FACTORS AFFECTING THE DISTRIBUTION OF SUNFISHES (CENTRARCHIDAE) IN SOUTHERN NEW JERSEY

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Camden, New Jersey

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ABSTRACT OF THE THESIS

Factors Affecting the Distribution of Sunfishes (Centrarchidae) in Southern New Jersey

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Thesis director: Professor Robert W. Hastings

At least three factors are at work limiting the distribution of species of *Enneacanthus* and *Lepomis* in southern New Jersey. These are: (1) the chemical characteristics of the aquatic habitat, especially pH, calcium, dissolved carbon dioxide, and toxic heavy metals; (2) interspecific competition; and (3) the productivity and trophic structure of the respective habitat types.

L. gibbosus and *L. macrochirus* are absent from most acid, dystrophic waters, while *E. chaetodon* and *E. obesus* are characteristic of these habitats. *E. gloriosus* is widely distributed in both dystrophic and eutrophic waters. *Enneacanthus* species are morphologically and behaviorally suited for nutrient poor dystrophic habitats where almost all production is associated with iron floc covering both aquatic macrophytes and substrate. *L. gibbosus* and *L. macrochirus* are at a disadvantage in these habitats. Very young *Lepomis* are primarily open water planktivores, a feeding niche that is conspicuously absent in

dystrophic waters. Water chemistry gives the illusion of having a direct effect on distribution, but is probably more important because of the way it affects habitat structure.

ACKNOWLEDGMENTS

I wish to express my deepest appreciation to my thesis committee, Dr. Robert W. Hastings, Dr. Ralph E. Good, and Dr. James B. Durand. Each contributed immensely to the development of this paper. I owe my interest in biogeography to Dr. Ralph E. Good, and my appreciation of aquatic productivity to Dr. James B. Durand. I learned about fish from Dr. Robert W. Hastings, my main thesis advisor. Most of the problems and ideas presented here were developed with Dr. Hastings during our many informal discussions.

John C. O'Herron III, Dr. Hastings, Dr. John Kohl, Catherine Chamberlin-Graham, and James J. Graham helped collect the fish. Dr. James E. Bohlke kindly allowed me to examine the collection of fishes at the Philadelphia Academy of Natural Science. Walter S. Murawski made available the files, collection data, and reports of the Freshwater Research and Development Section of the N.J. Bureau of Fisheries at Lebanon, New Jersey.

I am especially grateful to my wife, Catherine Chamberlin-Graham, for typing, proofreading, and helping with the research and collecting. Without her constant moral support, love, and sense of purpose, this thesis would have never come to be.

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I. INTRODUCTION

The distribution of organisms in nature is determined by various factors, both abiotic and biotic, operating in time upon all members of a species community. Early zoogeographers stressed historical influences on broad patterns of distribution (Darlington 1957). Ecologists, studying the local distribution of organisms, were more interested in abiotic limitations on individual species. Some limnologists believed that the local distribution of fishes in fresh water was clearly related to pH (Coker 1925, Creaser 1930). This view has been strongly criticized by many authors (Jewell and Brown 1929, Hutchinson 1957, Odum 1975). Dissolved oxygen, temperature, current, and substrate are usually considered to be more important characteristics of the aquatic environment (Hynes 1970). Recent trends in ecological thought have favored biological explanations for the local distribution of organisms. Ivlev (1961) considered biotic factors, especially feeding, to be more decisive than abiotic factors. Competition and predation are important mechanisms influencing the composition of fish communities (Zaret and Rand 1971, Fryer and Iles 1972, Lowe-McConnell 1975) and the local distribution of individual species. The interaction between species is determinative because of the way it amplifies differences in the abiotic environment, habitat structure, and the species themselves.

Certain sunfishes in the family Centrarchidae have been the subject of speculation concerning the role of pH, water chemistry, and competition on their distribution. The disjunct distribution of the blackbanded sunfish, *Enneacanthus chaetodon* (Baird), in North America is attributed to a variety of factors. Bailey (1938) echoed the sentiments of many earlier naturalists and aquarists when he stated that *E. chaetodon* does not thrive in higher pH water. Smith (1953) argued that competition from other species may be more important than water chemistry in determining the distribution of *E. chaetodon*. At the same time, he speculated that high acidity may be a limiting factor for the pumpkinseed, *Lepomis gibbosus* (Linnaeus), in the New Jersey Pine Barrens. Recently, Foster (in a paper given at the 1976 Annual Meeting of the New Jersey Academy of Science) proposed that reproductive success in *Enneacanthus* (or lack of it in other species) may be related to the low calcium content of highly acidic or dystrophic waters.

The purpose of this paper is to examine the factors affecting the distribution of sunfishes, including *Enneacanthus chaetodon*, *E. obesus* (Girard), *E. gloriosus* (Holbrook), *Lepomis gibbosus*, and *L. macrochirus* Rafinesque, in southern New Jersey. Two types of aquatic habitat are contrasted: (1) the dystrophic waters of the New Jersey Pine Barrens, and (2) the mesotrophic and eutrophic waters of the Inner Coastal Plain and agricultural areas within the Pine Barrens. This dichotomy presents an opportunity for the evaluation of many interrelated factors, including (1) water chemistry, (2) trophic structure, (3) habitat, (4) species morphology and behavior, and (5) interspecific competition.

II. INTRODUCTION TO THE ECOLOGY OF *ENNEACANTHUS* AND *LEPOMIS*

Among the centrarchid fishes, the Enneacanthini stand out as a specialized group, quite distinct from other sunfishes (Bailey 1938). Three species, *E. chaetodon* (blackbanded sunfish), *E. obesus* (banded sunfish), and *E. gloriosus* (bluespotted sunfish), are included in the genus. They are characterized by loss and reduction of dental characters, small size (to 75 mm SL), reduction in the number of vertebrae (Bailey 1938), and reduced acoustico-lateralis canals (Branson and Moore 1962). Species of *Enneacanthus* are restricted to the Atlantic Coastal Drainages and several river systems draining into the Gulf of Mexico, except where *E. gloriosus* has invaded the Lake Ontario Drainage (Werner 1972).

All of the Enneacanthini possess a short and deeply compressed body. They frequent waters with little or no current, especially in dense vegetation, leafy debris, tangled branches, or other concealing structures. Small size, vertical banding, reduced jaw size, and a rounded caudal fin are adaptations to this environment (Sweeney 1972). A complete review of the distribution and taxonomy of this genus is presented by Sweeney (1972). Life histories and habits of individual species can be found in Bailey (1941), Reid (1950), and Schwartz (1961) for

E. chaetodon, and Breder and Redmond (1929) for E. gloriosus. A life history of E. obesus is being prepared by Alan Cohen at the University of Connecticut.

Lepomis is the largest and most widespread sunfish genus, ranging throughout the Mississippi River Drainage, the Gulf of Mexico Coastal Drainages, and the Atlantic Coastal Drainages into southern Canada (Moore 1968). Five members of the genus are reported from New Jersey, but only L. gibbosus (pumpkinseed) and L. macrochirus (bluegill) are common in the study area. (L. macrochirus is an introduced species that has been stocked throughout the state.) L. auritus (redbreast sunfish) is more common in Piedmont streams, while L. gulosus (warmouth) is only reported from the Delaware River (Fowler 1905) and may be extinct in New Jersey. L. cyanellus (green sunfish) is a newcomer, from eastern Pennsylvania, which has been introduced into the Delaware River Drainage.

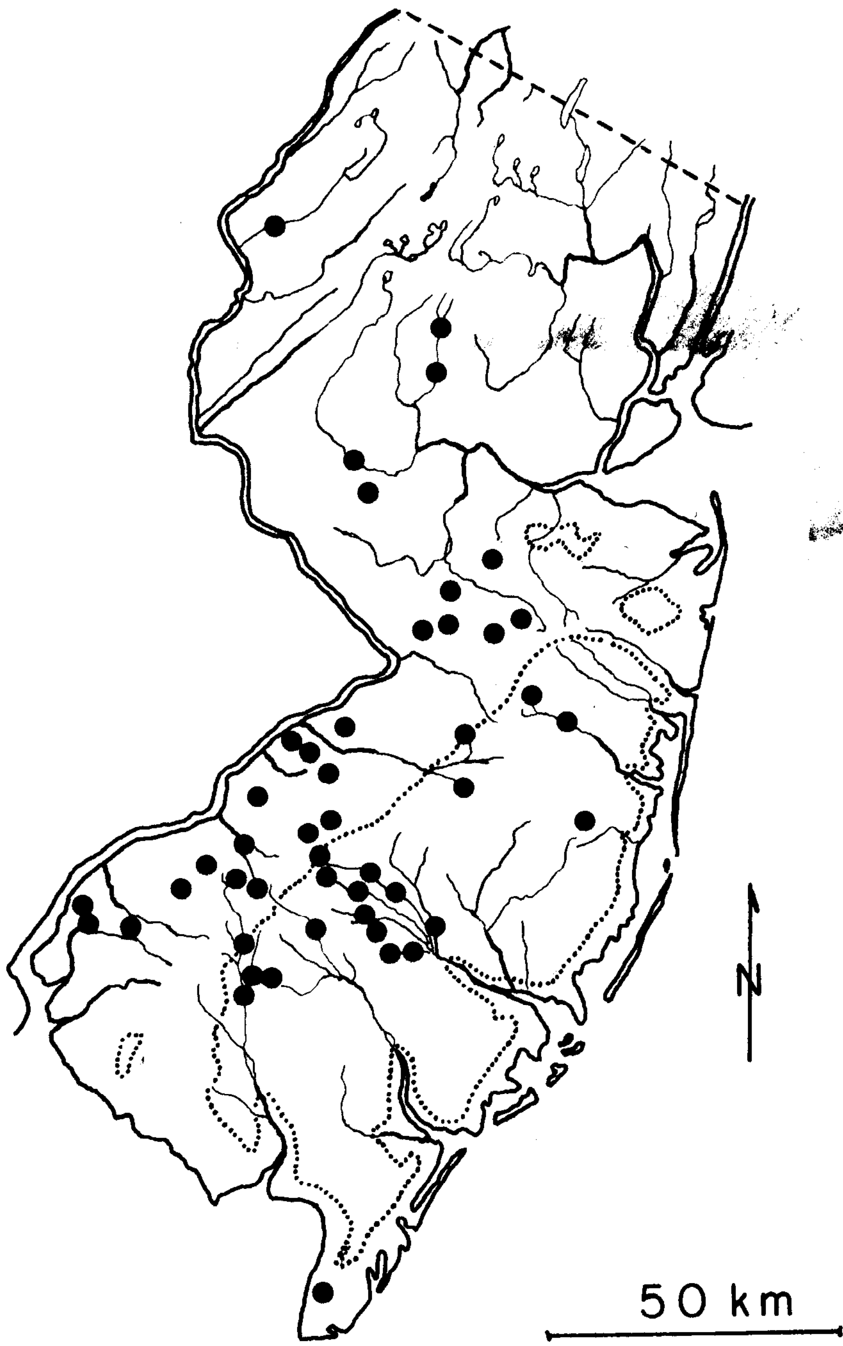
Both L. gibbosus and L. macrochirus reach more than twice the maximum standard length of Enneacanthus. They are deeply compressed, or gibbose, as adults and have an emarginate caudal fin. Keast and Webb (1968) point out that these structural features are directly associated with hanging or hovering in the water. Members of this genus are well known for their aggressive territoriality during courtship and spawning (Greenburg 1947, Breder and Rosen 1966.)

III. STUDY AREA

Southern New Jersey can be divided into two distinct geographic regions. The Inner Coastal Plain is a heavily populated corridor some 20 to 30 km in width bordering the Delaware River and extending from Delaware Bay to Raritan Bay. It was formerly covered with deciduous forest, a part of Braun's (1950) Oak-Chestnut Region, which has been replaced with agricultural, urban, and suburban development. Cretaceous deposits of sand, silt, and clay make up most of the surface geology (Kummel 1940). The soils contain low to moderate quantities of the essential nutrients (Toth and Smith 1960), but cultural eutrophication has enhanced the nutrient load entering this region's streams and ponds. The surface waters tend to be moderately soft, and productive, with a pH close to neutrality.

In contrast to the populous Inner Coastal Plain, the sparsely populated Pine Barrens occupy most of the Outer Coastal Plain and a very small portion of the Inner Coastal Plain (Figure 1). Braun (1950) described this area as an "extensive plain, clothed with forests of pitch pine and scrubby oaks, which are interrupted here and there by expanses of shrubby oaks and pines... and by bogs and swamps." The Cohansey Formation, a post-Eocene deposit

Figure 1. Collection localities in New Jersey. The approximate boundary of the Pine Barrens is indicated by a dotted line (after McCormick 1970).


N
50 km

of fine to coarse quartz sand, influences the character of this region. The soils contain very low quantities of the essential elements (Toth and Smith 1960) and virtually no sources of phosphorus (Wilkerson et al. 1948). The streams draining these soils are exceedingly soft, acid, and deeply stained with humic substances. Further information on the hydrography of the Pine Barrens can be found in Smith (1960), Fikslin and Montgomery (1971) and Rhodehamel (1970, 1973).

I made extensive collections throughout these regions (Figure 1), but Atco Lake was the site for most of my observations. This impoundment is located on upper Hays Creek in the Mullica River Drainage, Atco Township, Camden County (Figure 2). The surface area of the lake is approximately 4 hectares, with a mean depth of 0.8 meters and a maximum depth of 1.5 meters at the dam (open file; N.J. Dept. Environ. Protection; Div. Fish, Game and Shellfisheries; Freshwater Laboratory; Lebanon, N.J.). A highway borders the lake at the dam, and a picnic grove and sand beach occupy the eastern shore. The upper lake is relatively undisturbed and is bordered by a remnant southern white cedar (Chamaecyparis thyoides) swamp which extends up Hays Creek.

The substrate of Atco Lake, along the eastern shore beach is mostly sand with increasing silt toward the middle of the lake. The substrate of the upper lake and backwater pools is fine silt and organic muck. The bottom is a mosaic of submerged Utricularia beds of varying depth, bare substrate, and columns of Myriophyllum which reach to the surface. Covering everything and suspended in the otherwise clear and lightly colored water is a yellow-brown flocculant material. Some of the backwater pools in the upper lake and swamp have a darker stain than the main body of water. The water is soft, with a reported methyl orange alkalinity (27 November 1973) of less than 2.0 ppm (open file, Lebanon Freshwater Laboratory), and an acid pH ranging from 5.4 to 6.4.

The local conservation officer (open file, Lebanon Freshwater Laboratory) reported accelerated deterioration of Atco Lake in 1973 due to a pig farm and housing development along Hays Creek. Most of the deterioration appears to be in the form of heavy siltation, and only minor eutrophication is evident. Atco Lake lies somewhere between dystrophy and eutrophy in the revised trophic series of Berg and Petersen (1956) and Rodhe (1969).

The flora and fauna of Atco Lake comprise an interesting combination of characteristic Pine Barrens species with acid intolerant species which are common to the Inner Coastal Plain. All of the centrarchids I consider in this paper are found in Atco Lake (a rare situation in such a small pond). A list of fish species is presented in Table 1, according to Hastings' (1978) classification of Pine Barrens fishes.

Figure 2. The Mullica River Drainage showing sites mentioned in the text.

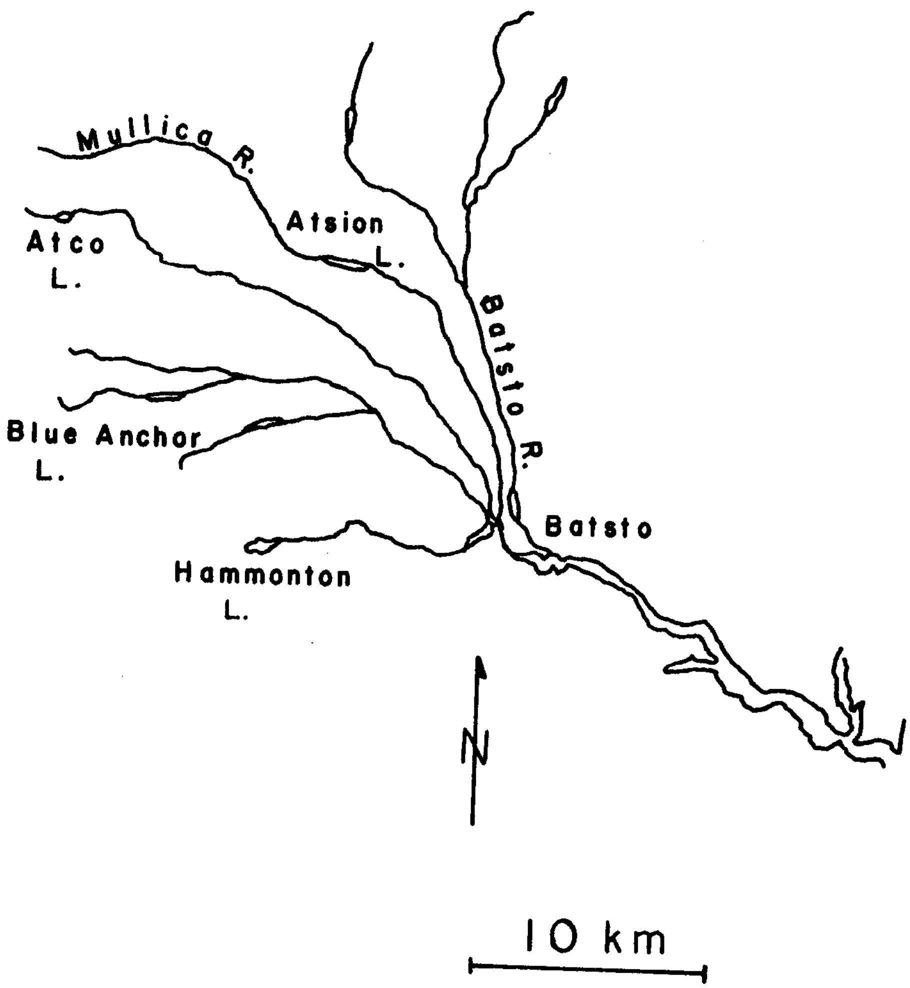

Mullica R.
Atsion L.
Atco L.
Batsto R.
Blue Anchor L.
Batsto
Hammonton L.
N
10 km

TABLE 1

FISH SPECIES COLLECTED FROM ATCO LAKE[1]

Characteristic species of the Pine Barrens

Acantharchus pomotis
Enneacanthus chaetodon
Enneacanthus obesus
Etheostoma fusiforme

Widely distributed species common in the Pine Barrens

Esox niger
Umbra pygmaea
Erimyzon oblongus
Enneacanthus gloriosus

Peripheral Pine Barrens species more characteristic of the Inner Coastal Plain

Notemigonus crysoleucas[2]
Ictalurus nebulosus
Fundulus diaphanus
Lepomis gibbosus

Exotic species (not tolerant of acid water)

Lepomis macrochirus
Micropterus salmoides

[1]Classification after Hastings (1978)

[2]*Notemigonus crysoleucas* was observed but not collected.

IV. METHODS AND MATERIALS

Distribution of Sunfishes in Southern New Jersey

I determined the distribution of species of *Enneacanthus* and *Lepomis* in the study area by making extensive collections, and supplementing these with the pre-existing collections of Robert W. Hastings (Rutgers University, Camden, N.J.), the collection of the Philadelphia Academy of Natural Sciences, the unpublished records of the New Jersey Department of Environmental Protection (open file, Lebanon Freshwater Laboratory), and a variety of other sources in the literature (Baird 1855, Cope 1862, 1896, Abbott 1883, 1885, Fowler 1905, 1911, 1915, 1918, 1921, 1938, 1940, Breder and Redmond 1929, N.J. Div. of Fish and Game 1951, 1953, 1957, Smith 1960, Mihursky 1962, Anselmini 1971, Thomas et al. 1974). I sampled field stations for at least an hour, or until all habitats were adequately covered, with a 15 foot seine (3/16 inch mesh) or with a shorter 5 foot seine in very small streams. I measured pH at each collection site, at first colorimetrically with Lamotte standardized indicators and later with a portable Beckman NB field pH meter.

I used the pH values of my collections, and of the N.J. Division of Fish and Game (1951, 1953, 1957) to determine the relationship between centrarchid distribution and aquatic pH. In order to determine the effect of agricultural and urban development on local aquatic systems, I measured the pH at 27 to 31 stations in the Mullica River Drainage on 8 and 22 August 1976 and 15 February 1977. Using McCormick's (1973) The Pine Barrens: Vegetation Geography, the appropriate geological survey quadrangles, and a Tacro cartometer, I estimated the stream mileage above each station and the relative contribution of streams draining pine-oak forest, oak-pine forest, cedar swamp forest, hardwood swamp forest, pitch pine lowland forest, agricultural regions and urban areas.

Dietary Analysis

I collected fishes from Atco Lake on 7 August 1975 and 20 June 1976. On 7 August, I seined in the northwest corner of the lake, while the 20 June collection was seined from the eastern shore beach and shallow backwaters on the southeastern shore. All collections were made with a 15 foot, 3/16 inch mesh nylon seine. Fishes were fixed in 10% formalin and stored in 70% ethanol. In the laboratory, I measured the standard length of each specimen. I examined the contents of the stomach and noted its fullness. Stomach contents (or rarely intestinal contents) were mounted on a microscope slide in Hoyer's solution. I identified food items in most cases to genus and estimated the volume of each item by assuming its shape to be cylindrical.

The species and numbers of fish examined is presented in Tables 2-14. I divided these into three subgroups based on size: (a) 10-15 mm SL (E. chaetodon only), (b) 20-35 mm SL, and (c) 35-50 mm SL. Some samples were too small to divide into separate groups (L. macrochirus and E. gloriosus in June 1976) and all data for that species is combined regardless of size.

