 1+ fish was roughly 2:1 (530 : 282-20 samples) for deep, roughly 4:1 (763 : 191-16 samples) for shallow areas sampled. Other environmental features had no obvious effect on the abundance of johnny darter in the river.

The other species were less abundant and more restricted in their distribution in the river. Iowa darter were scarce throughout 1968, with a total of four taken in all sampling. River darter and logperch were both present, and their distribution and abundance in the river fluctuated seasonally. Very few individuals of either species were caught in August and September.

Appendix 2: PATTERN OF SAMPLING DURING 1969

Stations visited and environments sampled in each collection period are given in Table 3 for the lake, and Table 4 for the river.

Table 3: Pattern of sampling in the lake during 1969, showing stations visited and environments sampled during the six collection periods.

Environments sampled are given number codes as follows:

'basic' environments	1	plant cover
	2	protected pebble-rubble
	3	exposed rubble
other	4	exposed pebble-rubble

Underlining denotes complete sampling is included. Asteriks denote that fewer than the customary three complete samples were taken.

Station	Time of Year: May 5-8 (early May)	May 26-28 (late May)	June 16-19 (June)	July 7-9 (early July)	July 27-Aug. 4 (early Aug.)	Sept. 18-20 (September)
L 1				1	1	
L 2	<u>2</u>, 3*	<u>2</u>, <u>3</u>	<u>2</u>	<u>2</u>, 3	<u>2</u>, 3	<u>2</u>
L 3					<u>1</u>, 2	1, 2
L 4			1		<u>1</u>	1
L 5					1	1
L 6	<u>3</u>*		<u>3</u>	3	<u>3</u>	3
L 7					3	
L 8	<u>3</u>*	<u>3</u>	<u>3</u>	<u>3</u>	<u>3</u>	<u>3</u>
L 9	<u>4</u>		<u>2</u>, <u>4</u>	<u>2</u>, <u>4</u>	<u>2</u>, <u>4</u>	<u>4</u>
L 13					1	
L 14					3	
L 15	<u>3</u>*	<u>3</u>	<u>3</u>	<u>3</u>	<u>3</u>	<u>3</u>
L 16	1, 2	<u>1</u>	<u>1</u>, 2	1, 2	<u>1</u>, 2	<u>1</u>, 2
L 17					2	

Table 4: Pattern of sampling in the river during 1969, showing stations visited and environments sampled during the six collection periods.

Environments sampled are given number codes, as follows:

'basic' environments	1	current
	2	shallow non-current
	3	deep non-current
other	4	non-current (any depth)

Underlining denotes complete sampling is included. Asteriks denote that fewer than the customary three complete samples were taken.

Station			Time of Year			
	May 5-8 (early May)	May 26-28 (late May)	June 16-19 (June)	July 7-9 (early July)	July 27-Aug.4 (early Aug.)	Sept. 18-20 (September)
R 1	4	4	4	4	4	4
R 2	1*, 3*, 4	1*, 4	1*, 4	1, 4	1, 2, 3	1, 4
R 3	3*, 4	4	4	4	4	4
R 4	1*, 4	1*, 4	1*, 4	1, 4	1, 4	1, 4
R 6	1*, 4	1*, 4	1, 4			1, 4
R 7	1*, 2*, 3*,4	4	1, 2, 3, 4	1, 2, 3, 4	1, 2, 3, 4	1, 2, 3, 4
R 9	1		1, 4			
R 10	1, 4	1, 4	4		1, 4	1, 4
R 11	1, 4					
R 12	1, 4	1, 4	1, 4			
R 13	4					
R 15	1, 2, 3				1, 2, 3	

Appendix 3: LENGTH-FREQUENCY DISTRIBUTIONS AND AGE DETERMINATION

To determine the age of darters, separate length-frequency histograms were constructed for fishes caught in the lake and the river during each collection period in 1968 and 1969. Where fewer than 30 fish were available the histograms were regarded as useless for age determination. It was expected that, for any species, growth rates in the river and the lake would be different. However, a survey of all length-frequency distributions showed that virtually all Iowa darter, river darter and logperch spent at least their first summer in the lake, while a disproportionately small number of johnny darter caught in the lake were young-of-the-year. To simplify the analysis, the separation of age classes for each period was based either on the fish caught in the lake, or those caught in the river, whichever were greater in number.