Functional Morphology

The morphology of the dietary apparatus was examined in collections from the Mullica River Drainage. I measured standard length, head length, snout length, length of upper jaw, length of the mandible, and gape width (Hubbs and Lagler 1958) using a Rostrei-Helios caliper (accurate to 0.1 mm, estimate to approximately ± 0.02 mm). I also determined compression or gibbosity in a collection from Atco Lake by plotting standard length against body depth.

Underwater Observations

Underwater observations were made in Atco Lake to determine the structure of the aquatic habitat and to observe the distribution and foraging habits of the fishes. I visited the lake for several hours each on 10 July, 7 August, and 5 October 1976. I recorded observations on a plastic slate while using face mask and snorkel.

Almost all observations were in water less than a meter deep, along the entire length of the eastern shore.

Aquarium Observations

I observed aquarium-held fishes for swimming movements, activity, methods of foraging, and general behavior. I obtained all specimens from Atco Lake and Hays Creek and transferred them to a 35 x 75 cm aquarium in the laboratory. The aquarium contained three individuals of each species (33.6 - 52.9 mm SL) except *L. macrochirus*, and was planted with *Myriophyllum* and an unidentified aquatic bryophyte. A grid, divided into 5 cm squares was placed on the back surface, for quantifying the activity of individual fish.

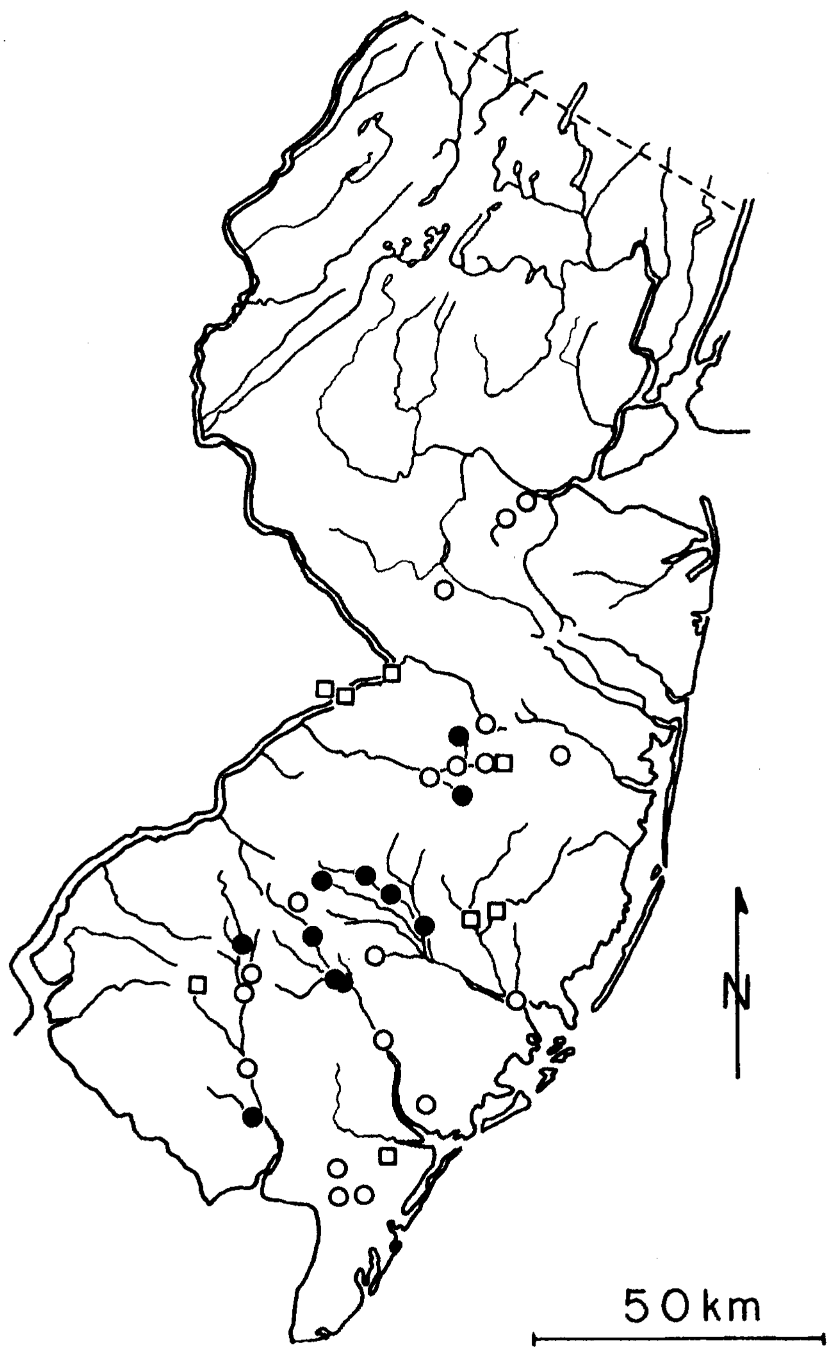
Using a tape recorder, counter and timer, I noted activity and foraging behavior for each fish. I estimated activity by facing the tank at a distance of 1 meter and counting the number of squares entered by the eye of a fish in a 5 minute period. Simultaneously, I noted the type of foraging: (1) at the substrate, (2) in the water column, (3) in the vegetation, or (4) at the surface. I observed fish for a total of 23 hours (1.9 hours per fish) on July 10, 11, and 14, 1976, from approximately 9:00 a.m. to 5:00 p.m. each day. Occasional observations were made on other fishes maintained in aquaria.

V. RESULTS

Distribution

Populations of E. chaetodon in North America are widely discontinuous, a phenomenon usually produced by widespread extinction within the area of disjunction. In New Jersey, E. chaetodon probably had a wider distribution in the past than it does today (Figure 3). Abbott (1883) and Fowler (1905, 1921) reported E. chaetodon in the tidewater region of the lower Delaware River, and at several sites in eastern Pennsylvania where it has not been collected since 1916 (Clark N. Shiffer, Herpetology and Endangered Species Coordinator, Pennsylvania Fish Commission, Division of Fisheries, Bellafonte, Pennsylvania, personal communication). Intensive collecting by Ichthyological Associates Inc. in the Delaware River, near some of these original collection sites, failed to yield any specimens (Anselmini 1971). In addition, it has apparently been extirpated in Grover's Mill Pond, in the Raritan-Millstone Drainage, sometime within the last 25 years. The New Jersey Division of Fish and Game (1957) reported E. chaetodon in Grover's Mill Pond in 1952, but no specimens were collected in 1969, after suburban development, increased pollution, and channelization of the tributary stream had occurred (open file, Lebanon Freshwater Laboratory). I failed to find E. chaeto-

Figure 3. Distribution of _Enneacanthus_ _chaetodon_ in New Jersey. Sites are classified as: (□) collection or report before 1930; (○) collection or report after 1930; (●) collection of Rutgers University, Camden (1974-1977).

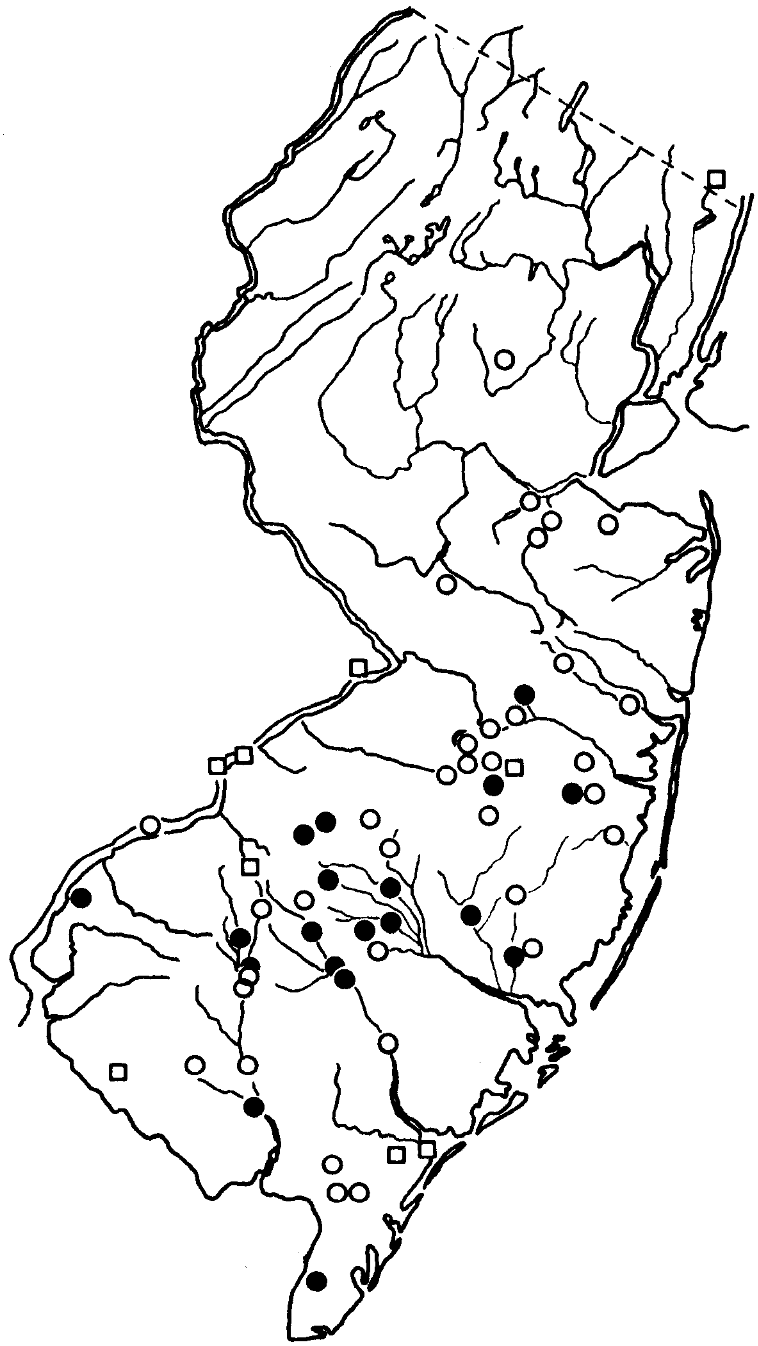

N
50km

don in either Grover's Mill Pond (June 1977) or in Big Bear Brook, its main tributary (August 1975).

The past distribution of E. obesus was similar to that of E. chaetodon in New Jersey, but with several exceptions (Figure 4). It ranged historically into the Hackensack River Drainage (Bean 1903) and is reported from Great Swamp (unpublished species list, National Wildlife Service, Great Swamp National Wildlife Refuge), whereas E. chaetodon only ranges into the southern tributaries of the Raritan River. Furthermore, remnant E. obesus populations have been reported in the Delaware River at the Eddystone Generating Station between Chester and Philadelphia, Pennsylvania (Clark N. Shiffer, personal communication), and have been collected in Game Creek, a Delaware River tributary near Penns Grove, New Jersey. The Eddystone site is near Tinicum Marsh, one of the last natural freshwater tidal marshes in Pennsylvania, while Game Creek drains a large undisturbed red maple (Acer rubrum) swamp. Like E. chaetodon, E. obesus has apparently been reduced or extirpated from many of its former habitats, including Grover's Mill Pond. Most of the sites where E. obesus and E. chaetodon occur today in New Jersey lie within the boundaries of the Pine Barrens.

In contrast, E. gloriosus is widely distributed throughout New Jersey, from the dystrophic waters of the Pine Barrens to the limestone streams of the Great Appalachian Valley, a region of alternating ridges and valleys

Figure 4. Distribution of Enneacanthus obesus in New Jersey. Sites are classified as: (□) collection or report before 1930; (○) collection or report after 1930; (●) collection of Rutgers University, Camden (1974-1977).



in the northwestern corner of the state (Figure 5). However, it is less numerous in the Pine Barrens than either E. chaetodon or E. obesus. L. gibbosus and L. macrochirus have similar distributions, being more widely distributed outside the Pine Barrens (Figures 6 and 7). Despite extensive stocking (open file, Lebanon Freshwater Laboratory), neither species has established populations in the more acid waters of the Pine Barrens.

The distribution of all New Jersey centrarchids seems to be influenced by the pH of the aquatic habitat (Figure 8). E. chaetodon and E. obesus occur more frequently in water ranging from pH 4.0 to 5.5 with a maximum of about pH 7.1. Their relative abundance in a habitat is lower where pH approaches neutrality. E. gloriosus, on the other hand, spans the entire pH range, but is more frequent in neutral to slightly basic waters. Both L. gibbosus and L. macrochirus are apparently absent from all waters below pH 4.9. In addition, their relative abundance in a habitat decreases as this lower limit of pH is reached.

The effect of agricultural development on the pH of waters in the Mullica River Drainage is presented in Figures 9,10, and 11. Even minor agricultural development in the watershed can raise the pH of downstream stations, particularly during periods of low water (e.g. 22 August). L. gibbosus and L. macrochirus have successfully invaded most of the waters affected by agricultural (or urban) development (e.g. Blue Anchor Lake, Hammonton Lake, and

Figure 5. Distribution of Enneacanthus gloriosus in New Jersey. Sites are classified as: (□) collection or report before 1930; (○) collection or report after 1930; (●) collection of Rutgers University, Camden (1974-1977).

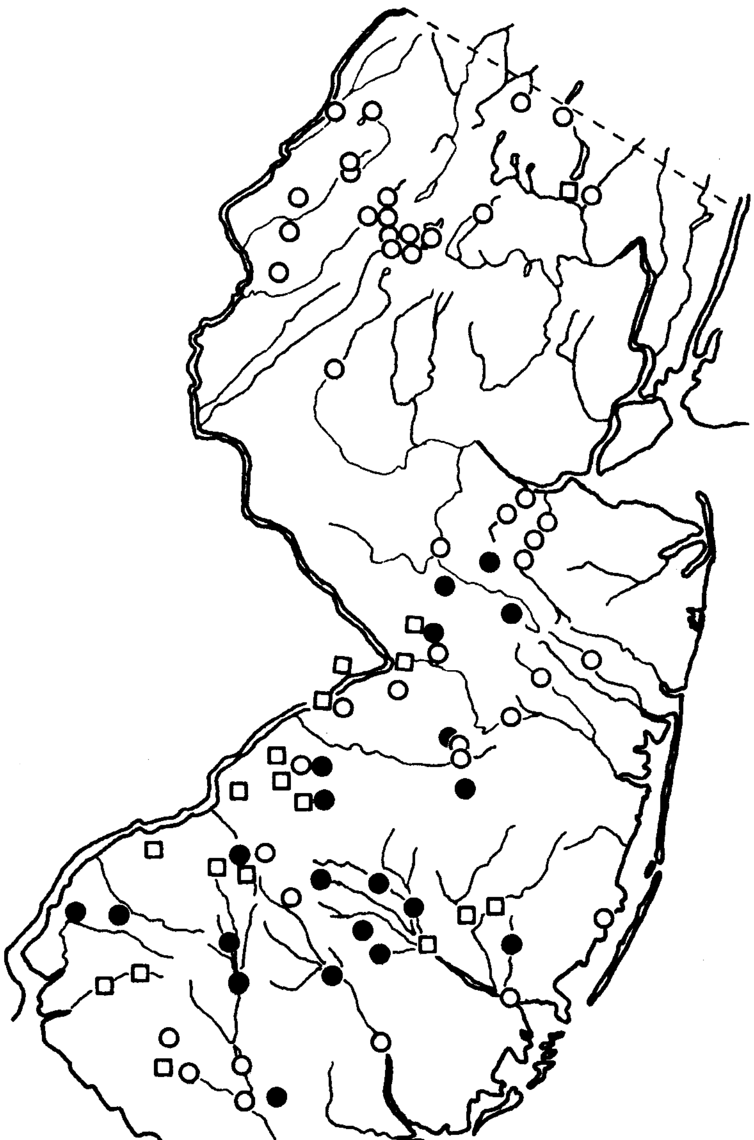


Figure 6. Distribution of Lepomis gibbosus in New Jersey. Sites are classified as: (□) collection or report before 1930; (○) collection or report after 1930; (●) collection of Rutgers University, Camden (1974-1977).

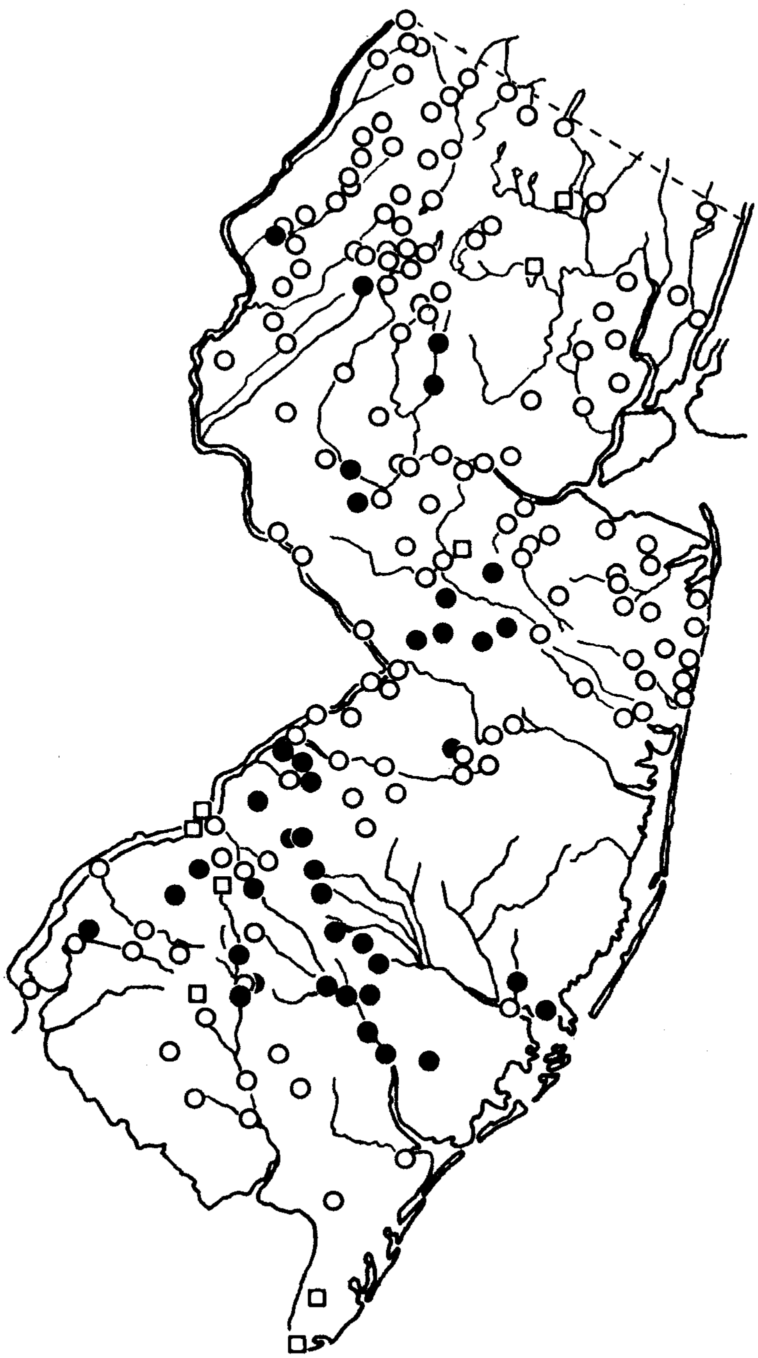


Figure 7. Distribution of Lepomis macrochirus in New Jersey. Sites are classified as: (□) collection or report before 1930; (○) collection or report after 1930; (●) collection of Rutgers University, Camden (1974-1977).

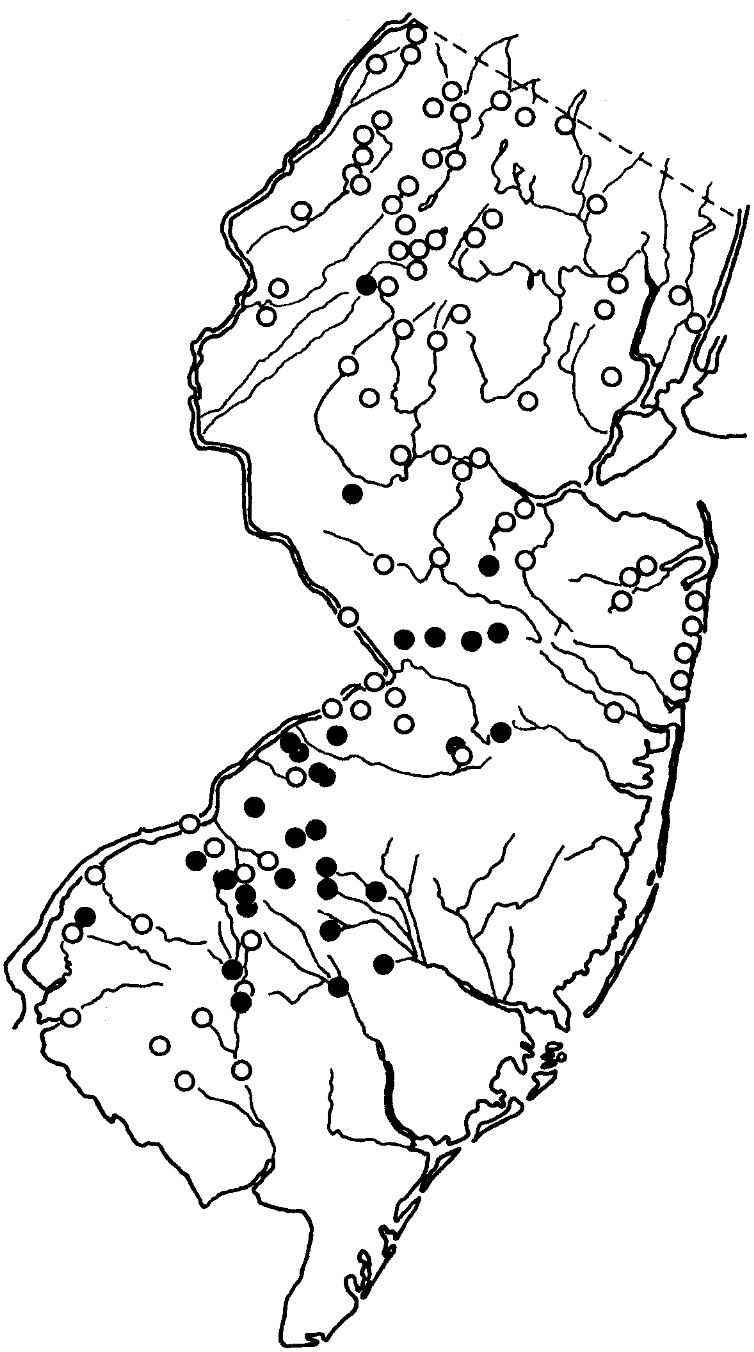


Figure 8. The effect of pH on the frequency of occurrence of *Enneacanthus chaetodon* (○), *E. obesus* (●), *E. gloriosus* (□), *Lepomis gibbosus* (△), and *L. macrochirus* (■) in 93 New Jersey ponds. (Modified from N.J. Div. Fish and Game 1951, 1953, 1957).

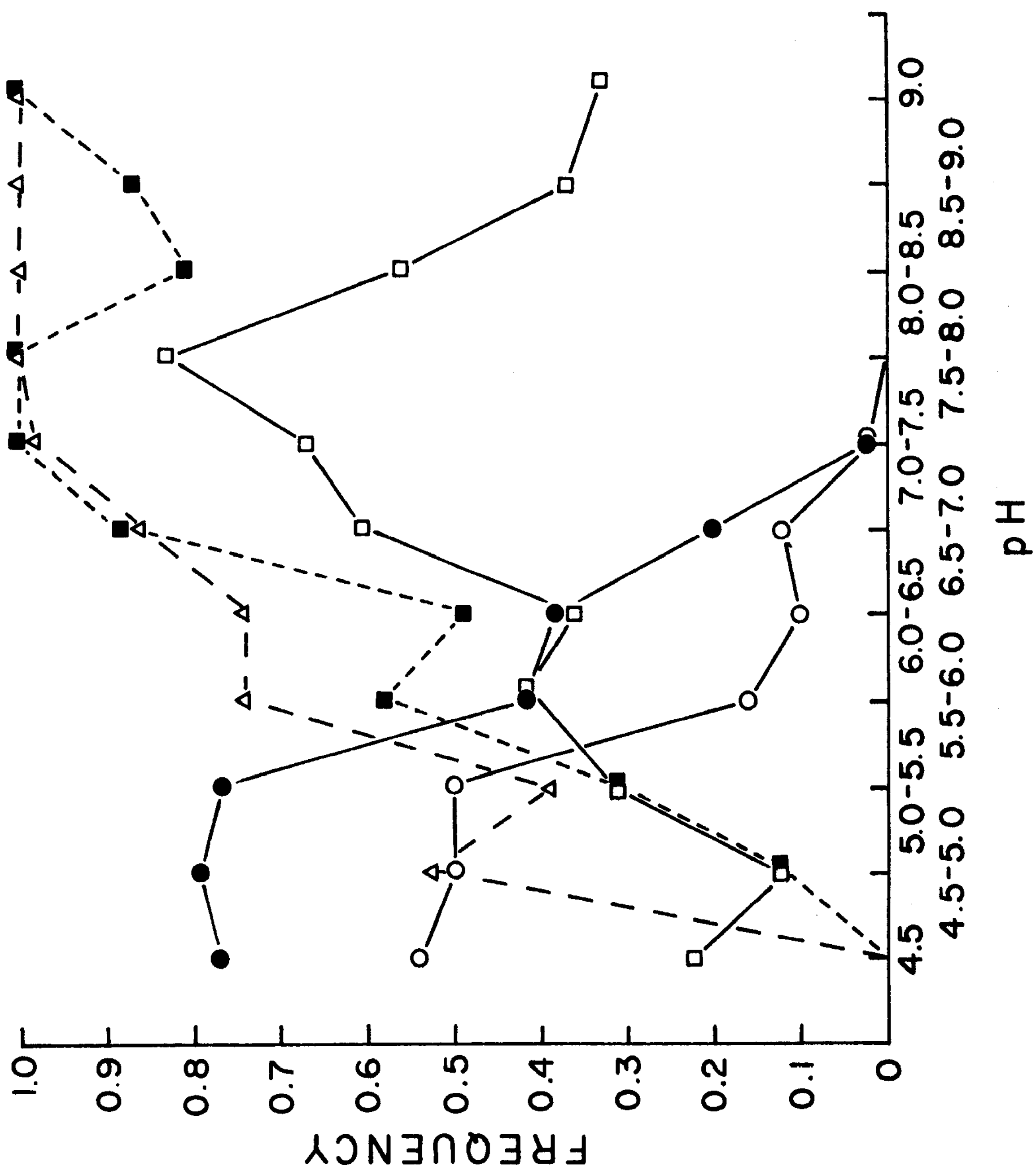
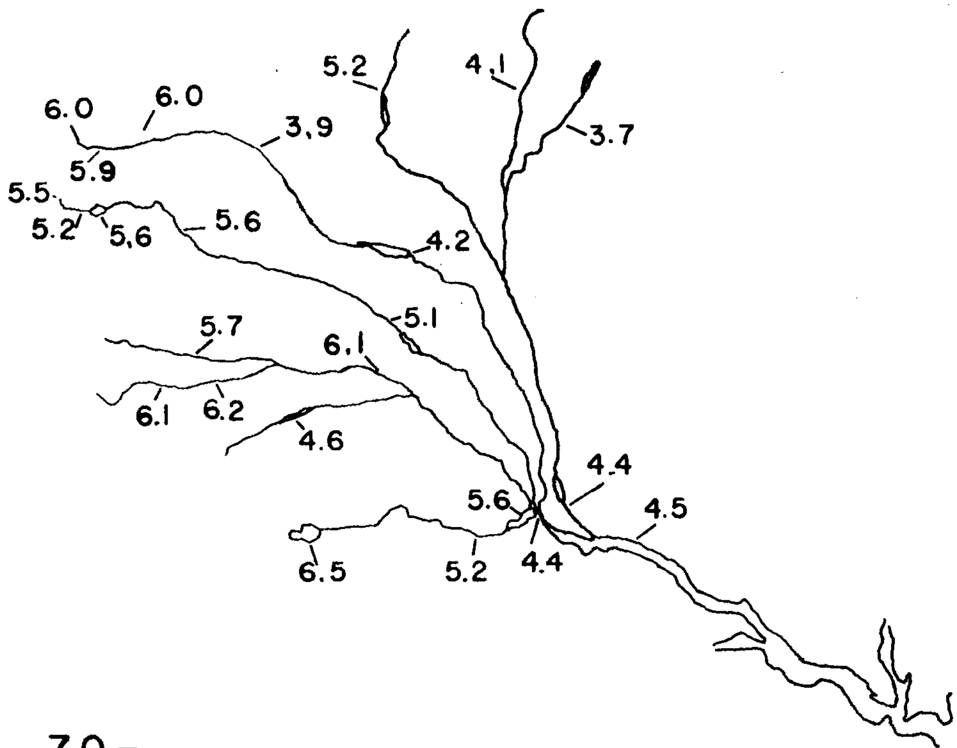

FREQUENCY
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
4.5
4.5-5.0
5.0-5.5
5.5-6.0
6.0-6.5
6.5-7.0
7.0-7.5
7.5-8.0
8.0-8.5
8.5-9.0
9.0
pH

Figure 9. The distribution of pH and its relationship to agricultural and urban development within the Mullica River Drainage (8 August 1976). First order streams are excluded from the lower graph. Percent agricultural and urban development was determined using McCormick (1973), the appropriate geological survey quadrangles, and a cartometer to estimate the stream mileage above each station, and the relative contribution of streams draining agricultural, urban, and forested areas.


5.2
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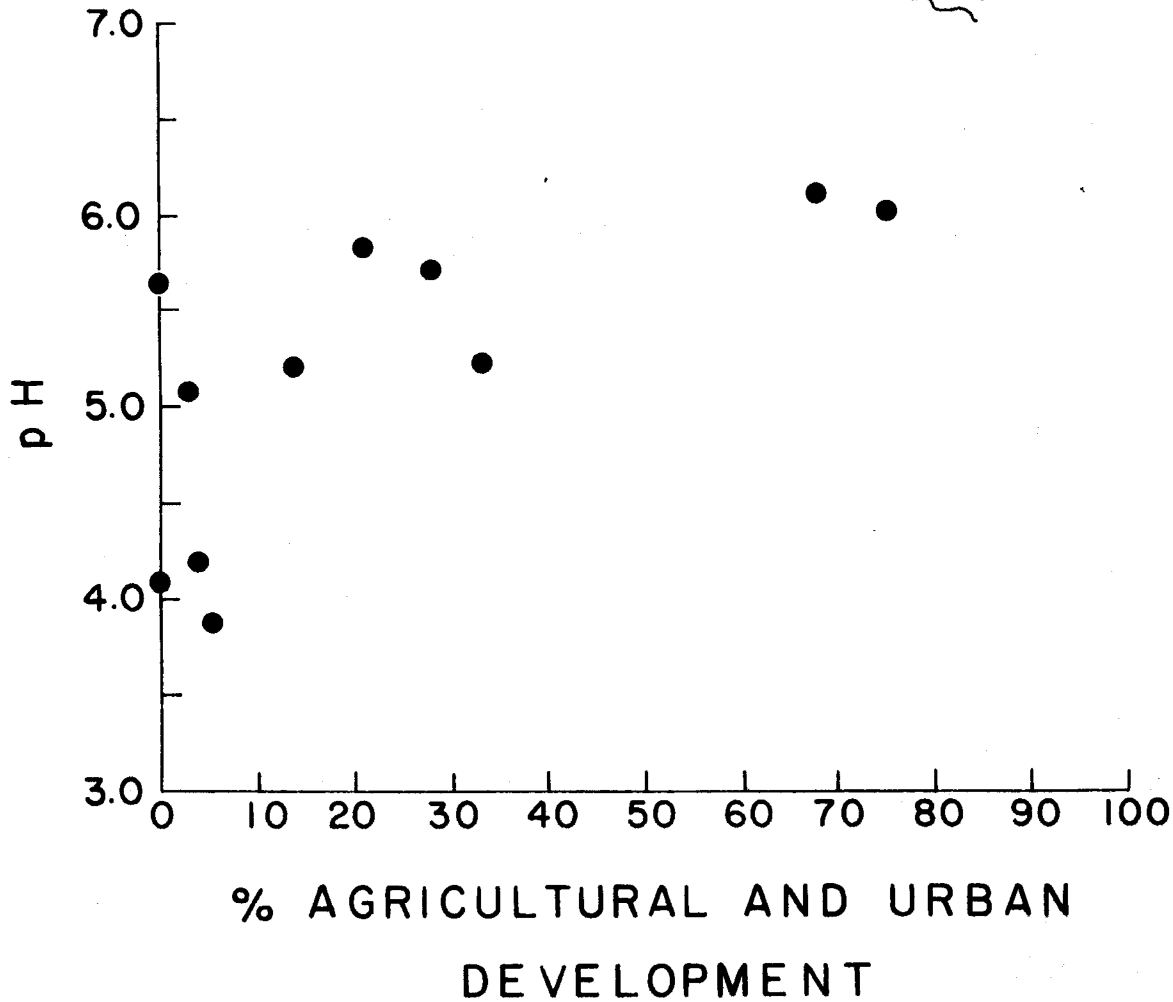
5.2
4.4


7.0
6.0
5.0
4.0
3.0
pH
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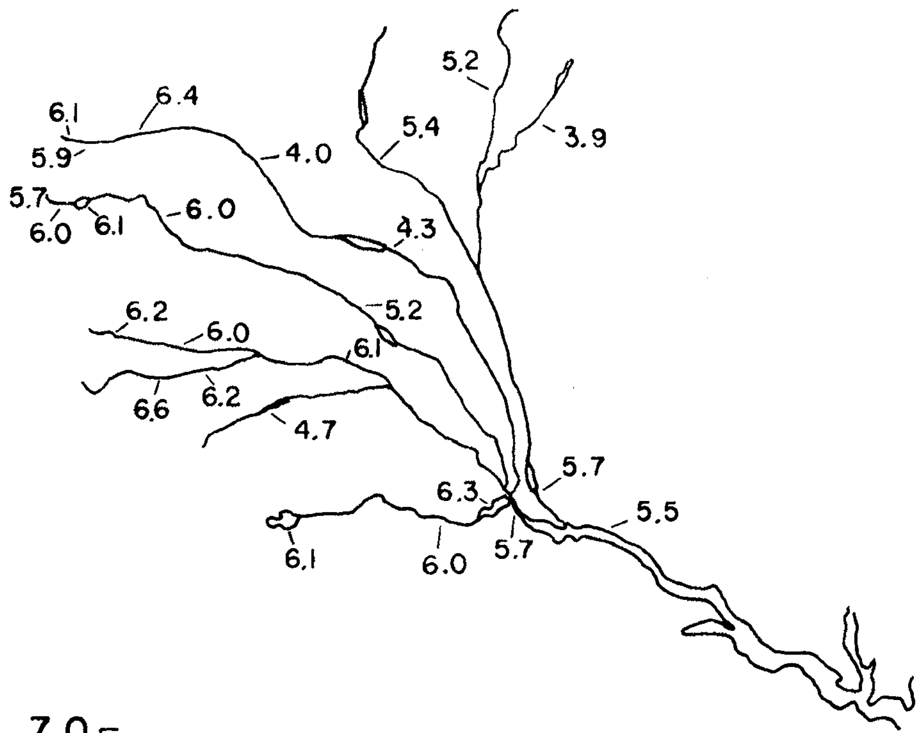
20
30
40
50
60
70
80
90
100
% AGRICULTURAL AND URBAN
DEVELOPMENT

Figure 10. The distribution of pH and its relationship to agricultural and urban development within the Mullica River Drainage (22 August 1976). First order streams are excluded from the lower graph. Percent agricultural and urban development was determined using McCormick (1973), the appropriate geological survey quadrangles, and a cartometer to estimate the stream mileage above each station, and the relative contribution of streams draining agricultural, urban, and forested areas.


5.2
6.4
6.1
5.4
3.9
5.9
4.0
5.7
6.0
6.0
6.1
4.3
5.2
6.2
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5.5
6.1
6.0
5.7

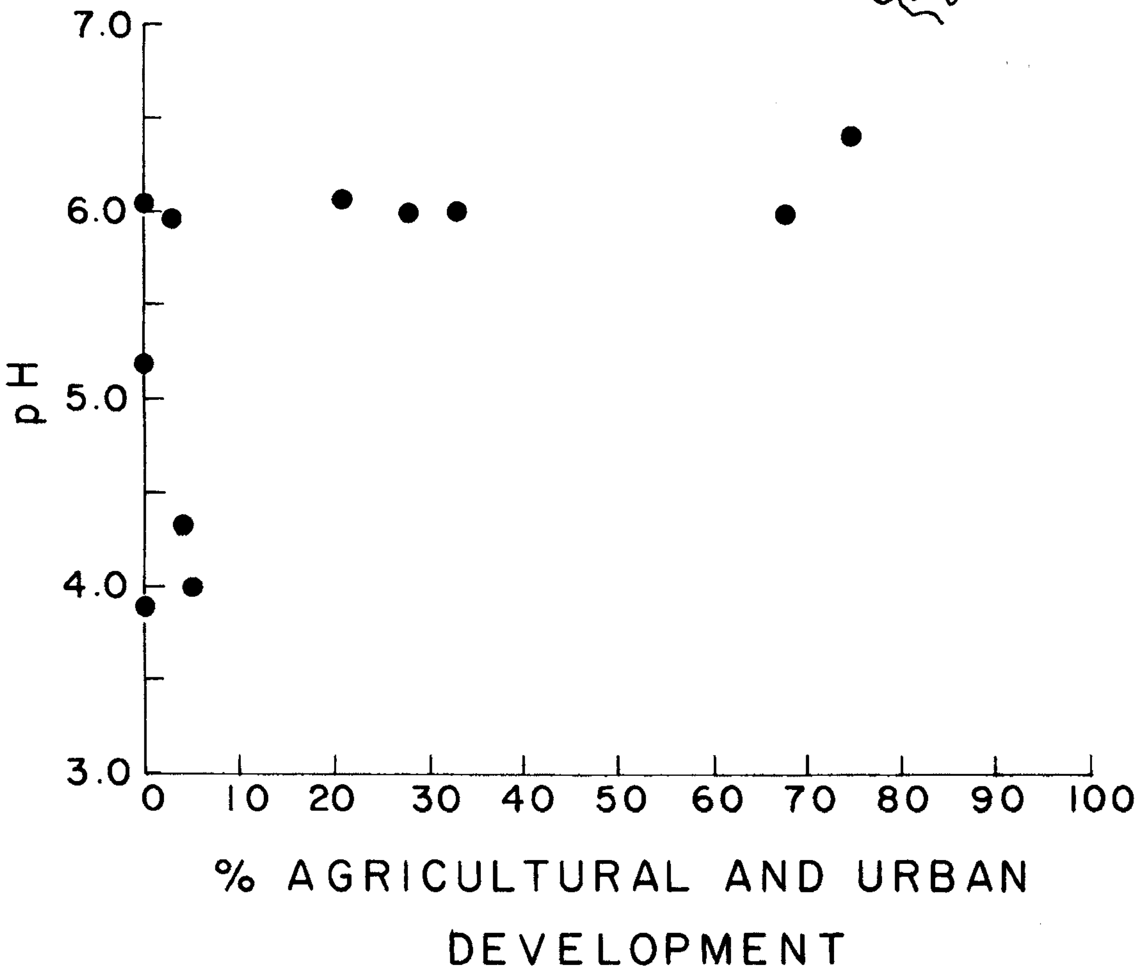
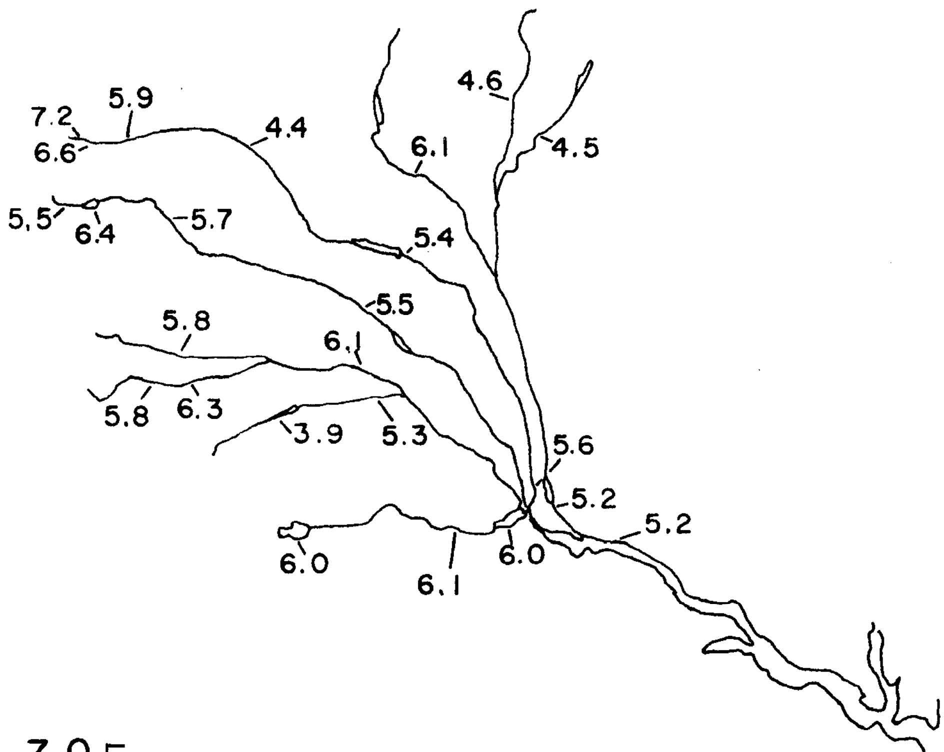

7.0
6.0
5.0
4.0
3.0
pH
0
10
20
30
40
50
60
70
80
90
100
% AGRICULTURAL AND URBAN DEVELOPMENT

Figure 11. The distribution of pH and its relationship to agricultural and urban development within the Mullica River Drainage (15 February 1977). First order streams are excluded from the lower graph. Percent agricultural and urban development was determined using McCormick (1973), the appropriate geological survey quadrangles, and a cartometer to estimate the stream mileage above each station, and the relative contribution of streams draining agricultural, urban, and forested areas.