Table 5: Length-frequency tables for johnny darter. Note that classes over 44-45 mm have been combined.

L Lake

R river

(triple underline) age 2+

(double underline) age 1+

(single underline) age 1

age 0 (no underlining)

--- age groups not separated

This legend applies to Tables 5-8.

Date	Frequency 12-13	14-15	16-17	18-19	20-21	22-23	24-25	26-27	28-29	30-31	32-33	34-35	36-37	38-39	40-41	42-43	44-45	46-71
L Aug. 1968.							1	2	4	2	7	6	1		4	5	16	132
L Sept. 1968.							1	2	6	7	21	16	5	2	2	2	2	24
L June 1969.							1	2	3	7	10	7	8	4	1			5
L July 1969.							2		3	2	8	7	5	13	8	2	1	8
L Aug. 1969.	1		3		1			4	4	2	5	3	14	24	25	34	25	25
L Sept. 1969.											1			1	2	1	3	22
R June 1968.							4	15	40	44	104	89	100	83	56	65	40	51
R July 1968.	Present but not measured							12	45	49	55	61	59	63	42	43	20	32
R Aug. 1968.	9	23	87	120	143		120	132	77	35	33	35	27	39	43	47	48	56
R Sept. 1968.		10	60	98	173		142	123	100	70	33	41	37	64	48	53	42	126

Continued on next page.

Table 5 contd.

Date	12-13	14-15	16-17	18-19	20-21	22-23	24-25	26-27	28-29	30-31	32-33	34-35	36-37	38-39	40-41	42-43	44-45	46-71
	Frequency																	
R Early May 1969.					6	8	18	10	9	11	8	8	17	18	12	8	6	27
R Late May 1969.						4	26	30	33	35	52	68	47	26	21	8	1	4
R June 1969						1	3	11	19	15	21	31	22	41	26	25	22	29
R July 1969.	1	3	9	17	20	15	5	4	10	15	12	19	21	22	28	19	14	15
R Late July 1969.	1	27	37	65	61	57	67	41	30	32	21	19	26	28	46	36	38	66
R Sept. 1969.				1	4	12	16	21	13	16	14	12	11	25	23	21	17	36

Table 6: Length-frequency tables for Iowa darter. Note that classes over 44-45 mm have been combined.

Date	Frequency																	
	12-13	14-15	16-17	18-19	20-21	22-23	24-25	26-27	28-29	30-31	32-33	34-35	36-37	38-39	40-41	42-43	44-45	46-59
L June 1968.										2	1	1	7	4	2	4	7	11
L July 1968.											1	1	2	3	9	17	9	14
L Aug. 1968.			11	27	38	26	15	16	11	9	1	1	4	2	3	4	2	14
L Sept. 1968.					1	1	1	2	5	8	10	20	20	14	7	5	6	15
L Early May 1969.							3	9	13	33	26	32	31	8	6		3	13
L Late May 1969.								2	10	3	8	10	5	1	1	1	2	
L June 1969.							2	1	11	19	31	31	28	11	4	6	2	16
L Early July 1969.									2	8	14	20	19	13	5	3	3	5
L Late July 1969.	3	59	387	326	212	112	72	20	8			7	13	22	16	11	3	10
L Sept. 1969.				2	6	18	21	47	68	97	90	49	41	12	6	5	7	5

Table 7: Length-frequency tables for river darter. Note that classes under 26-27 mm have been combined, as have classes above 56-57 mm.