4.6
5.9
7.2
4.4
6.6
6.1
4.5
5.5
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5.5
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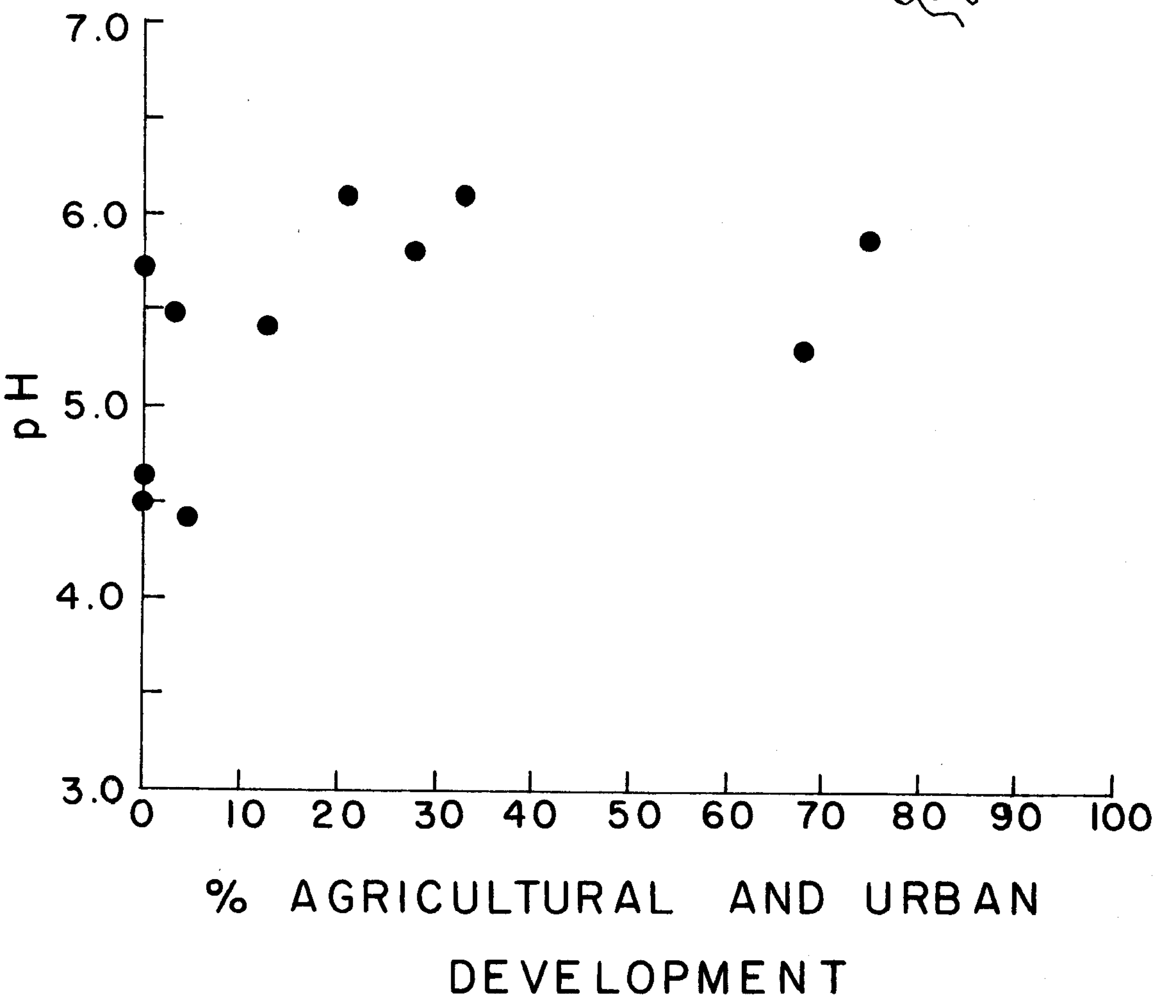
6.0
6.1



7.0
6.0
5.0
4.0
3.0
pH
0
10
20
30
40
50
60
70
80
90
100
% AGRICULTURAL AND URBAN DEVELOPMENT

Atco Lake), while *Enneacanthus* populations are minimal or absent in some disturbed habitats (e.g. Blue Anchor Lake) even though they are native to the drainage (Figure 2).

Food Habits

The dietary habits of fishes reflect the morphological and behavioral adaptations of each individual species (Keast and Webb 1966). Although feeding habits may change with locality and season (Kapoor et al. 1975), this is usually due to changes in prey availability. Diet is strongly influenced by the predator's spatial distribution, feeding apparatus, and behavior (see Tables 2-14 and Appendixes 1, 2, and 3).

Adult *E. chaetodon* preyed consistently on larval chironomids, Cladocera, and Ephemeroptera. *Calopsectra* and *Pseudochironomus* were the most important chironomids in the August 1975 sample, while *Pentaneura*, *Hydrobaenus*, and *Chironomus* were important in the July 1976 sample. The largest *E. chaetodon* (40.0 - 44.2 mm SL) also preyed on *Caenis* (Ephemeroptera), *Oxyethira* (Trichoptera), *Hyallela azteca* (Amphipoda) and some Odonata. These were the largest prey items injested. *Ceriodaphnia* spp. were the most important cladocerans, especially for juveniles and young adult *E. chaetodon*. In juveniles (10.7 - 14.4 mm SL), Cladocera (*Sida crystallina* and *Ceriodaphnia reticulata*), cyclopoid copepods, rotifers, and

Hydrobaenus (Chironomidae) were the most important food items.

E. chaetodon utilizes Utricularia as a substrate for food items. Plant material, such as Utricularia bladders, indicate some time was spent in vegetation searching for food. Utricularia bladders and stems were frequently found in E. chaetodon guts, but never in the other species (Appendixes 1, 2, and 3). Sida crystallina, a cladoceran which attaches directly to vegetation via a small gland on the back of its head (Quade 1969), composed 12.4% (relative abundance) of the food items (71.1% frequency) in juvenile E. chaetodon (10.4 - 14.4 mm SL) and 0.72% to 2.3% relative abundance in adult fish. S. crystallina was absent from the guts of the other species. Items indicating a bottom feeding habit were rarely found in the gut of E. chaetodon. (In the August sample, the 7.7% frequency for sand grains consisted of a single grain in one fish.)

E. obesus preyed chiefly on ostracods, dipteran larvae, Cladocera, and cyclopoid copepods. Ostracods were especially abundant in the August sample when they composed 42.7% of the total food items. In contrast, ostracods were never an important item in the diet of E. chaetodon. Probezzia (Ceratopogonidae) were the most important dipteran larvae in August, while Chironomus and Pentaneura (Chironomidae) were important in July. Cladocera were not included in the diet during August, but

Alona affinis, Chydorus, and thirteen other species were common in July. Most specimens of E. obesus contained at least one or more larger food items, including Hyallela azteca (Amphipoda), Caenis nymphs (Ephemeroptera), Oxyethira and Oecetis larvae (Trichoptera), larval Notonecta (Hemiptera), and larval Coleoptera.

E. gloriosus was similar to E. obesus in its choice of food items. Dipteran larvae, Cladocera, Ostracoda, cyclopoid copepods, and Ephemeroptera nymphs were the most important foods. The chironomids Calopsectra and Pentaneura, and the ceratopogonid Probezzia were common food items in August, while Chironomus and Pentaneura were more important in June. Cladocerans were unimportant in the August sample, but Chydorus bicornutus and Alona affinis were common in the June sample. As with E. obesus, most stomachs contained one or more larger food items, including Ameletus and Caenis (Ephemeroptera), Hyallela azteca (Amphipoda), Oxyethira and Oecetis (Trichoptera), and larval Coleoptera.

Both E. obesus and E. gloriosus ingest items associated with the bottom. E. obesus consumed leeches, Limnodrilus, abundant ostracods, occasional detritus (5.3% frequency in the June sample), and sand grains (20% frequency in the August sample). E. gloriosus guts contained ostracods, abundant sand grains (71.4% frequency and up to 50 grains in one fish) and some detritus (14.3% frequency in the August sample). Both species also contained plant material, but never in large amounts.

L. gibbosus (23.6 - 47.1 mm SL) preyed primarily on chironomid larvae, Cladocera, cyclopoid copepods, and ostracods. *Hydrobaenus* and *Calopsectra* were the dominant chironomids in the August sample, while *Chironomus* and *Hydrobaenus* were important in June. Cladocera were unimportant in August, but *Latona parviremus*, *Alona affinis* and *Ceriodaphnia* were common food items in June. *Ferrissia* (Gastropoda) was moderately abundant in the diet during June.

Cladocera, chironomid larvae, ostracods, and cyclopoid copepods were the most important food items of *L. macrochirus* in June. *Bosmina longirostris* and *Alona affinis* were the dominant food items (51% total relative abundance). *Bosmina longirostris*, a relatively small cladoceran, was rarely encountered in the guts of the other species. *Chironomus* and *Pentaneura* were the most numerous chironomids.

L. gibbosus and *L. macrochirus* consumed items that suggest diverse feeding habits. Guts of both species contained sand grains, detritus, and moderate numbers of ostracods. *L. gibbosus* consumed plant material, especially filamentous algae, and both species infrequently foraged at the surface on terrestrial ants (Hymenoptera).

TABLE 2

MAJOR FOOD CATEGORIES CONSUMED BY *Enneacanthus chaetodon*
20.7 - 32.3 mm SL (25.8 mm ave. SL)
13 SPECIMENS, 7 AUGUST 1975

Food Items	Total No.	No. Stomachs With Items	$\bar{x}$ No. Items	Percent Stomach With Items	Percent Total Items
Gastrotricha	-	-	-	-	-
Nematoda	3	1	0.23	8.0	0.5
Annelida	-	-	-	-	-
Rotatoria	-	-	-	-	-
Amphipoda	3	3	0.23	23.1	0.5
Copepoda	49	12	3.77	92.3	8.7
Cladocera	291	12	22.38	92.3	51.8
Ostracoda	5	4	0.38	30.8	0.9
Hydracarina	9	6	0.69	46.2	1.6
Odonata	5	4	0.38	30.8	0.9
Ephemeroptera	40	12	3.08	92.3	7.1
Trichoptera	5	4	0.38	30.8	0.9
Hemiptera	1	1	0.23	8.0	0.2
Coleoptera	-	-	-	-	-
Diptera	138	13	10.62	100.0	24.6
Hymenoptera	-	-	-	-	-
Gastropoda	1	1	0.23	8.0	0.2
Unid. Insecta	12	5	0.92	38.5	2.1
Dig. Anim. Mat.	-	-	-	-	-
Plant Material	*	3	0.62	23.1	-

*Present

TABLE 3

MAJOR FOOD CATEGORIES CONSUMED BY *Enneacanthus chaetodon*
40.0 - 44.2 mm SL (42.5 mm ave. SL)
5 SPECIMENS, 7 AUGUST 1975

Food Items	Total No.	No. Stomachs With Items	$\bar{x}$ No. Items	Percent Stomach With Items	Percent Total Items
Gastrotricha	1	1	0.20	20.0	0.8
Nematoda	3	3	0.60	60.0	2.3
Annelida	-	-	-	-	-
Rotatoria	-	-	-	-	-
Amphipoda	5	3	1.00	60.0	3.9
Copepoda	3	3	0.60	60.0	2.3
Cladocera	4	1	0.80	20.0	3.1
Ostracoda	-	-	-	-	-
Hydracarina	7	3	1.40	60.0	5.4
Odonata	1	1	0.20	20.0	0.8
Ephemeroptera	28	4	5.60	80.0	21.7
Trichoptera	7	3	1.40	60.0	5.4
Hemiptera	-	-	-	-	-
Coleoptera	1	1	0.20	20.0	0.8
Diptera	66	5	13.20	100.0	51.1
Hymenoptera	-	-	-	-	-
Gastropoda	-	-	-	-	-
Unid. Insecta	2	2	0.40	40.0	1.6
Dig. Anim. Mat.	1	1	0.20	20.0	0.8
Plant Material	*	3		60.0	-

*Present

TABLE 4

MAJOR FOOD CATEGORIES CONSUMED BY *Enneacanthus chaetodon*
10.7 - 14.4 mm SL (12.5 mm ave. SL)
7 SPECIMENS, 20 JUNE 1976

Food Items	Total No.	No. Stomachs With Items	$\bar{x}$ No. Items	Percent Stomach With Items	Percent Total Items
Gastrotricha	-	-	-	-	-
Nematoda	1	1	0.14	14.3	0.8
Annelida	-	-	-	-	-
Rotatoria	23	4	3.29	57.1	18.2
Amphipoda	-	-	-	-	-
Copepoda	38	6	5.43	85.7	30.2
Cladocera	50	7	7.14	100.0	39.7
Ostracoda	-	-	-	-	-
Hydracarina	-	-	-	-	-
Odonata	-	-	-	-	-
Ephemeroptera	-	-	-	-	-
Trichoptera	1	1	0.14	14.3	0.8
Hemiptera	-	-	-	-	-
Coleoptera	-	-	-	-	-
Diptera	13	6	1.86	85.7	10.3
Hymenoptera	-	-	-	-	-
Gastropoda	-	-	-	-	-
Unid. Insecta	-	-	-	-	-
Dig. Anim. Mat.	-	-	-	-	-
Plant Material	-	-	-	-	-

TABLE 5

MAJOR FOOD CATEGORIES CONSUMED BY *Enneacanthus chaetodon*
35.9 - 36.7 mm SL (36.3 mm ave. SL)
2 SPECIMENS, 20 JUNE 1976

Food Items	Total No.	No. Stomachs With Items	$\bar{x}$ No. Items	Percent Stomach With Items	Percent Total Items
Gastrotricha	-	-	-	-	-
Nematoda	-	-	-	-	-
Annelida	-	-	-	-	-
Rotatoria	2	1	1	50	4.8
Amphipoda	-	-	-	-	-
Copepoda	2	1	1	50	4.8
Cladocera	10	2	5	100	23.8
Ostracoda	-	-	-	-	-
Hydracarina	3	2	1.5	100	7.1
Odonata	-	-	-	-	-
Ephemeroptera	-	-	-	-	-
Trichoptera	-	-	-	-	-
Hemiptera	-	-	-	-	-
Coleoptera	1	1	.50	50	2.4
Diptera	24	2	12.0	100	57.1
Hymenoptera	-	-	-	-	-
Gastropoda	-	-	-	-	-
Unid. Insecta	-	-	-	-	-
Dig. Anim. Mat.	-	-	-	-	-
Plant Material	-	-	-	-	-

TABLE 6

MAJOR FOOD CATEGORIES CONSUMED BY *Enneacanthus obesus*
22.9 - 45.7 mm SL (32.9 mm ave. SL)
5 SPECIMENS, 7 AUGUST 1975

Food Items	Total No.	No. Stomachs With Items	$\bar{x}$ No. Items	Percent Stomach With Items	Percent Total Items
Gastrotricha	-	-	-	-	-
Nematoda	-	-	-	-	-
Annelida	-	-	-	-	-
Rotatoria	-	-	-	-	-
Amphipoda	3	2	0.60	40	4.0
Copepoda	11	4	2.20	80	14.7
Cladocera	-	-	-	-	-
Ostracoda	32	4	6.40	80	42.7
Hydracarina	4	3	0.80	60	5.3
Odonata	1	1	0.20	20	1.3
Ephemeroptera	3	3	0.60	60	4.0
Trichoptera	-	-	-	-	-
Hemiptera	3	2	0.60	40	4.0
Coleoptera	-	-	-	-	-
Diptera	15	5	3.00	100	20.0
Hymenoptera	-	-	-	-	-
Gastropoda	-	-	-	-	-
Unid. Insecta	2	2	0.40	40	2.7
Dig. Anim. Mat.	1	1	0.20	20	1.3
Plant Material	*	1	-	20	-

*Present

TABLE 7

MAJOR FOOD CATEGORIES CONSUMED BY *Enneacanthus obesus*
23.8 - 34.1 mm SL (28.3 mm ave. SL)
19 SPECIMENS, 20 JUNE 1976

Food Items	Total No.	No. Stomachs With Items	$\bar{x}$ No. Items	Percent Stomach With Items	Percent Total Items
Gastrotricha	-	-	-	-	-
Nematoda	7	5	0.37	26.3	1.4
Annelida	-	-	-	-	-
Rotatoria	28	4	1.47	21.1	5.6
Amphipoda	-	-	-	-	-
Copepoda	29	7	1.53	36.8	5.8
Cladocera	223	19	11.74	100.0	44.6
Ostracoda	34	9	1.79	47.4	6.8
Hydracarina	21	6	1.11	31.6	4.2
Odonata	-	-	-	-	-
Ephemeroptera	1	1	0.05	5.3	0.2
Trichoptera	8	5	0.42	26.3	1.6
Hemiptera	1	1	0.05	5.3	0.2
Coleoptera	8	5	0.42	26.3	1.6
Diptera	131	18	6.89	94.7	26.2
Hymenoptera	-	-	-	-	-
Gastropoda	-	-	-	-	-
Unid. Insecta	9	8	0.47	42.1	1.8
Dig. Anim. Mat.	-	-	-	-	-
Plant Material	-	-	-	-	-

TABLE 8

MAJOR FOOD CATEGORIES CONSUMED BY *Enneacanthus obesus*
35.0 - 42.2 mm SL (39.1 mm ave. SL)
6 SPECIMENS, 20 JUNE 1976

Food Items	Total No.	No. Stomachs With Items	$\bar{x}$ No. Items	Percent Stomach With Items	Percent Total Items
Gastrotricha	-	-	-	-	-
Nematoda	2	2	0.33	33.3	0.8
Annelida	2	2	0.33	33.3	0.8
Rotatoria	7	1	1.17	16.7	2.9
Amphipoda	1	1	0.17	16.7	0.4
Copepoda	10	4	1.67	66.7	4.2
Cladocera	70	6	11.67	100.0	29.3
Ostracoda	5	2	0.83	33.3	2.1
Hydracarina	6	4	1.00	66.7	2.5
Odonata	-	-	-	-	-
Ephemeroptera	-	-	-	-	-
Trichoptera	3	2	0.50	33.3	1.3
Hemiptera	2	1	0.33	16.7	0.8
Coleoptera	1	1	0.17	16.7	0.4
Diptera	119	6	19.83	100.0	49.8
Hymenoptera	-	-	-	-	-
Gastropoda	5	2	0.83	33.3	2.1
Unid. Insecta	6	2	1.00	33.3	2.5
Dig. Anim. Mat.	-	-	-	-	-
Plant Material	*	2	-	33.3	-

*Present

TABLE 9

MAJOR FOOD CATEGORIES CONSUMED BY *Enneacanthus gloriosus*
29.1 - 35.8 mm SL (32.9 mm ave. SL)
7 SPECIMENS, 7 AUGUST 1975

Food Items	Total No.	No. Stomachs With Items	$\bar{x}$ No. Items	Percent Stomach With Items	Percent Total Items
Gastrotricha	-	-	-	-	-
Nematoda	1	1	0.14	14.3	0.8
Annelida	-	-	-	-	-
Rotatoria	-	-	-	-	-
Amphipoda	6	3	0.86	42.9	4.9
Copepoda	6	2	0.86	28.6	4.9
Cladocera	4	2	0.57	28.6	3.3
Ostracoda	31	3	4.43	42.9	25.2
Hydracarina	-	-	-	-	-
Odonata	1	1	0.14	14.3	0.8
Ephemeroptera	23	6	3.29	85.7	18.7
Trichoptera	2	2	0.29	28.6	1.6
Hemiptera	-	-	-	-	-
Coleoptera	-	-	-	-	-
Diptera	46	7	6.57	100.0	37.4
Hymenoptera	-	-	-	-	-
Gastropoda	-	-	-	-	-
Unid. Insecta	2	2	0.29	28.6	-
Dig. Anim. Mat.	1	-	0.14	-	0.8
Plant Material	*	2	-	28.6	-

*Present

TABLE 10

MAJOR FOOD CATEGORIES CONSUMED BY *Enneacanthus gloriosus*
23.8 - 40.0 mm SL (28.7 mm ave. SL)
6 SPECIMENS, 20 JUNE 1976

Food Items	Total No.	No. Stomachs With Items	$\bar{x}$ No. Items	Percent Stomach With Items	Percent Total Items
Gastrotricha	-	-	-	-	-
Nematoda	-	-	-	-	-
Annelida	-	-	-	-	-
Rotatoria	3	1	0.50	16.7	1.9
Amphipoda	-	-	-	-	-
Copepoda	14	5	2.33	83.3	8.8
Cladocera	59	6	9.83	100.0	36.9
Ostracoda	2	2	0.33	33.3	1.2
Hydracarina	2	1	0.33	16.7	1.2
Odonata	-	-	-	-	-
Ephemeroptera	-	-	-	-	-
Trichoptera	3	2	0.50	33.3	1.9
Hemiptera	-	-	-	-	-
Coleoptera	2	2	0.33	33.3	1.2
Diptera	72	6	12.0	100.0	45.0
Hymenoptera	-	-	-	-	-
Gastropoda	-	-	-	-	-
Unid. Insecta	3	3	0.50	33.0	1.9
Dig. Anim. Mat.	-	-	-	-	-
Plant Material	-	-	-	-	-

TABLE 11

MAJOR FOOD CATEGORIES CONSUMED BY **Lepomis gibbosus**
23.6 - 28.6 mm SL (26.0 mm ave. SL)
10 SPECIMENS, 7 AUGUST 1975

Food Items	Total No.	No. Stomachs With Items	$\bar{x}$ No. Items	Percent Stomach With Items	Percent Total Items
Gastrotricha	-	-	-	-	-
Nematoda	2	2	0.20	20.0	0.6
Annelida	-	-	-	-	-
Rotatoria	2	1	0.20	10.0	0.6
Amphipoda	2	2	0.20	20.0	0.6
Copepoda	32	8	3.20	80.0	10.3
Cladocera	5	5	0.50	50.0	1.6
Ostracoda	28	8	2.80	80.0	9.0
Hydracarina	7	5	0.70	50.0	2.2
Odonata	-	-	-	-	-
Ephemeroptera	4	3	0.40	30.0	1.3
Trichoptera	-	-	-	-	-
Hemiptera	-	-	-	-	-
Coleoptera	-	-	-	-	-
Diptera	229	10	22.9	100.0	73.4
Hymenoptera	-	-	-	-	-
Gastropoda	-	-	-	-	-
Unid. Insecta	-	-	-	-	-
Dig. Anim. Mat.	1	1	0.10	10.0	0.3
Plant Material	*	2	-	20.0	-

*Present

TABLE 12

MAJOR FOOD CATEGORIES CONSUMED BY *Lepomis gibbosus*
32.9 - 34.6 mm SL (33.7 mm ave. SL)
2 SPECIMENS, 20 JUNE 1976

Food Items	Total No.	No. Stomachs With Items	$\bar{x}$ No. Items	Percent Stomach With Items	Percent Total Items
Gastrotricha	-	-	-	-	-
Nematoda	1	1	.50	0.50	1.4
Annelida	-	-	-	-	-
Rotatoria	-	-	-	-	-
Amphipoda	-	-	-	-	-
Copepoda	7	2	3.5	1.0	9.5
Cladocera	40	2	20.0	1.0	54.1
Ostracoda	12	2	6.0	1.0	16.2
Hydracarina	-	-	-	-	-
Odonata	-	-	-	-	-
Ephemeroptera	-	-	-	-	-
Trichoptera	-	-	-	-	-
Hemiptera	-	-	-	-	-
Coleoptera	-	-	-	-	-
Diptera	14	2	7.0	1.0	18.9
Hymenoptera	-	-	-	-	-
Gastropoda	-	-	-	-	-
Unid. Insecta	-	-	-	-	-
Dig. Anim. Mat.	-	-	-	-	-
Plant Material	-	-	-	-	-

TABLE 13

MAJOR FOOD CATEGORIES CONSUMED BY *Lepomis gibbosus*
36.3 - 47.1 mm SL (41.9 mm ave. SL)
16 SPECIMENS, 20 JUNE 1976

Food Items	Total No.	No. Stomachs With Items	$\bar{x}$ No. Items	Percent Stomach With Items	Percent Total Items
Gastrotricha	-	-	-	-	-
Nematoda	12	8	0.75	5.0	.6
Annelida	3	3	0.19	18.7	0.7
Rotatoria	-	-	-	-	-
Amphipoda	-	-	-	-	-
Copepoda	59	15	3.69	93.7	13.8
Cladocera	98	16	6.12	100.0	22.9
Ostracoda	41	12	2.56	75.0	9.6
Hydracarina	3	2	0.19	12.5	0.7
Odonata	2	1	0.12	6.2	0.5
Ephemeroptera	1	1	0.06	6.2	0.2
Trichoptera	2	2	0.12	12.5	0.5
Hemiptera	1	1	0.06	6.2	0.2
Coleoptera	4	4	0.25	25.0	0.9
Diptera	161	16	10.06	100.0	37.6
Hymenoptera	1	1	0.06	6.2	0.2
Gastropoda	36	7	2.25	43.7	8.4
Unid. Insecta	4	4	0.25	25.0	0.9
Dig. Anim. Mat.	-	-	-	-	-
Plant Material	*	3	-	-	-

*Present

TABLE 14

MAJOR FOOD CATEGORIES CONSUMED BY *Lepomis macrochirus*
39.1 - 44.2 mm SL (41.9 mm ave. SL)
7 SPECIMENS, 20 JUNE 1976

Food Items	Total No.	No. Stomachs With Items	$\bar{x}$ No. Items	Percent Stomach With Items	Percent Total Items
Gastrotricha	-	-	-	-	-
Nematoda	-	-	-	-	-
Annelida	1	1	0.14	14.3	0.1
Rotatoria	12	3	1.71	42.9	1.0
Amphipoda	1	1	0.14	14.3	0.1
Copepoda	63	7	9.00	100.0	5.4
Cladocera	744	7	106.3	100.0	64.2
Ostracoda	122	7	17.40	100.0	10.5
Hydracarina	46	6	6.57	85.7	4.0
Odonata	-	-	-	-	-
Ephemeroptera	1	1	0.14	14.3	0.1
Trichoptera	1	1	0.14	14.3	0.1
Hemiptera	5	5	0.71	71.4	0.4
Coleoptera	4	1	0.57	14.3	0.3
Diptera	153	7	21.86	100.0	13.2
Hymenoptera	1	1	0.14	14.3	0.1
Gastropoda	2	1	0.29	14.3	0.2
Unid. Insecta	3	3	0.43	42.9	0.3
Dig. Anim. Mat.	-	-	-	-	-
Plant Material	*	1	-	14.3	-

*Present

Dietary Overlap

I examined overlap in the utilization of major food categories using the overlap measure of Morisita (1959) as modified by Horn (1966) and used by Zaret and Rand (1971) for tropical stream fishes. The overlap coefficient,

$$C = \frac{2 \sum_{i=1}^{s} x_i \, y_i}{\sum_{i=1}^{s} x_i^2 + \sum_{i=1}^{s} y_i^2}$$

where s is the total number of food categories and x_i and y_i are the proportions of the total diet of species x and y taken from a given category of food i. The overlap coefficient varies from 0, when no overlap in food categories occurs, to 1, when both species consume the same proportions of each category. I used the percentage relative abundance of the major food categories, as presented in Tables 2 to 14, in calculating overlap.

Tables 15 and 16 show the overlap coefficients for August and June samples, respectively. In their analysis of tropical stream fishes, Zaret and Rand (1971) take any value over 0.60 to be significant. In my August sample, four interspecies pairs surpassed Zaret and Rand's significance value. In the June sample, 25 out of 28 possible interspecific and intraspecific combinations were significant. The overlaps are meaningful if the

TABLE 15

DIETARY OVERLAP AMONG SUNFISH SPECIES FROM ATCO LAKE, 7 AUGUST 1975. THE OVERLAP MEASURE IS FROM MORISITA (1959) AS MODIFIED BY HORN (1966).

	E. chaetodon 20.7-32.3 mm SL	*E. chaetodon* 40.0-44.2 mm SL	*E. obesus* 22.9-45.7 mm SL	*E. gloriosus* 29.1-35.8 mm SL	*L. gibbosus* 23.6-28.6 mm SL
E. chaetodon 20.7-32.3 mm SL		.49	.24	.44	.44
E. chaetodon 40.0-44.2 mm SL			.42	.84	.87
E. obesus 22.9-45.7 mm SL				.80	.50
E. gloriosus 29.1-35.8 mm SL					.76
L. gibbosus 23.6-28.6 mm SL					

TABLE 16

DIETARY OVERLAP AMONG SUNFISH SPECIES FROM ATCO LAKE, 20 JUNE 1976. THE OVERLAP MEASURE IS FROM MORISITA (1959) AS MODIFIED BY HORN (1966).

	E. chaetodon 10.7-14.4 mm SL	E. chaetodon 35.9-36.7 mm SL	E. obesus 23.8-34.1 mm SL	E. obesus 35.0-42.2 mm SL	E. gloriosus 23.8-40.0 mm SL	L. gibbosus 32.9-34.6 mm SL	L. gibbosus 36.3-47.1 mm SL	L. macrochirus 39.1-44.2 mm SL
E. chaetodon 10.7-14.4 mm SL		.51	.81	.59	.70	.80	.66	.78
E. chaetodon 35.9-36.7 mm SL			.78	.98	.95	.64	.89	.56
E. obesus 23.8-34.1 mm SL				.87	.92	.95	.85	.92
E. obesus 35.0-42.2 mm SL					.98	.74	.93	.66
E. gloriosus 23.8-40.0 mm SL						.83	.93	.76
L. gibbosus 32.9-34.6 mm SL							.75	.97
L. gibbosus 36.3-47.1 mm SL								.63
L. macrochirus 39.1-44.2 mm SL								

fishes occupy the same habitat. Competition for food items should be intense between all three Enneacanthus and between both Lepomis species. In addition, overlap between species of Lepomis and Enneacanthus is high but there is probably lower competition since they occupy different habitats within Atco Lake (see field observations below).

Size Selection of Food Items

Closely related organisms occupying the same habitat frequently reduce competition by dividing resources on the basis of size (Darlington 1972). In examining this possibility, I plotted the percent relative abundance of intact food items against the logarithm of their volume, a procedure which makes the curve more symmetrical (MacArthur 1972). In general, considerable overlap exists in the size of food items selected by individuals of all five species. Figures 12-16 are designed so that congenerics from the same collection are presented together. In Figure 12, the most frequent food size for E. obesus is more than an order of magnitude smaller than that for E. gloriosus of similar size, even though the range of food size is equivalent. In the June collection (Figure 14) this is not repeated, and the overlap is considerable. Both species relied heavily on cladocerans in June, while the greater number of large food items for E. gloriosus in August is due to a high percentage

(18.7%) of Ephemeroptera in its diet.

Two size groups of *E. chaetodon* are represented in both the August and June collections. In Figures 12 and 13, a distinct shift toward larger food items occurs with increased size. However, the range of food sizes is similar in the August sample. Both June curves are bimodal and overlap in the middle range of food sizes. However, the bimodal shape of the 36.3 mm group may be an artifact due to small sample size (2 individuals). A slight shift toward smaller food items with no reduction in the range of food sizes can also be seen in the June sample for two size groups of *E. obesus* (Figure 14). Changes in diet associated with increased size is best documented for *E. chaetodon* in Figure 15. Large food items such as Ephemeroptera nymphs and larval Diptera become more important in larger fish, while rotifers, copepods, and Cladocera decrease in importance.

The sizes of food items utilized by *L. gibbosus* (both August and June samples) and the June sample of *L. macrochirus* is presented in Figure 16. The two size groups of *L. gibbosus* from the June sample have very similar curves. *L. macrochirus* from this sample selects smaller food items, within a reduced size range, than *L. gibbosus* .

Figure 12. Frequency distribution of prey size, expressed as the log of their volume (mm), in the stomachs of *E. chaetodon* - 20.7-32.3 mm SL (■), *E. chaetodon* - 40.0-44.2 mm SL (□), *E. obesus* - 22.9-45.7 mm SL (●), and *E. gloriosus* - 29.1-34.8 mm SL (○), 7 August 1975.

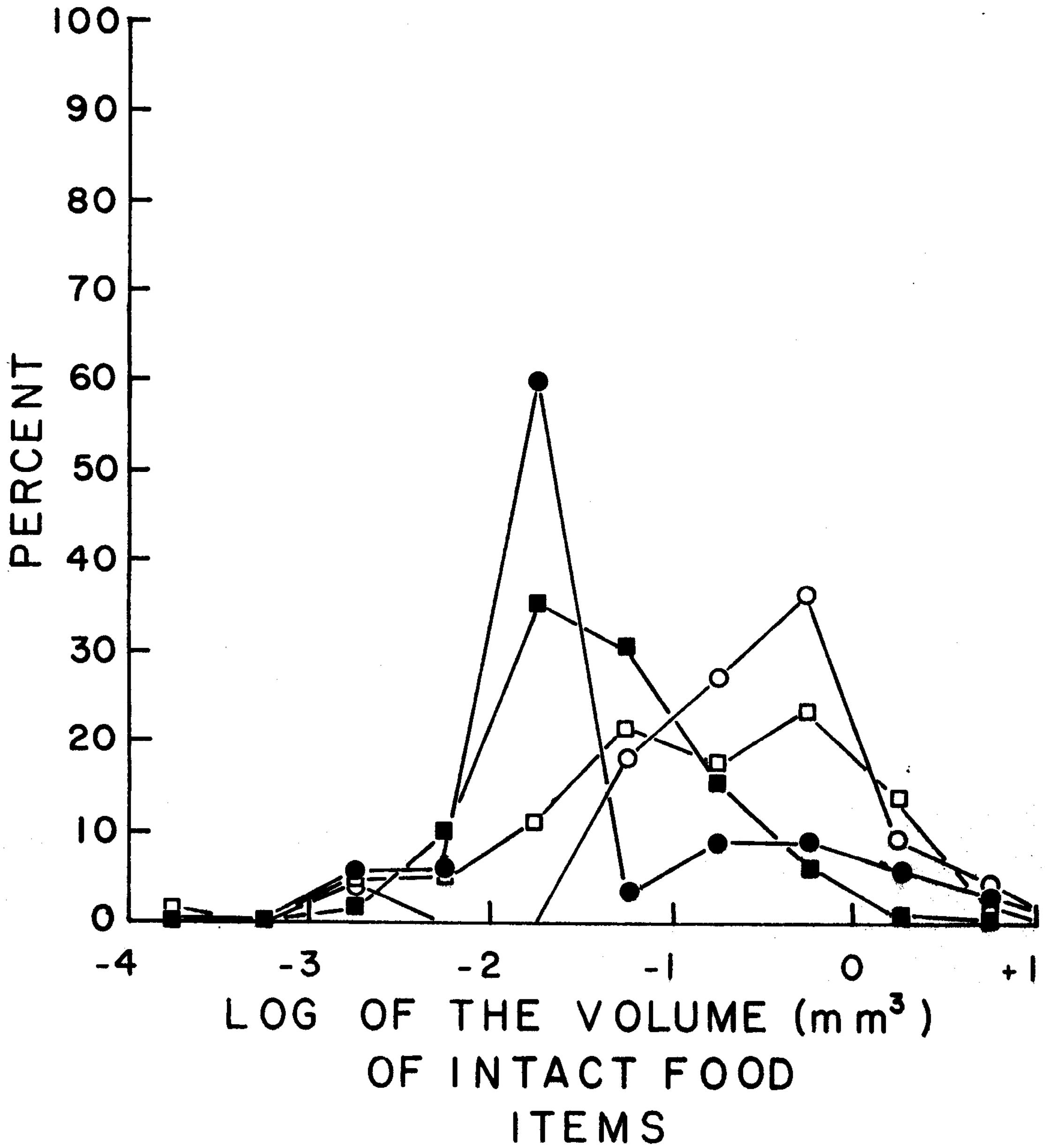

100
90
80
70
60
50
40
30
20
10
0
PERCENT
-4
-3
-2
-1
0
+1
LOG OF THE VOLUME (mm³)
OF INTACT FOOD
ITEMS

Figure 13. Frequency distribution of prey size, exnressed as the log of their volume (mm), in the stomachs of *E. chaetodon* - 10.7-14.4 mm SL (■), and *E. chaetodon* - 35.9-36.7 mm SL (●), 20 June 1976.

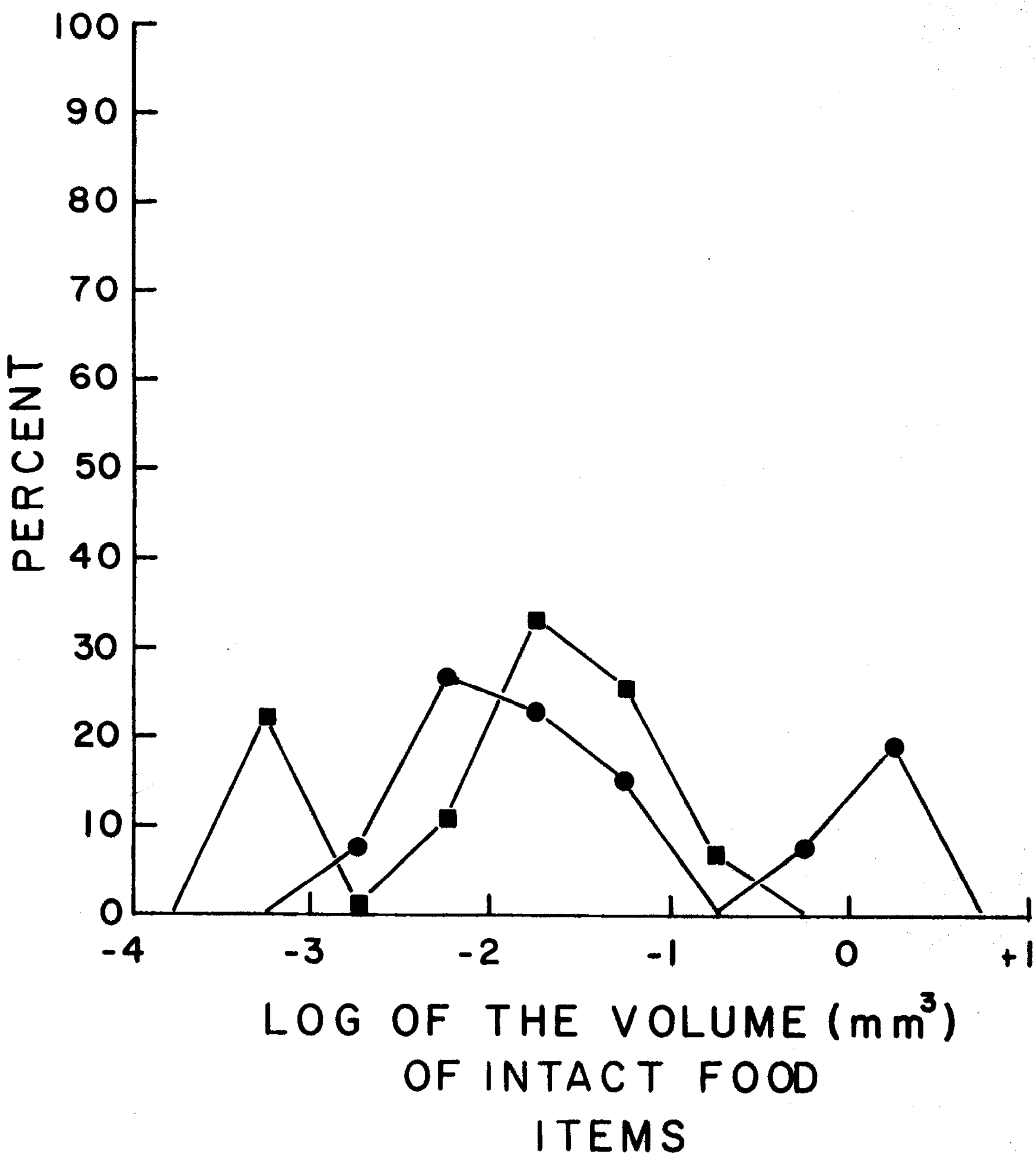

100
90
80
70
60
50
40
30
20
10
0
PERCENT
-4
-3
-2
-1
0
+1
LOG OF THE VOLUME (mm³)
OF INTACT FOOD
ITEMS

Figure 14. Frequency distribution of prey size, expressed as the log of their volume (mm), in the stomachs of E. obesus - 23.8-34.1 mm SL (△), E. obesus - 35.0-42.2 mm SL (□), and E. gloriosus - 23.0-40.0 mm SL (○), 20 June 1976.