	Frequency																	
Date	20-25	26-27	28-29	30-31	32-33	34-35	36-37	38-39	40-41	42-43	44-45	46-47	48-49	50-51	52-53	54-55	56-57	58-71
L June 1968.						1	2	3	7	7	2	1		4	13	15	15	19
L July 1968.									1	1		2	4	1	17	11	16	19
L Aug. 1968.	10	2	8	14	36	33	30	15		1		8	4	18	34	34	17	56
L Sept. 1968.	1		1		5	14	27	22	2			1	3	4	5	11	5	19
L May 1969.					1	2	10	2				1	2		11	4	4	4
L June 1969.				2	9	36	49	48	52	16	1		4	13	32	32	47	48
L July 1969.			1		1	9	15	40	45	51	45	12	5	19	41	49	28	32
L Late July 1969.	1	5	7	5	2			1	4	9	9	28	43	31	16	8	4	3
L Sept. 1969.					1	2	5	6	7	4			1	3	3	10	3	14
R June 1968							2	2					4	8	21	13	6	2

Table 8: Length-frequency tables for logperch. Note that classes under 46-47 mm have been combined in groups of four, and classes over 70-71 mm have been lumped.

Date	Frequency																	
	20-27	28-35	36-43	44-45	46-57	48-49	50-51	52-53	54-55	56-57	58-59	60-61	62-63	64-65	66-67	68-69	70-71	72-95
L June 1968.						1	4	4	6	19	3	2	1					2
L July 1968.							1	1		3	3	1	4	10	9	7	4	12
L Aug. 1968.		4	6	8	6	3	1	2						1	2	1	4	51
L July 1969.				2	1	2	2	2	2	4	12	4	3	1				1
L Late July 1969.		1	4	1				2	3		3	2	5	5	3	2	7	7
R June 1968.									1		1			1	4	5	12	74
R July 1968.													3	1	3	6	2	17
R May 1969.				1	1							1	2	3	4	4	6	11

Appendix 4: VARIATION AMONG STATIONS IN THE DENSITIES OF DARTERS IN EARLY AUGUST, 1969

The amount of variation occuring among stations in the density of a particular species and age group, in a given environment, was assessed by examining range and standard deviation about the mean. In addition, a coefficient of variation was computed. The coefficient was not useful at very low densities, where frequent samples without a darter almost invariably produced values of about 1.7. Thus the coefficient of variation was arbitrarily considered as meaningless if none of the densities from which it was calculated exceeded 0.14 fish/m^2. For densities obtained during early August, 1969, the above mentioned measures are given in Table 9.

A coefficient of variation exceeding 0.5 can be arbitrarily considered high. A survey of the (meaningful) coefficients listed in Table 9 shows that for 12 of 13 mean densities, variation among stations within any environment was high.

Table 9: Mean densities and variation among stations for basic environments sampled during early August, 1969. Coefficients of variation based on a set of three densities of which none exceeded 0.14 fish/m^2 are not shown. The means for each environment were obtained from densities at three stations.

$$CV = \text{Coefficient of variation} = \frac{s}{\bar{\bar{x}}}$$

Environment	Species	Age	Range	Mean	Standard Deviation	CV
LAKE:	Johnny d.	0	0-.08	.03	.05	
Plant-cover		1+	0-.05	.02	.03	
	Iowa d.	0	3.61-6.8	4.81	1.74	.36
		1+	0-.1	.03	.06	
	River d.	0	0-.03	.01	.02	
Protected pebble-rubble	Johnny d.	0	0-.09	.04	.05	
		1+	.06-.92	.44	.44	.99
	Iowa d.	0	.09-.34	.17	.14	.83
		1+	0-.75	.25	.43	1.73
	River d.	0	0-.02	.01	.01	
		1+	0-.23	.13	.12	.91
	Logperch	0	0-.09	.03	.05	
		1+	.05-.11	.07	.03	
Exposed rubble	Johnny d.	1+	0-.02	.01	.01	
	Iowa d.	0	.17 -1.92	.89	.92	1.03
		1+	0-.03	.01	.02	
	River d.	0	0-.02	.01	.01	
		1+	.03-.38	.18	.18	1.0
	Logperch	1+	0-.05	.02	.03	
RIVER:	Johnny d.	0	0-1.54	.55	.86	1.58
Current		1+	.14 -.98	.59	.42	.71
Shallow non-current	Johnny d.	0	.44-4.02	2.33	1.80	.77
		1+	.43-1.76	.88	.76	.87
Deep non-current	Johnny d.	0	0-2.77	1.34	1.39	1.04
		1+	.49-2.18	1.22	.71	.7
	Logperch	1+	0-.06	.02	.04	

Appendix 5: RATIOS OF NUMBERS OF DARTERS CAUGHT IN LAKE ENVIRONMENTS THROUGHOUT 1969, AND CHI-SQUARE VALUES OBTAINED IN COMPARING THESE RATIOS

Numbers shown in Table 10 were obtained from both complete and incomplete samples, but incomplete samples in which some darters had been discarded were not included.