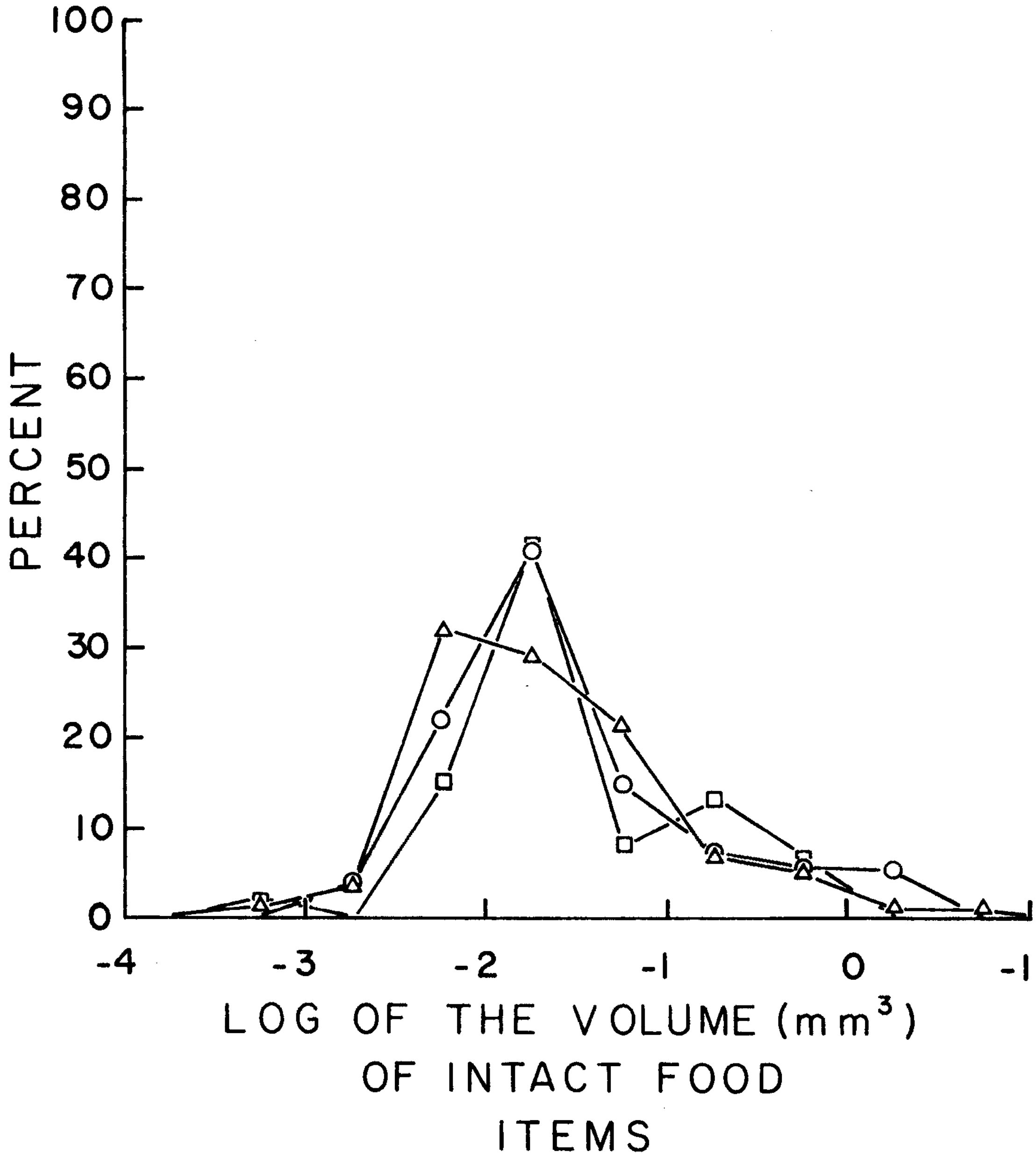
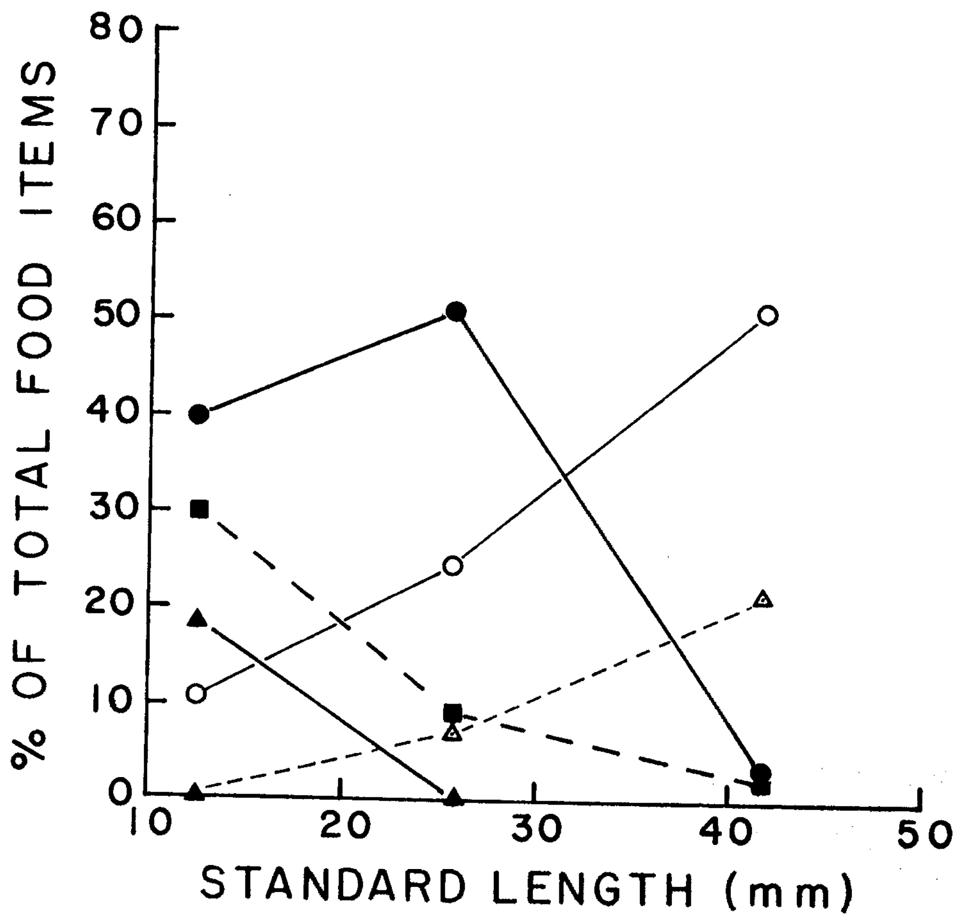
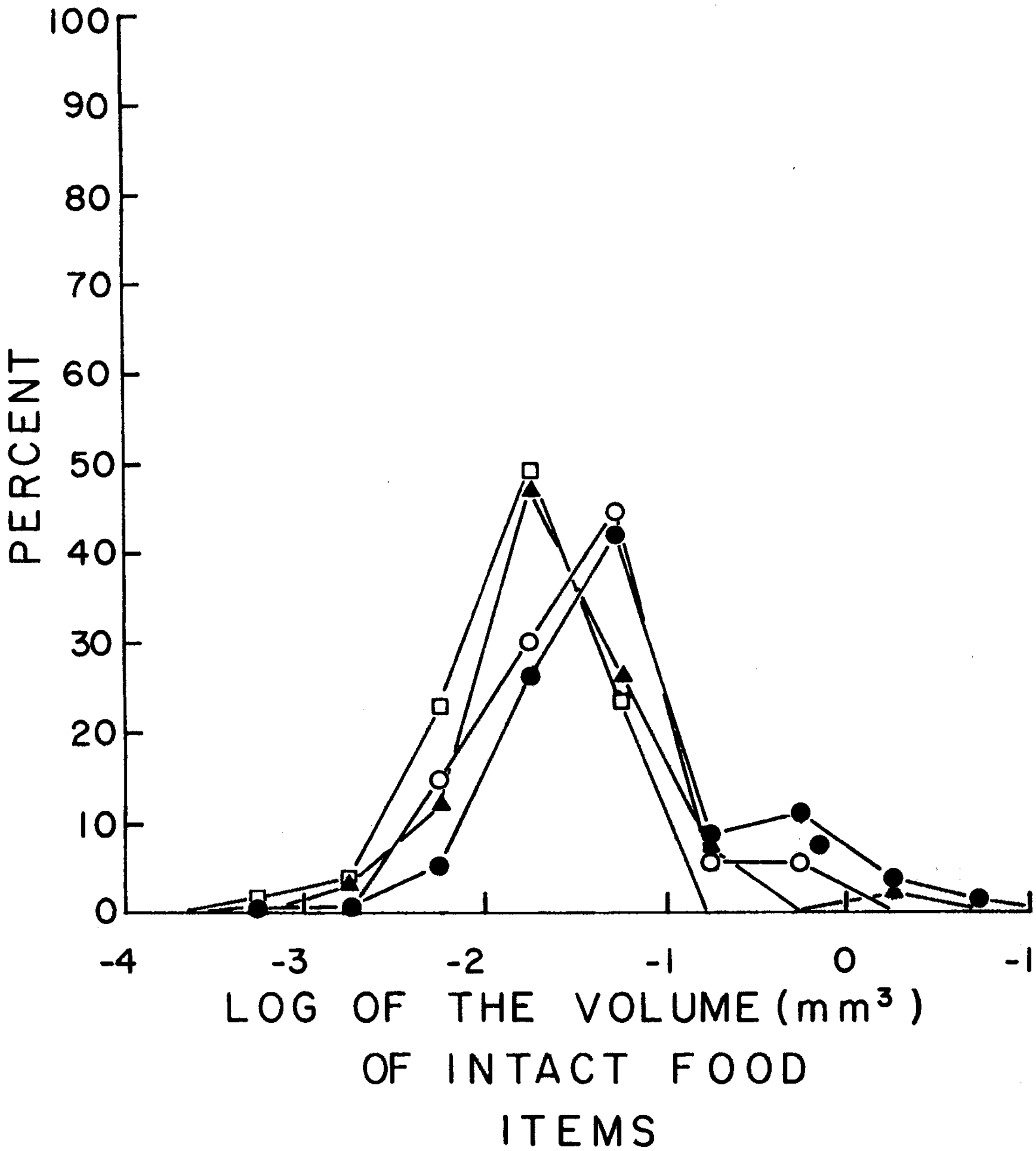

100
90
80
70
60
50
40
30
20
10
0
PERCENT
-4
-3
-2
-1
0
-1
LOG OF THE VOLUME (mm³)
OF INTACT FOOD
ITEMS

Figure 15. Changes in the relative abundance of rotifers (▲), cyclopoid copepods (■), cladocerans (●), ephemeropteran nymphs (△), and dipteran larvae (○) in the diet of three size groups of *E. chaetodon*. The smallest size group is from 20 June 1976, the other two are from 7 August 1975.



80
70
60
50
40
30
20
10
0
% OF TOTAL FOOD ITEMS
10
20
30
40
50
STANDARD LENGTH (mm)

Figure 16. Frequency distribution of prey size, expressed as the log of their volume (mm), in the stomachs of _L_. _gibbosus_ - 32.9-34.6 mm SL (○), _L_. _gibbosus_ - 36.3-47.1 mm SL (●), and _L_. _macrochirus_ - 39.1-44.2 mm SL (□), on 20 June 1976 and _L_. _gibbosus_ - 23.6-28.6 mm SL (▲), 7 August 1976.


100
90
80
70
60
50
40
30
20
10
0
PERCENT
-4
-3
-2
-1
0
-1
LOG OF THE VOLUME (mm³)
OF INTACT FOOD
ITEMS

Functional Morphology

Gape widths are compared in Figures 17 and 18 for all five species of sunfish. *E. obesus* and *E. gloriosus* have comparable gape widths, while *E. chaetodon* has a distinctly smaller gape. The mouth is directed forward in all species. The gape widths of *L. gibbosus* and *L. macrochirus* are generally similar (Figure 18). The mandibles and maxilla are fleshier in *L. gibbosus* than in *L. macrochirus*. Comparing *Lepomis* and *Enneacanthus*, *Lepomis* has a gape intermediate between *E. obesus* - *E. gloriosus* and *E. chaetodon*.

Important differences exist in the body design of *Enneacanthus* and *Lepomis*. Both genera are compressed, or gibbose, as adults, but juvenile *Lepomis* are compressed fusiform, whereas *Enneacanthus* are compressed even as juveniles (Figure 19 and 20). The caudal fin in *Enneacanthus* is rounded whereas it is emarginate in *Lepomis*.

Field Observations

E. chaetodon is almost always associated with dense vegetation in Atco Lake. On 10 July, when vegetative growth was slightly to moderately developed in the lower lake, I observed no *E. chaetodon* in that portion of the lake. Seining data indicate movement of *E. chaetodon* adults into the shallow water on the eastern shore beach only when *Utricularia* and *Myriophyllum*

Figure 17. The relationship between gape width (mm) and standard length (mm) in *E. chaetodon* (▲), *E. obesus* (○), and *E. gloriosus* (●).

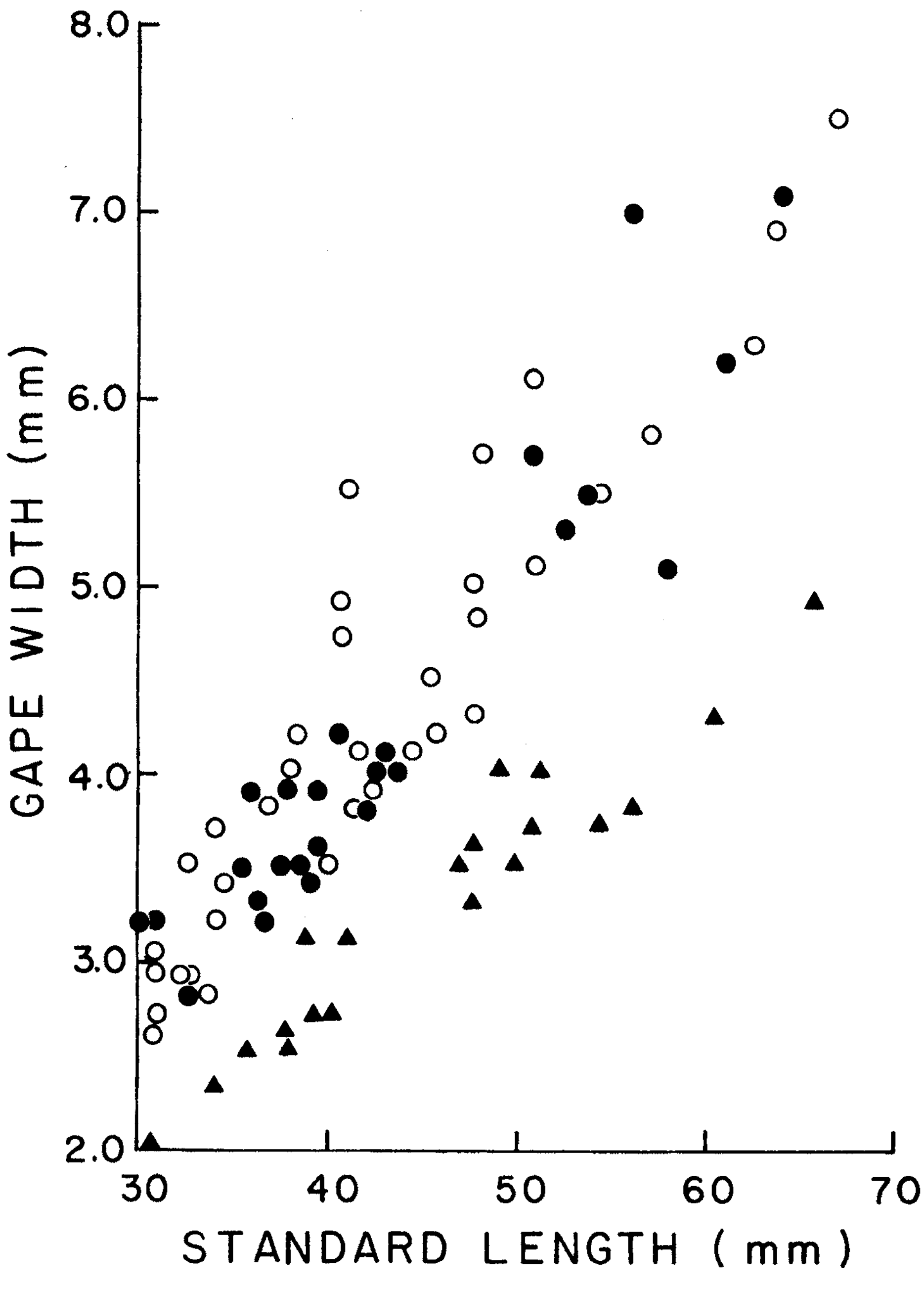

8.0
7.0
6.0
5.0
4.0
3.0
2.0
GAPE WIDTH (mm)
30
40
50
60
70
STANDARD LENGTH (mm)

Figure 18. The relationship between gape width (mm) and standard length (mm) in *L. gibbosus* (●) and *L. macrochirus* (○).

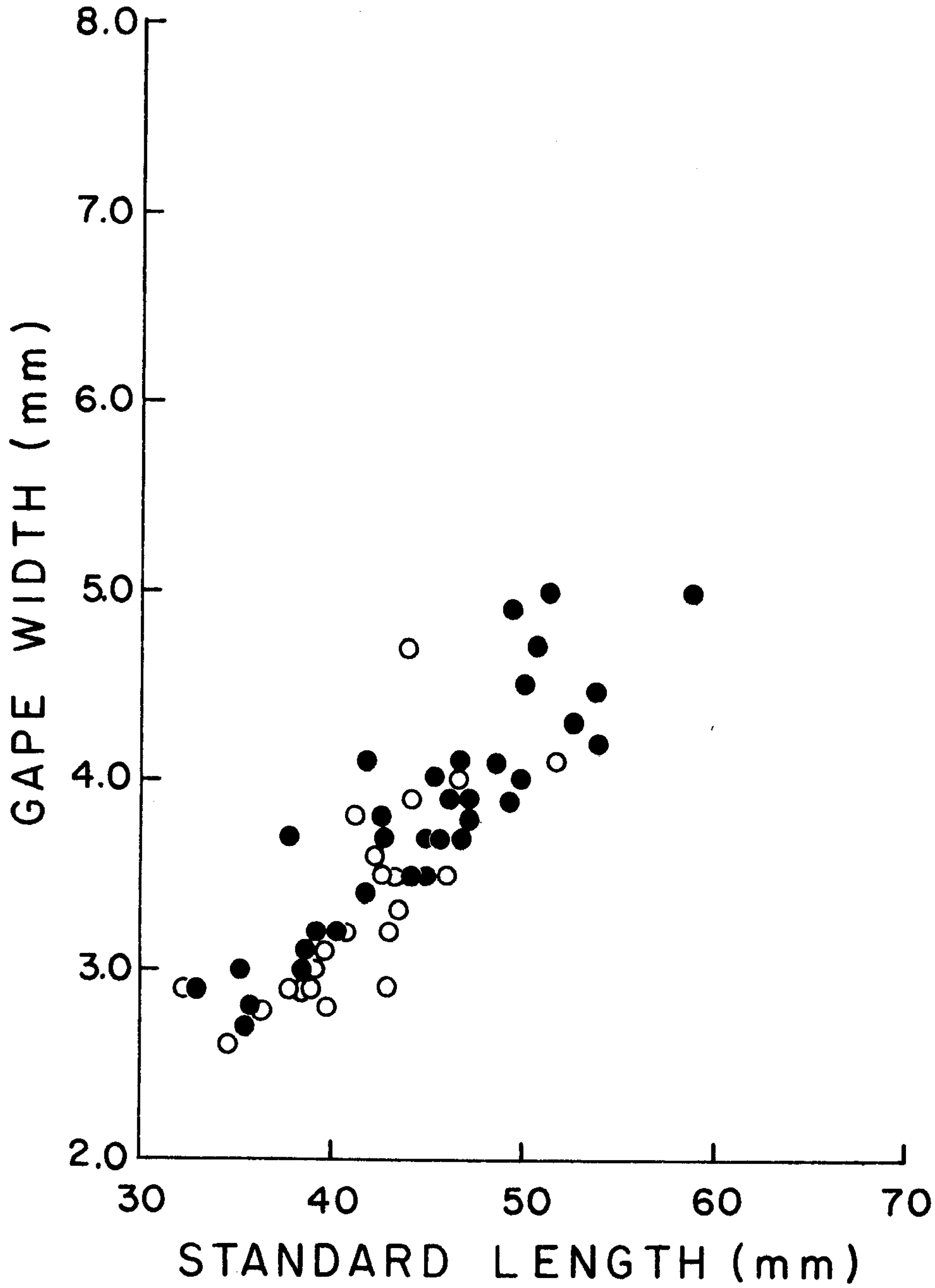

8.0
7.0
6.0
5.0
4.0
3.0
2.0
GAPE WIDTH (mm)
30
40
50
60
70
STANDARD LENGTH (mm)

Figure 19. Lateral compression (or gibbosity) presented as body depth (mm) against standard length (mm) in *E. chaetodon* (●), *E. obesus* (■), *E. gloriosus* (▲), *L. gibbosus* (○), and L. *macrochirus* (△).