Table 10: Numbers of darters caught in three lake environments throughout 1969. For early August, numbers of age 0 and 1+ darters are given separately, in that order.

S stations A area-m^2 pc plant-cover environment

ppr protected pebble-rubble er exposed rubble

Date	Environ-ment	No. S	No. A	Number caught of each species J.D.	I.D.	R.D.	L.
Early May	pc	1	73		14		
	ppr	1	57	23	89	4	
	er	4	193		10	8	
Late May	pc	1	26		24		
	ppr	1	37	6	19	4	
	er	3	100	6	1	32	3
June	pc	2	124	12	68		
	ppr	3	196	37	40	102	17
	er	3	277		20	172	3
Early July	pc	2	118	7	14		
	ppr	3	208	52	57	139	24
	er	4	310	2	21	212	
Early Aug.	pc	6	254	0/1	724/6	1/0	
	ppr	6	211	22/69	115/52	1/13	3/12
	er	6	481	2/8	187/1	9/42	4/7
Sept.	pc	3	92		206		
	ppr	3	189	22	115	1	3
	er	3	180	4	49	60	11

Table 11: Individual and total chi-square values obtained for comparisons of the ratios of numbers of darters in pairs of environments. Individual chi-square values which appear to contribute heavily to total chi-square are underlined, and the environment in which the species concerned was relatively more abundant is shown. A dash indicates that the species was caught in neither environment (in which case chi-square was calculated for a 2 x 3 contingency table).

x^2 individual chi-square

X^2 total chi-square

\+ more than 20% of expected values 5

critical X^2 for 2 x 4 contingency table
at 5% level of significance = 7.8
at 1% level of significance = 11.3
for 2 x 3 contingency table,
at 5% level of significance = 6.0
at 1% level of significance = 9.2

pc plant-cover environment

ppr protected pebble-rubble environment

er exposed rubble environment

Date	Environments	x^2 for each species				x^2
		J.D.	I.D.	R.D.	L.	
Early May	ppr vs er	3.5	1.5	29.5er	---	34+
Late May	ppr vs er	0.3	23.6ppr	13.6er	1.3	39
June	pc vs ppr	0.5	60.6pc	41.7ppr	6.8	110
	pc vs er	29.2pc	99.0pc	70.5er	1.3	200+
	ppr vs er	37.0ppr	6.5ppr	18.3er	9.8ppr	71
Early July	pc vs ppr	2.6	16.7pc	10.8ppr	1.8	32
	pc vs er	61.5pc	46.3pc	19.0er	---	127+
	ppr vs er	39.4ppr	11.9ppr	27.9er	10.7ppr	90
Early Aug.	pc vs ppr	114.6ppr	1.4	9.9	---	126+
	pc vs er	3.1	0.8	27.0er	13.8er	44
Age 0	ppr vs er	22.2ppr	0.5	0.4	0.9	24+
Age 1+	pc vs ppr	2.2	4.2pc	0.6	0.6	7.7+
	pc vs er	0	38.2pc	5.0	0.9	44+
	ppr vs er	12.3ppr	18.4ppr	62.4er	0.7	94
Sept.	ppr vs er	16.5ppr	18.8ppr	65.4er	5.6	106

Appendix 6: NUMBERS OF DARTERS CHOOSING EACH ENVIRONMENT IN ENVIRONMENT PREFERENCE EXPERIMENTS

Table 12: Numbers of darters choosing each environment in environment preference experiments. For each test (individual experiment) the ratio of fish choosing each environment while sampling without replacement, and (if additional sampling with replacement was necessary) the final ratios of choices, are given. Preference for an environment is indicated by an asterik after the number of choices for that environment.