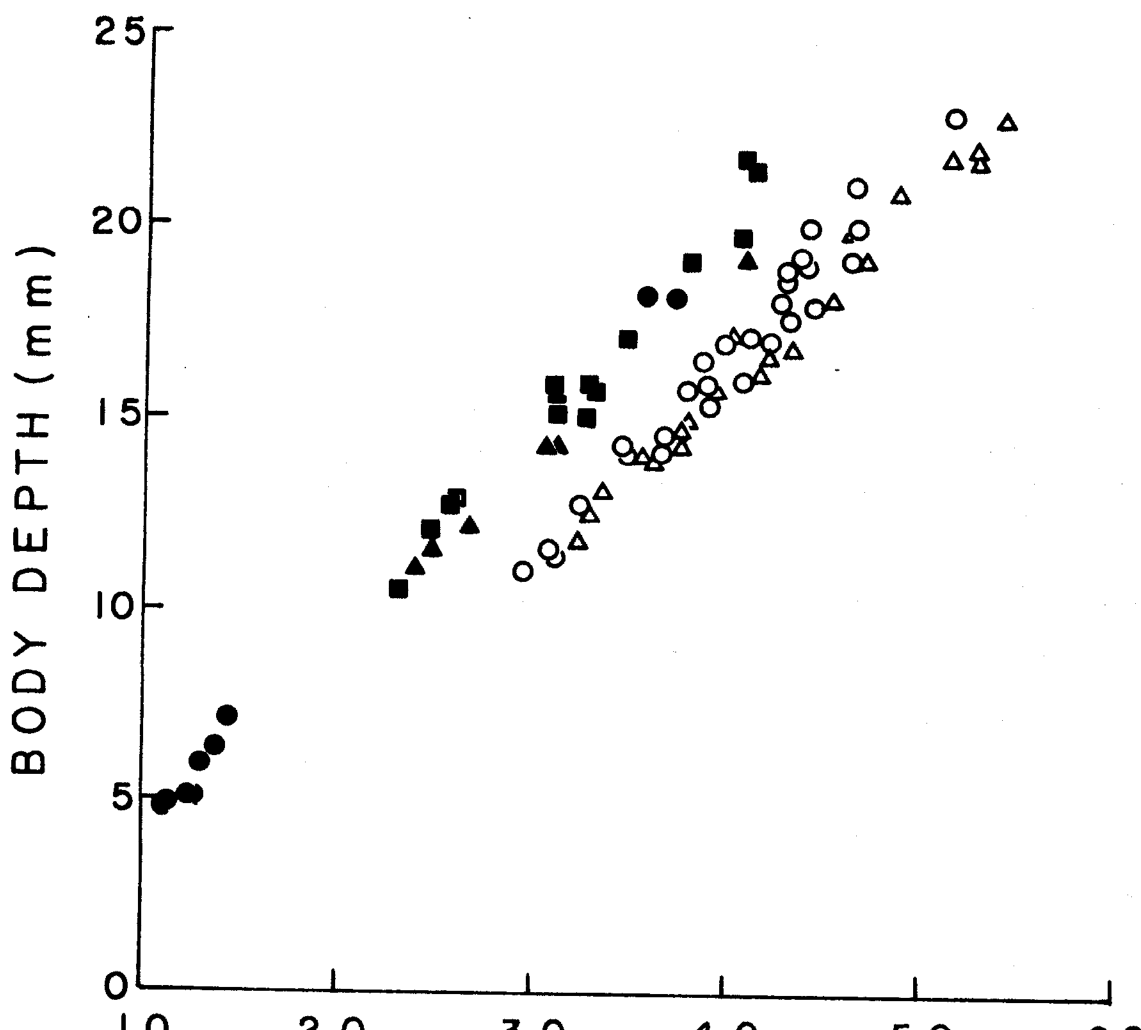
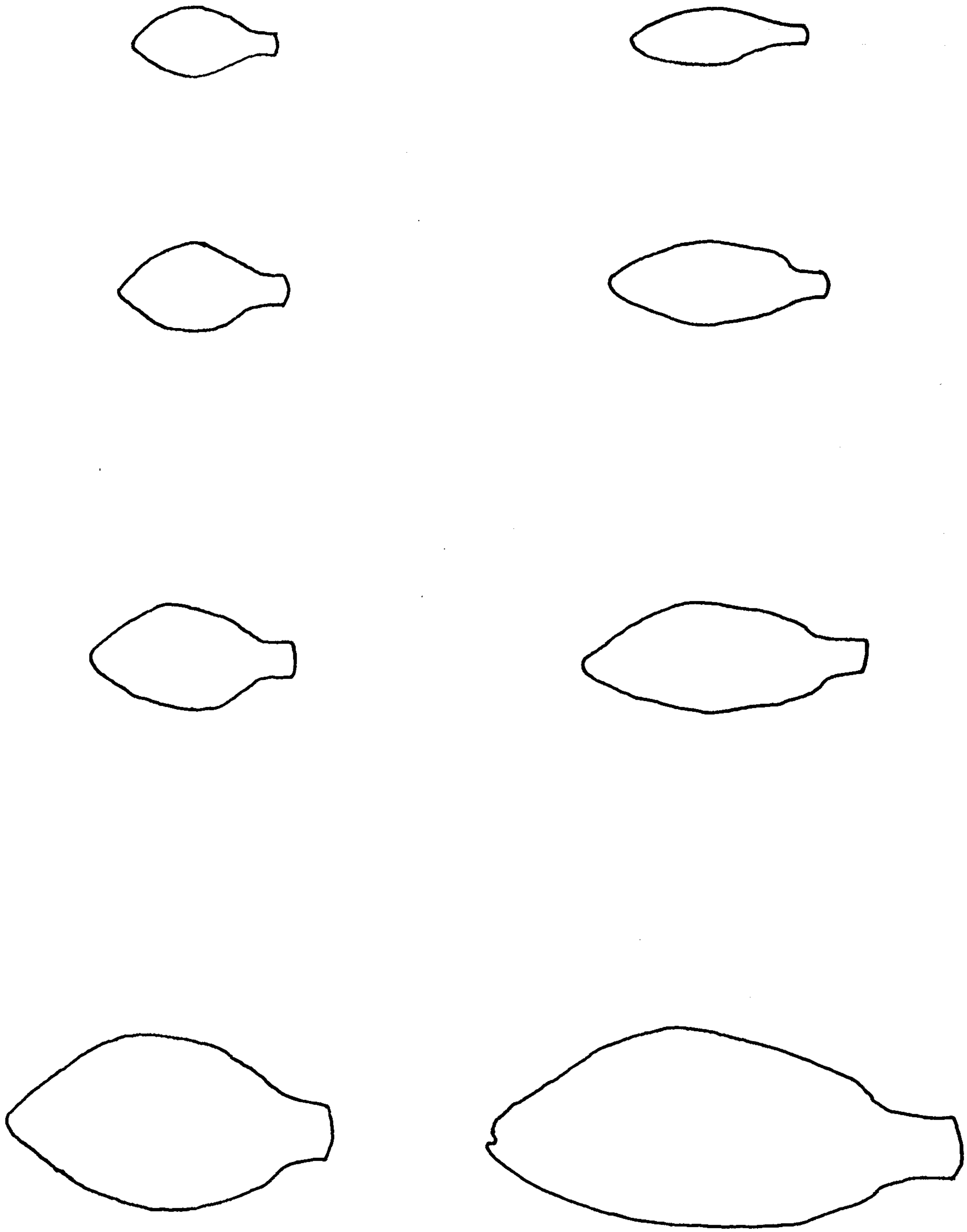

BODY DEPTH (mm)
STANDARD LENGTH (mm)
0
5
10
15
20
25
10
20
30
40
50
60

Figure 20. Silhouettes of *Enneacanthus chaetodon* and *Lepomis gibbosus* showing changes in body form with increased size. Drawings are to scale.



Enneacanthus chaetodon

Lepomis gibbosus

became extremely overgrown in the lower lake. The only adults collected in June came from the swampy upper lake and tributary. On 7 August, both *Utricularia* and *Myriophyllum* were overgrown throughout the lake, but especially in the shallow upper half. I observed four *E. chaetodon* (20-40 mm) on that date in approximately 0.5 meter of water, 3 meters from shore on the upper beach. By 5 October, some die-back of vegetation had occurred. On this date *E. chaetodon* was abundant along the shallow upper beach. *E. chaetodon* is timid, and when alarmed it either moves away in rapid jerks or dives directly into the vegetation. Individuals were frequently seen within recesses in the *Utricularia*. The coloration and markings of this fish conceal it in *Utricularia*, but when swimming in open water above the vegetation it is quite conspicuous.

At no time did I observe *E. obesus* or *E. gloriosus* while snorkeling. However, I collected both species while seining in water that was too shallow and dark to observe fish. During June, I collected many *E. obesus* and a few *E. gloriosus* in a shallow (less than 10 cm) cove and backwater filled with decomposing vegetation, leaf litter, and other detritus.

Both *L. gibbosus* and *L. macrochirus* occupy spatial and behavioral niches very different from the species of *Enneacanthus.* The smallest *Lepomis* observed (10-20 mm SL) foraged on zooplankton in schools of 25 to 50 individuals, usually in the vicinity of tall *Myriophyllum*, and always in mid-water. (It was impossible to differentiate between young *L. gibbosus* and young *L. macrochirus* in the field). Juveniles of *L. gibbosus*, 40-60 mm long, generally foraged in small groups of 2 to 4 individuals. The usual foraging behavior of these larger juveniles consisted of searching restricted patches of bare sediment. These fishes poised above the bottom at a sharp angle and sorted through mouthfuls of sediment, rejecting non-edible material and ingesting food items. In contrast to *E. chaetodon* of similar size, *L. gibbosus* hovered well away from any submerged vegetation. Even when momentarily alarmed, they usually moved away in the water column instead of seeking cover. Both *L. gibbosus* and *L. macrochirus* are counter-shaded in such a way that they are not conspicuous in open water. I have no data on the foraging activities of *L. macrochirus* in Atco Lake since it was less numerous than *L. gibbosus*. Werner and Hall (1975) reported adult *L. macrochirus* frequenting the middle water column in Michigan ponds, while *L. gibbosus* adults were more closely associated with substrate.

Aquarium Observations

While the data obtained from aquarium observations on a small test group were far from conclusive, they were interesting enough to include. *E. chaetodon* in a community tank containing abundant vegetation, was usually associated with the upper few inches of vegetation. It used the vegetation as a refuge and frequently swam in the open water just above the vegetation. Three *E. chaetodon* in the 40 gallon aquarium did 80% of their foraging amongst vegetation (Table 17). These fish are agile, and capable of approaching a strand of vegetation from almost any angle or direction.

Both *E. obesus* and *E. gloriosus* differ from *E. chaetodon* in their apparent affinity for the bottom, under a cover of vegetation which they only leave on brief excursions. Foraging behavior in aquarium held fishes indicates more dependence on the substrate and water column for feeding (Table 17).

L. gibbosus and *L. macrochirus* juveniles actively patrolled the water column in community aquaria. They were much faster than any of the *Enneacanthus*, and consistently beat them to commercial food offered at the surface. *L. gibbosus* spent almost 70% of its foraging activity on the bottom.

TABLE 17

AQUARIUM OBSERVATIONS OF SUNFISH FORAGING BEHAVIOR, 10 AND 11 JUNE 1976

Species	Frequency (%) of Foraging			
	Bottom	Vegetation	Water-column	Surface
E. chaetodon	4.7	87.5	7.4	0.6
E. obesus	22.0	17.9	58.8	1.4
E. gloriosus	45.3	1.0	53.7	0
L. gibbosus	69.6	12.5	7.2	10.8

VI. DISCUSSION

The pH of the aquatic environment is the most obvious factor limiting the distribution of fishes in southern New Jersey. Adult fish exposed to low pH water are killed by coagulation film anoxia (Westfall 1954, Beamish 1972), or by salt loss (Dunson and Martin 1973). The effect of low pH on adult centrarchids is similar for all species tested. L. macrochirus can withstand acid water to approximately pH 4.0 (Trama 1954, Calabrese 1969). I have captured adult E. obesus from bog waters as low as pH 3.7 $\pm$ 0.1, but this is close to the limit for all fish species (Smith 1953, N.J. Div. of Fish and Game 1957).

Early stages in the life history of fishes are more susceptible to low pH (Jones 1964, Mount 1973). For species of Lepomis in New Jersey, reproduction is inhibited below pH 5.0 (Smith 1953). Dystrophic waters which have been artificially neutralized with hydrated lime, $Ca(OH)_2$, are capable of supporting reproducing populations of L. gibbosus (N.J. Dept. Environ. Protection 1972). The lower limit for species of Enneacanthus is unknown, but it must be close to, or slightly lower than, pH 4.0, since reproducing populations exist in this pH range.

At the other end of the pH spectrum, there is little evidence that neutral or alkaline waters in New Jersey are detrimental to E. chaetodon or E. obesus. Both species are sometimes found in waters over pH 7.0 (Schwartz 1961, N.J. Div. of Fish and Game 1951, 1953, 1957). Hoedeman (1974) states that E. chaetodon reproduces in neutral or alkaline water.

The pH of water may not be the only chemical factor of potential toxicity to fish. Dissolved carbon dioxide (Kelley 1946, Alderdice et al. 1958, Smith 1960) and heavy metals (Smith 1960, Hynes 1970, Wetzel 1975) may be present in toxic quantities in dystrophic waters. In addition, low dissolved calcium increases the toxicity of heavy metals (Jones 1938, 1964). Foster (1976) considers dissolved calcium because of its disproportionate influence on the permeability of exposed membranes, the most important chemical characteristic affecting fish distribution. Yet many fishes are tolerant of a wide range of dissolved calcium. E. gloriosus populations exist in both the very low dissolved calcium waters of the Pine Barrens and also in the calcium rich limestone streams of northern New Jersey (N.J. Div. of Fish and Game 1951, 1953, 1957).

Compared to water chemistry, the trophic structure of the aquatic habitat has received little attention in relation to its possible importance to fishes. Dystrophic habitats receive most of their organic matter in the form of humic substances (Wetzel 1975). Primary productivity in the water column is extremely low, and littoral plants completely dominate the metabolism of dystrophic lake systems (Berg and Petersen 1956, Smith 1960, Wetzel 1975). A yellow-brown flocculant material of complexed ferrous iron and humic acids forms a loose aggregate, which covers the substrate and littoral macrophytes. In Turkey Lake, a dystrophic pond in the New Jersey Pine Barrens, most of the primary and secondary production is associated with the floc flora and fauna (Smith 1960).

The niche occupied by the planktivore is reduced or entirely absent in dystrophic waters. Rudolfs and Lackey (1929) attributed mosquito death in bog waters to the lack of planktonic food organisms. Minnows (family Cyprinidae) and other strictly planktivorous fishes are rare or absent in most dystrophic waters in the Pine Barrens. The survival of larval fish in particular is dependent upon a minimal concentration of plankton organisms (Lisivnenko 1961, Laurence 1974, Lasker 1975, Dabrowski 1976). Searching for food items in the water column is a poor feeding strategy for any fish in dystrophic habitats. A much better approach utilizes the localized food resource associated with macrophytes or substrate.

The feeding strategy of all 3 species of *Enneacanthus* is adaptive in dystrophic habitats. *E. chaetodon* is closely associated with aquatic vegetation where it feeds on invertebrates living on leaves and stems.

Schwartz (1961) claimed E. chaetodon to be a bottom feeder of nocturnal habits, but none of his data support this notion. (No exclusively benthic invertebrates are mentioned in his dietary description. In Atco Lake, E. chaetodon is active during the day.) The small mouth and tubular buccal cavity in E. chaetodon allow a greater speed and distance of suction (Alexander 1970). This is an obvious advantage in dense vegetation where access to food items is limited. The rounded caudal fin is characteristic of slow-swimming fish, which seize prey items in a sudden strike (Keast and Webb 1967). This may be adaptive in dense vegetation where movement of the predator is restricted and abundant cover is available to the prey.

E. obesus and E. gloriosus seem to have very similar habitat requirements, but E. obesus is associated with darkly stained waters more often than E. gloriosus. Dietary data from other authors support my contention that E. obesus and E. gloriosus forage close to the substrate in dense vegetation or cover. Abbott (1883) noted Pisidium (Pelycepoda) in the diet of E. gloriosus from the lower Delaware River. E. gloriosus examined in Florida by McLane (1955) contained food items associated with both substrate and vegetation. E. obesus collected in Florida by McLane also contained benthic food items.

In comparison to Enneacanthus, L. gibbosus and L. macrochirus are poorly adapted to an environment with little zooplankton. Miller (1964) reported a positively phototactic response in larval *L. gibbosus* which caused them to swim within 6-20 cm of the surface. For the first five days out of the nest, all foraging activity was in mid water. *L. macrochirus* fry show a preference for the limnetic zone and the surface waters of the littoral zone (Werner 1967). The compressed fusiform body and emarginate caudal fin of young *Lepomis* are adaptive in an open water habitat where a rapid escape in the water column is the best means of predator avoidance.

The combination of high acidity and low nutrient availability in dystrophic waters usually precludes high planktonic productivity (Wetzel 1975). Agricultural development and nutrient loading in the Pine Barrens has created conditions in certain waters favorable to *L. gibbosus* and *L. macrochirus* by (1) increasing the pH to a level suitable for reproduction and (2) increasing planktonic productivity. At the same time, eutrophication and turbidity may destroy *Enneacanthus* habitat by limiting the growth of submerged macrophytes. Schwartz (1964) blamed the disappearance of *E. chaetodon* in Maryland on habitat disruption and draining operations made to improve fishing.

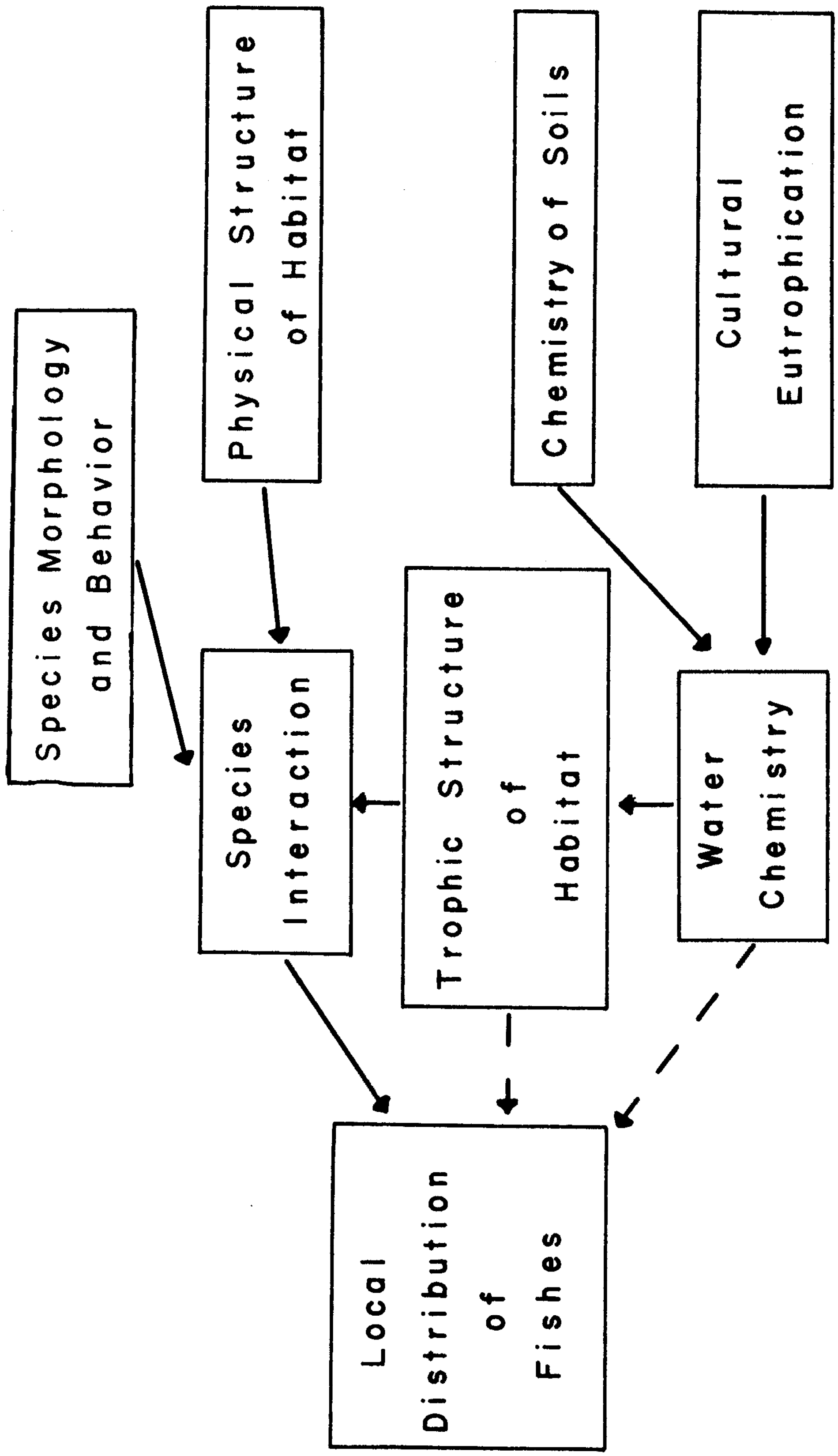
Within the Mullica River Drainage, replacement of species of *Enneacanthus* has occurred in several portions of the watershed, following habitat disruption and subsequent invasion by related centrarchids. Invasion is often accomplished by human introduction of exotic game and forage fishes (e.g. Lepomis). Blue Anchor Lake is heavily disturbed from extensive agriculture and effluent from the county hospital. I collected no Enneacanthus in either the lake or its tributary, but L. gibbosus and L. macrochirus were abundant. In Hammonton Lake, which is in the city of Hammonton, extinction seems likely for E. chaetodon. Only 24 specimens were collected when the entire 31 hectare lake was drained and poisoned with rotenone (N.J. Dept. Environ. Protection 1971). Over 1100 L. gibbosus, 460 L. macrochirus, and 135 L. auritus were collected in that operation. According to MacArthur and Wilson (1967), for small populations in the tens or small hundreds, extinction can be rapid. When competitors are present, the survival time is roughly the cube root of what it would be without competitors (MacArthur 1972).

Extinction is not always a result of invasion. Instances of coexistence are common and instructive. In Atco Lake, coexistence of potential competitors is possible because of the diversity of habitats (i.e. swamp, cedar bog, undisturbed tributary stream, dense aquatic vegetation and open water). In comparison, Blue Anchor Lake and Hammonton Lake have very little diversity that might permit coexistence. Impoundments of large size, or with extensive upstream tributaries, may allow more species to coexist than would be possible in a smaller body of water. Farrington Lake (117 hectares) and Union Lake (364 hectares) are two large non-dystrophic impoundments where coexisting populations of Enneacanthus and Lepomis occur.

The scarcity of E. chaetodon and E. obesus outside the Pine Barrens may be the result of competition from related centrarchids. Competition may also contribute to the exclusion of L. gibbosus and L. macrochirus from most dystrophic waters. In order for Lepomis to evolve the adaptation needed for egg survival in acid waters, the larvae must also solve the problem of obtaining adequate nourishment once their yolk sac is exhausted. This would require a relatively more "complex" change in morphology and behavior needed to compete with other species (e.g. Enneacanthus) which are better adapted to dystrophic habitats. In situations where competitors are present, Lepomis may not be able to make the behavioral and reproductive modifications needed to maintain a population.

No simple answer exists to explain the distribution of sunfishes in southern New Jersey. Water chemistry, trophic structure, habitat structure, species morphology and behavior, and interspecific competition all interact in complex ways (Figure 21). Water chemistry gives the illusion of having a direct effect on distribution, but is probably more important because of the way it affects habitat structure. Dystrophic habitats may or may not impose a direct limitation on planktivorous fishes. Behavioral plasticity may be great enough in juvenile *L. gibbosus* and *L. macrochirus* to allow a niche shift to a non-planktivorous way of life in the absence of competitors. The interaction between species is decisive because of the way it amplifies differences in water chemistry, habitat structure, and the species themselves to determine the local distribution of sunfishes in southern New Jersey.

Figure 21. Summary of important factors influencing the distribution of sunfishes in southern New Jersey. Refer to text for discussion.


Species Morphology and Behavior
Physical Structure of Habitat
Chemistry of Soils
Cultural Eutrophication
Species Interaction
Trophic Structure of Habitat
Water Chemistry
Local Distribution of Fishes

SUMMARY

1. *E. chaetodon* and *E. obesus* are characteristic inhabitants of dystrophic waters in the Pine Barrens. *E. gloriosus* is widely distributed in quiet waters throughout New Jersey but is less common in dystrophic habitats. *L. gibbosus* and *L. macrochirus* are widespread but have not established populations in the more acid waters of the Pine Barrens.

2. The distribution of all five species is related to the pH of the aquatic habitat. Other factors associated with low pH (i.e. low calcium, high dissolved carbon dioxide, and high toxic heavy metals) are probably equally as important.