Environments: (a) non-cover
(b) plant-cover
(c) pebble-bottom
(d) rubble bottom

s.w.r. sampling without replacement
n near end of aquarium
f far end of aquarium

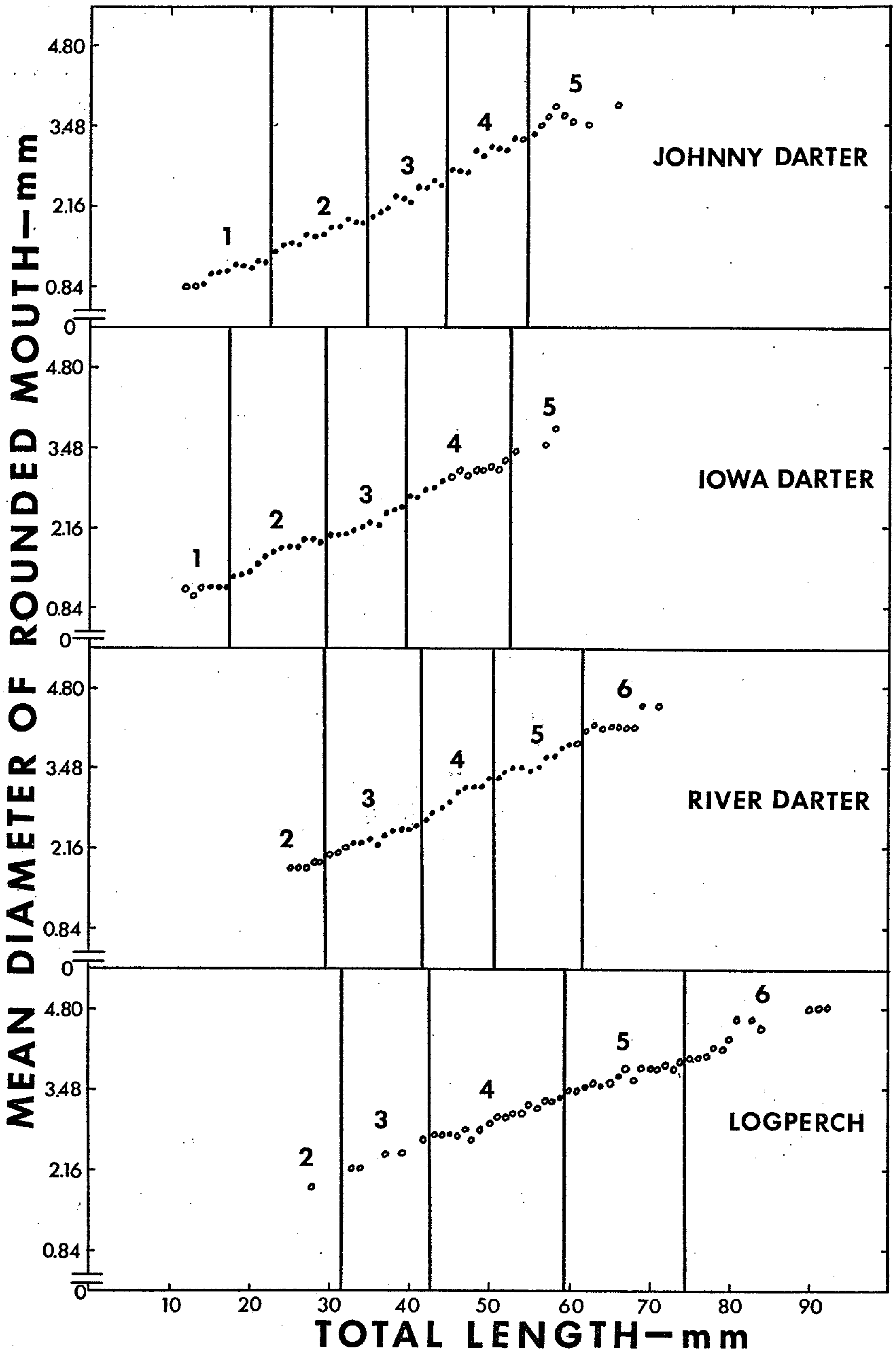
Aquarium	Environments n vs f	Species	Age	Ratio s.w.f n:f	Final ratio n:f
1	(d)vs (a)	Johnny d.	0	7:2	11*:2
			1+	7:2	11*:2
		Iowa d.	0	3:5	8:11
			1+	6:4	22*:6
		River d.	0	10:4	18:10
			1+	0:7*	---
		Logperch	0	6:0	7*:0
			1+	9*:1	---
2	(d)vs(c)	Johnny d.	0	1:0	8:10
			1+	7:3	19:11
		Iowa d.	0	5:2	14:9
			1+	4:5	6:6
		River d.	0	6:7	---
			1+	7:19	10:28*
		Logperch	0	6:1	9*:1
			1+	7:4	11:8
3	(d)vs(b)	Johnny d.	0	1:0	7:6
			1+	6:5	6:6
		Iowa d.	0	3:4	9:14
			1+	6:5	6:6
		River d.	0	1:9*	---
			1+	6:6	---
		Logperch	0	4:3	24*:7
			1+	7:4	28:13
4	(c)vs)a)	Johnny d.	0	0:1	14*:3
			1+	7*:0	---
		Iowa d.	0	4:2	17*:4
			1+	5:5	6:6
		River d.	0	1:9	---
			1+	6:17	11:19

Table 12 cont'd.

Aquarium	Environments n vs f	Species	Age	Ratio s.w.f. n:f	Final ratio n:f
4	(c)vs(a)	Logperch	0	4:0	11*:2
			1+	7*:0	---
5	(c)vs(b)	Johnny d.	0	22*:6	---
			1+	4:4	8:10
		Iowa d.	0	3:4	9:14
			1+	6:5	6:6
		River d.	0	4:8	7:24*
			1+	6:20	6:22*
		Logperch	0	3:3	8:12
			1+	2:7	6:22
6	(a)vs(b)	Johnny d.	0	0:2	1:9*
			1+	0:7*	---
		Iowa d.	0	0:7*	---
			1+	0:7*	---
		River d.	0	3:10	8:26*
			1+	6:21	6:22*
		Logperch	0	0:4	0:7*
			1+	1:9*	---

Appendix 7: THE RELATIONSHIP BETWEEN MOUTH-SIZE AND TOTAL LENGTH FOR THE FOUR SPECIES OF DARTERS.

Figure 1: The relationship between mean mouth-size and total length for the four species, showing division into classes. Solid dots represent means of ten measurements. Circles represent means of fewer than ten measurements


JOHNNY DARTER
IOWA DARTER
RIVER DARTER
LOGPERCH
MEAN DIAMETER OF ROUNDED MOUTH—mm
TOTAL LENGTH—mm
4.80
3.48
2.16
0.84
0
10
20
30
40
50
60
70
80
90

Appendix 8: DIURNAL VARIATION IN INTENSITY OF FEEDING

Table 12: Diurnal variation in intensity of feeding by large darters caught in protected pebble-rubble environment in early August. Large johnny darter and Iowa darter include classes of mouth-size 3 and 4, river darter classes 4 and 5, and logperch class 5. Figures given are means, with the number of fish examined appearing in parentheses. For an individual fish, intensity of feeding is given by:

$$\frac{\text{Weight in gm of all stomach contents (except parasites)}}{\text{Weight of entire fish}} \times 100$$

Station	Species	Time of Day 5:30	11:30	17:30	23:30
L2	Johnny d.	0.01 (15)	0.78 (18)	0.31 (11)	0.69 (20)
	River d.	0.05 (12)	---	0.41 (13)	0.47 (12
L 16	Johnny d.	0.43 (14)	0.52 (12)	1.05 (7)	1.02 (13)
	Iowa d.	0.60 (16)	1.15 (12)	1.10 (11)	1.89 (13)
	River d.	1.03 (14)	1.15 (12)	0.35 (10)	0.33 (13)
	Logperch	0.37 (10)	0.87 (10)	1.39 (7)	0.24 (10)