3. *L. gibbosus* and *L. macrochirus* have invaded habitats in the Pine Barrens which have been disturbed by agricultural and urban runoff. Even minor agricultural development in a watershed can raise the pH of downstream stations to a level high enough to permit *Lepomis* reproduction.

4. *Enneacanthus* species are morphologically and behaviorally suited for nutrient poor dystrophic habitats, where almost all production is associated with aquatic macrophytes and substrate. *E. chaetodon* in Atco Lake utilizes *Utricularia* as a substrate for food items, while

E. obesus and *E. gloriosus* are largely benthic feeders in dense vegetation or cover.

5. *L. gibbosus* and *L. macrochirus* are at a disadvantage in dystrophic habitats. Very young *Lepomis* were observed feeding in open water on zooplankton. This is a feeding niche that is conspicuously absent in dystrophic waters. Juvenile *L. gibbosus* (40-60 mm) are primarily benthic foragers in shallow open water. *L. macrochirus* (39.1-44.2 mm SL) is primarily an open water planktivore.

6. *Enneacanthus* and *Lepomis* in Atco Lake select similar types and sizes of food items. Resource allocation appears to be largely on the basis of microhabitat utilization.

7. Interspecific competition is possibly the most important factor influencing the distribution of sunfishes in southern New Jersey.

APPENDIX 1

PERCENT RELATIVE ABUNDANCE (%RA) AND PERCENT RELATIVE FREQUENCY (%RF) OF FOOD ITEMS OF Enneacanthus AND Lepomis, 7 AUGUST 1976

Food Items	E. chaetodon 20.7-32.3 mm %RA	E. chaetodon 20.7-32.3 mm %RF	E. chaetodon 40.0-44.2 mm %RA	E. chaetodon 40.0-44.2 mm %RF	E. obesus 22.9-45.7mm %RA	E. obesus 22.9-45.7mm %RF	E. gloriosus 29.1-35.8 mm %RA	E. gloriosus 29.1-35.8 mm %RF	L. gibbosus 23.6-28.6 mm %RA	L. gibbosus 23.6-28.6 mm %RF
Gastrotricha										
Chaetonotus			0.72	20.0						
Rotatoria									0.62	10.0
Annelida										
Limnodrilus										
Amphipoda										
Hyallela										
azteca	0.54	23.1	0.36	60.0	3.95	40.0	4.89	42.9	0.62	20.0
Copepoda										
Cyclopoidea	8.94	92.3	2.17	60.0	14.47	80.0	4.89	42.9	11.46	1.00
Harpacticoidea	0.18	7.7								
Cladocera										
Sida										
crystallina			0.72	20.0						
Latona										
parviremus										
Ceriodaphnia										
sp.	49.55	92.3	0.72	20.0			2.44	28.6	0.62	20.0
C. reticulata										
C. quadrangula										
C. megalops										
Bosmina										
longirostris	0.18	7.7								

APPENDIX 1 CONTINUED

Food Items	*E. chaetodon* 20.7-32.3 mm %RA	%RF	*E. chaetodon* 40.0-44.2 mm %RA	%RF	*E. obesus* 22.9-45.7mm %RA	%RF	*E. gloriosus* 29.1-35.8 mm %RA	%RF	*L. gibbosus* 23.6-28.6 mm %RA	%RF
Acantholebris curvirostris										
Leydigia sp.	0.18	7.7								
L. quadrangularis	0.18	7.7								
Acroperus sp.	0.18	7.7								
Alona affinis										
Chydorus sp.										
C. globosus										
C. sphaericus										
C. bicornutus										
Alonella nana										
Eurycercus lamellatus										
Ophryoxus gracilus										
Unidentified	1.79		2.17	20.0			0.81	14.3	0.93	30.0
Ostracoda	0.89	30.8			42.11	80.0	26.02	57.1	8.98	80.0
Hydracarina										
adult	1.61	46.2	5.07	60.0	5.26	60.0			2.17	50.0
larva										
Ephemeroptera										
Caenis	4.47	61.5	18.4	80.0	1.32	20.0	9.76	71.4	1.24	30.0
Ameletus	2.15	61.5					8.94	71.4		
Unidentified	0.54				2.63	40.0	0.81	14.3		

APPENDIX 1 CONTINUED

Food Items	*E. chaetodon* 20.7-32.3 mm %RA	%RF	*E. chaetodon* 40.0-44.2 mm %RA	%RF	*E. obesus* 22.9-45.7 mm %RA	%RF	*E. gloriosus* 29.1-35.8 mm %RA	%RF	*L. gibbosus* 23.6-28.6 mm %RA	%RF
Odonata										
Hagenius brevistylus	0.36	7.7								
Libellulidae										
Damselfly larva	0.36	15.4								
Unidentified Odonata	0.18	7.7	0.72	20.0	1.32	20.0	0.81	14.3		
Trichoptera										
Oxyethira	0.89	30.8	5.07	60.0						
Oecetis							1.63	28.6		
Hemiptera										
Corixidae										
adult										
nymph	0.18	7.7								
Notonectidae										
Notonecta					3.95	40.0				
Coleoptera										
Hydrophilidae										
Berosus larva			0.72	20.0						
Elmidae										
Haliplus larva										
Peltodytes larva										
Dytiscidae larva										

APPENDIX 1 CONTINUED

Food Items	*E. chaetodon* 20.7-32.3 mm %RA	%RF	*E. chaetodon* 40.0-44.2 mm %RA	%RF	*E. obesus* 22.9-45.7 mm %RA	%RF	*E. gloriosus* 29.1-35.8 mm %RA	%RF	*L. gibbosus* 23.6-28.6 mm %RA	%RF
Unidentified Coleoptera			0.72	20.0						
Hymenoptera										
ant (terrestrial)										
Diptera										
Chironomidae										
Pentaneura	2.86	69.2	1.45	40.0	3.95	60.0	7.32	57.1	2.17	60.0
Coelotanypus	1.43	23.1	0.72	20.0			0.81	14.3		
Procladius										
Hydrobaenus	6.44	53.8	1.45	20.0			3.25	42.9	29.10	1.00
Metriocnemus										
Pseudochironomus	1.61	53.8	9.42	1.00			1.63	28.6	4.95	80.0
Calopsectra	5.90	53.8	18.84	80.0	1.32	20.0	8.94	57.1	13.31	1.00
Polypedilum	0.18	7.7	0.72	20.0						
Stenochironomus							0.81	14.3		
Microtendipes					1.32	20.0	0.81	14.3	0.62	20.0
Zavreliella									0.31	10.0
Lauterborniella									0.62	20.0
Chironomus	0.18	7.7							0.31	10.0
Unidentified larva	3.94		11.59	80.0	2.63	20.0	6.50	42.9	16.10	90.0
Unidentified pupa			0.72	20.0					0.31	10.0

APPENDIX 1 CONTINUED

Food Items	*E. chaetodon* 20.7-32.3 mm %RA	%RF	*E. chaetodon* 40.0-44.2 mm %RA	%RF	*E. obesus* 22.9-45.7 mm %RA	%RF	*E. gloriosus* 29.1-35.8 mm %RA	%RF	*L. gibbosus* 23.6-28.6 mm %RA	%RF
Ceratopogonidae										
Probezzia	1.79	46.2	5.07	60.0	11.84	60.0	7.32	85.7	2.79	50.0
Stilobezzia									0.93	30.0
Palpomyia									0.31	10.0
Dasyhelea										
Unidentified larva	0.18								0.62	20.0
Unidentified pupa			0.72	20.0						
Unidentified Insecta	1.97				2.63	40.0	1.63	14.3		
Gastropoda										
Ferrissia										
Unidentified helical snail	0.18	7.7								
Nematoda	0.54	15.4	2.90	60.0			0.81	14.3	0.62	20.0
Protozoa										
Difflugia										
Unidentified Organism			2.17	60.0	1.32	20.0	0.81	14.3	0.31	10.0
Utricularia Bladders	0.34	15.4	2.90	60.0						

APPENDIX 1 CONTINUED

Food Items	*E. chaetodon* 20.7-32.3 mm %RA	%RF	*E. chaetodon* 40.0-44.2 mm %RA	%RF	*E. obesus* 22.9-45.7 mm %RA	%RF	*E. gloriosus* 29.1-35.8 mm %RA	%RF	*L. gibbosus* 23.6-28.6 mm %RA	%RF
Plant Material	*	23.1	*	40.0	*	40.0	*	28.6	*	10.0
Ephyppia										
Invertebrate eggs	*	38.5	*	40.0						
Detritus			*	20.0			*	14.3		
Sand grains	*	7.7			*	20.0	*	71.4	*	80.0

*Present

APPENDIX 2

PERCENT RELATIVE ABUNDANCE (%RA) AND PERCENT RELATIVE FREQUENCY (%RF) OF FOOD ITEMS OF *Enneacanthus*, 20 JUNE 1976

Food Items	*E. chaetodon* 10.7-14.4 mm %RA	*E. chaetodon* 10.7-14.4 mm %RF	*E. chaetodon* 35.9-36.1 mm %RA	*E. chaetodon* 35.9-36.1 mm %RF	*E. obesus* 23.8-34.1 mm %RA	*E. obesus* 23.8-34.1 mm %RF	*E. obesus* 35.0-42.2 mm %RA	*E. obesus* 35.0-42.2 mm %RF
Gastrotricha								
Chaetonotus								
Rotatoria	19.0	57.1	4.6	50.0	5.1	21.1	3.0	33.3
Annelida								
Hirudinea							0.4	16.7
Limnodrilus							0.4	16.7
Amphipoda								
Hyallela azteca							0.4	16.7
Copepoda								
Cyclopoidea	28.1	85.7	4.6	50.0	5.3	42.1	3.7	66.7
Harpacticoidea					0.2	5.3		
Cladocera								
Sida crystallina	12.4	71.4	2.3	50.0				
Latona parviremus	1.7	14.3			0.7	15.8		
Ceriodaphnia sp.					6.4	36.8	0.4	16.7
C. reticulata	12.4	71.4	13.6	50.0	0.4	10.5	0.7	16.7
C. quadrangula	8.26	14.3						
C. megalops					0.4	5.3		
Bosmina longirostris	3.31	28.6					0.4	16.7

APPENDIX 2 CONTINUED

Food Items	E. chaetodon 10.7-14.4 mm %RA	%RF	E. chaetodon 35.9-36.1 mm %RA	%RF	E. obesus 23.8-34.1 mm %RA	%RF	E. obesus 35.0-42.2 mm %RA	%RF
Acantholebris curvirostris					0.2	5.3		
Leydigia sp.								
L. quadrangularis								
Acroperus sp.								
Pleuroxus denticulatus					0.4	5.3		
Pleuroxus striatus					0.6	5.3		
Pleuroxus sp.					0.4	5.3		
Alona affinis			6.8	100.0	8.8	52.6	2.2	66.7
Chydorus sp.					3.1	36.8	3.7	50.0
C. globosus					7.3	36.8	6.7	33.3
C. sphaericus								
C. bicornutus					0.7	10.5	3.3	33.3
Alonella nana					0.4	5.3		
Eurycercus lamellatus					4.2	31.6	3.7	33.3
Ophryoxus gracilus	0.8	14.3						
Unidentified Cladoceran	0.8	14.3			7.2	47.4	5.2	16.7
Ostracoda					6.2	47.4	2.2	33.3
Hydracarina adult			6.8	100.0	1.8	21.1	0.7	33.3
Hydracarina larva					2.0	15.8	1.5	33.3
Ephemeroptera								
Caenis					0.2	5.3		
Ameletus								
Unidentified Ephemeroptera								
Odonata								
Hagenius brevistylus								
Libellulidae								
Damselfly larva								

APPENDIX 2 CONTINUED

Food Items	*E. chaetodon* 10.7-14.4 mm %RA	%RF	*E. chaetodon* 35.9-36.1 mm %RA	%RF	*E. obesus* 23.8-34.1 mm %RA	%RF	*E. obesus* 35.0-42.2 mm %RA	%RF
Unidentified Odonata								
Trichoptera								
Oxyethira					0.2	5.3	0.4	16.7
Oecetis					1.5	26.3	1.1	33.3
Unidentified Trichoptera	0.8	14.3						
Hemiptera								
Unidentified Hemiptera							0.7	16.7
Corixidae adult					0.2	5.3		
Corixidae nymph								
Notonectidae								
Notonecta								
Coleoptera								
Hydrophilidae								
Berosus larva					0.2	5.3		
Elmidae Unidentified			2.3	50.0				
Haliplus larva								
Peltodytes larva					0.7	15.8		
Dytiscidae larva							0.4	16.7
Unidentified Coleoptera					0.6	15.8		
Hymenoptera								
ant (terrestrial)								
Diptera								
Chironomidae								
Pentaneura	1.7	28.6	15.9	100.0	5.1	63.2	7.4	83.3
Coelotanypus								
Procladius					0.6	15.8	0.7	33.3
Hydrobaenus	6.6	57.1	4.6	50.0	0.6	10.5	3.0	66.7

APPENDIX 2 CONTINUED

Food Items	E. chaetodon 10.7-14.4 mm %RA	E. chaetodon 10.7-14.4 mm %RF	E. chaetodon 35.9-36.1 mm %RA	E. chaetodon 35.9-36.1 mm %RF	E. obesus 23.8-34.1 mm %RA	E. obesus 23.8-34.1 mm %RF	E. obesus 35.0-42.2 mm %RA	E. obesus 35.0-42.2 mm %RF
Metriocnemus								
Brillia								
Pseudochironomus					0.4	10.5	0.7	16.7
Calopsectra			2.3	50.0	1.5	36.8	1.5	50.0
Polypedilum					0.2	5.3	0.4	16.7
Stenochironomus								
Microtendipes					0.4	5.3	0.4	16.7
Zavreliella								
Lauterborniella								
Chironomus	1.7	14.3	6.8	100.0	12.3	78.9	25.6	83.3
Unidentified larva	1.7	14.3	4.6	100.0	4.2	57.9	0.4	16.7
Unidentified pupa			13.6	100.0				
Ceratopogonidae								
Probezzia					0.4	10.5	3.0	50.0
Stilobezzia								
Palpomyia								
Dasyhelea			2.3	50.0	0.2	5.3	0.7	16.7
Unidentified larva					0.2	5.3		
Unidentified pupa							0.4	16.7
Unidentified Insecta					1.7	36.8	2.2	33.3
Gastropoda								
Ferrissia							0.4	16.7
Unidentified snail							1.5	33.3
Nematoda	0.8	14.3			1.3	26.3	0.7	33.3
Protozoa								

APPENDIX 2 CONTINUED

Food Items	*E. chaetodon* 10.7-14.4 mm %RA	%RF	*E. chaetodon* 35.9-36.1 mm %RA	%RF	*E. obesus* 23.8-34.1 mm %RA	%RF	*E. obesus* 35.0-42.2 mm %RA	%RF
Difflugia			9.1	50.0	3.7	42.1	1.5	50.0
Unidentified Organism								
Utricularia Bladder								
Plant Material							*	50.0
Ephyppia					2.2	31.6	8.9	33.3
Invertebrate Eggs	*	14.3	*	100.0				
Detritus					*	5.3		
Sand grains								

*Present

APPENDIX 3

PERCENT RELATIVE ABUNDANCE (%RA) AND PERCENT RELATIVE FREQUENCY (%RF) OF FOOD ITEMS OF *Enneacanthus* AND *Lepomis*, 20 JUNE 1976

Food Items	*E. gloriosus* 23.8-40.0 mm %RA	%RF	*L. gibbosus* 32.9-34.6 mm %RA	%RF	*L. gibbosus* 36.3-47.1 mm %RA	%RF	*L. macrochirus* 39.1-44.9 mm %RA	%RF
Gastrotricha								
Chaetonotus								
Rotatoria	1.8	16.7					2.3	42.9
Annelida								
Hirudinea								
Limnodrilus					0.7	18.8	0.2	14.3
Amphipoda								
Hyallela azteca							0.2	14.3
Copepoda								
Cyclopoidea	8.4	100.0	9.3	100.0	13.3	93.8	8.3	100.0
Harpacticoidea								
Cladocera								
Sida crystallina								
Latona parviremus			20.0	100.0	5.3	56.3	1.9	42.9
Ceriodaphnia sp.	1.8	16.7	13.3	50.0	1.6	31.3	1.7	42.9
C. reticulata	1.2	33.3						
C. quadrangula								
C. megalops								
Bosmina longirostris	0.6	16.7					27.9	57.1
Acantholebris curvirostris					0.2	6.3		
Leydigia sp.								

APPENDIX 3 <u>CONTINUED</u>

Food Items	*E. gloriosus* 23.8-40.0 mm %RA	%RF	*L. gibbosus* 32.9-34.6 mm %RA	%RF	*L. gibbosus* 36.3-47.1 mm %RA	%RF	*L. macrochirus* 39.1-44.9 mm %RA	%RF
L. quadrangularis								
Acroperus sp.								
Pleuroxus denticulatus								
Pleuroxus striatus								
Pleuroxus sp.								
Alona affinis	6.0	83.3	14.7	100.0	12.2	81.3	23.1	85.7
Chydorus sp.					0.5	12.5	0.8	57.1
C. globosus					0.5	12.5	0.2	14.3
C. sphaericus	0.6	16.7			0.2	6.3	0.8	14.3
C. bicornutus	14.5	83.3	1.3	50.0	0.9	25.0	1.7	28.6
Alonella nana								
Eurycercus lamellatus								
Ophryoxus gracilus								
Unidentified Cladoceran	10.2	66.7	6.7	50.0	1.2	31.3	2.7	28.6
Ostracoda	1.2	33.3	14.7	100.0	9.6	75.0	6.5	100.0
Hydracarina adult					0.2	6.25	1.7	85.7
Hydracarina larva	1.2	16.7			0.5	12.5	1.7	42.9
Ephemeroptera								
Caenis								
Ameletus					0.2	6.3	0.2	14.3
Unidentified Ephemeroptera								
Odonata								
Hagenius brevistylus								
Libellulidae					0.5	6.3		
Damselfly larva								
Unidentified Odonata								

APPENDIX 3 CONTINUED

Food Items	*E. gloriosus* 23.8-40.0 mm %RA	%RF	*L. gibbosus* 32.9-34.6 mm %RA	%RF	*L. gibbosus* 36.3-47.1 mm %RA	%RF	*L. macrochirus* 39.1-44.9 mm %RA	%RF
Trichoptera								
Oxyethira								
Oecetis	1.8	16.7			0.2	6.3		
Unidentified Trichoptera	0.6	16.7			0.2	6.3	0.2	14.3
Hemiptera								
Unidentified Hemiptera								
Corixidae adult								
Corixidae nymph					0.2	6.3	0.4	28.6
Notonectidae								
Notonecta								
Coleoptera								
Hydrophilidae								
Berosus larva								
Unidentified Elmidae					0.7	18.8		
Haliplus larva							0.4	14.3
Peltodytes larva							0.2	14.3
Dytiscidae larva	1.2	33.3						
Unidentified Coleoptera								
Hymenoptera					0.2	6.3	0.2	14.3
ant (terrestrial)								
Diptera					0.2	6.3	0.2	14.3
Chironomidae								
Pentaneura								
Coelotanypus	6.6	66.7			4.1	56.3	3.9	71.4
Procladius								
Hydrobaenus	0.6	16.7	1.3	50.0	2.5	37.5		
Metriocnemus	1.2	33.3	5.3	100.0	4.1	50.0	1.4	71.4

APPENDIX 3 CONTINUED

Food Items	*E. gloriosus* 23.8-40.0 mm %RA	%RF	*L. gibbosus* 32.9-34.6 mm %RA	%RF	*L. gibbosus* 36.3-47.1 mm %RA	%RF	*L. macrochirus* 39.1-44.9 mm %RA	%RF
Brillia								
Pseudochironomus	1.2	33.3			0.7	12.5	1.0	57.1
Calopsectra	4.8	50.0	1.3	50.0	3.2	43.8	1.5	57.1
Polypedilum					0.2	6.3	0.2	14.3
Stenochironomus								
Microtendipes	1.2	33.3			0.9	12.5		
Zavreliella								
Lauterborniella								
Chironomus	18.7	83.3	4.0	100.0	8.7	93.8	4.1	71.4
Unidentified larva	4.82	50.0	2.7	50.0	9.9	75.0	1.0	57.1
Unidentified pupa	1.8	50.0	2.7	50.0	2.1	50.0	0.4	28.6
Ceratopogonidae								
Probezzia	1.2	33.3	1.3	50.0	0.7	18.8	0.4	28.6
Stilobezzia								
Palpomyia								
Dasyhelea								
Unidentified larva	1.2	33.3						
Unidentified pupa								
Unidentified Insecta	1.8	50.0			0.9	25.0	0.6	42.9
Gastropoda								
Ferrissia					6.7	18.8	0.4	14.3
Unidentified snail					1.8	31.3		
Nematoda			1.3	50.0	2.8	50.0		
Protozoa								
Difflugia	2.4	33.3			1.4	25.0	1.0	57.1
Unidentified Organism								

APPENDIX 3 CONTINUED

Food Items	*E. gloriosus* 23.8-40.0 mm %RA	%RF	*L. gibbosus* 32.9-47.1 mm %RA	%RF	*L. gibbosus* 36.3-47.1 mm %RA	%RF	*L. macrochirus* 39.1-44.9 mm %RA	%RF
Utricularia Bladder								
Plant Material					*	12.5		
Ephyppia	1.2	33.3					0.8	42.9
Invertebrate Eggs					*	6.3	*	14.3
Detritus					*	18.8	*	14.3
Sand grains								

*Present

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