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PREDATION BY LARVAL CENTRARCHIDS ON ZOOPLANKTON
IN LAKE ITASCA, MINNESOTA

A Thesis
Presented for the
Master of Science
Degree
The University of Tennessee, Knoxville

Catherine Ann Justis

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ABSTRACT

The distribution and diets of larval Pomoxis nigromaculatus (Lesueur) and Lepomis spp. were estimated from collections during the summer of 1984 from Lake Itasca, Minnesota. Zooplankton was sampled concurrently with fish and used to estimate changes in zooplankton density and to calculate electivity indices in comparison with the fish stomach contents. Black crappies (Pomoxis nigromaculatus) hatched during the first two weeks of June, moved into the limnetic zone for approximately one month, and returned to the littoral zone. Sunfish (Lepomis spp.) hatched from mid-June to mid-July; some of the larvae undertook a pelagic migration, but many apparently remained inshore. Larval crappies ate copepod nauplii at the initiation of feeding, but soon switched to and fed primarily upon cyclopoid copepods. Larval sunfish ate predominantly rotifers and copepod nauplii.

During the first week of July, a decline was observed in numbers of pelagic zooplankton which concurred with intensive feeding by young crappies and sunfish. Crappies were probably not abundant enough to be a major factor in this decline. An increase in the mean size of zooplankton over the summer was probably due to the decrease in the numbers of rotifers, which could have resulted from larval fish predation. Predation by larval fish may play a part in structuring zooplankton communities by eliminating small size classes, and may also be a major factor in the mid-summer decline of zooplankton. Larval centrarchids interact with a combination of fishes to produce these effects.

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I. INTRODUCTION

The importance of predators in structuring zooplankton communities has been a subject of much interest since Brooks and Dodson (1965) set forth the hypothesis that fish will select the largest size classes of prey available in the environment, effecting a shift toward a smaller mean size in the community. Since then, the potential for dramatic impact upon the zooplankton by juvenile and adult fishes has been well documented (e.g., Werner and Hall 1974, Brooks 1968, Galbraith 1967, Wong and Ward 1972).

Recent work (Whiteside et al. 1985) has suggested that age 0+ or larval fish may also influence the zooplankton community for a number of reasons. Because larval fish are gape-limited, they are obligate planktivores and are restricted to small sizes of prey (Keast 1980, Lemly and Dimmick 1982, Zaret 1980); they also demonstrate the high metabolic rate associated with periods of rapid growth and development. Furthermore, in most species, larvae are produced in high numbers each year in order to compensate for high mortality rates (Snyder 1983).

This study represents a preliminary effort to elucidate the relationship between predation by larval fish and changes in the zooplankton community of Lake Itasca, Minnesota. It is also an attempt to add to the comparatively small body of literature available on larval stages of fish. The family of fishes chosen for study was the Centrarchidae, represented by Pomoxis nigromaculatus and three species of Lepomis.

II. LITERATURE REVIEW

Centrarchid Life History and Distribution

Members of the family Centrarchidae are gibbose-bodied water hangers (Keast and Webb 1966) which characteristically spawn in late spring to early summer. A male fish constructs a nest by fanning out a shallow depression in the bottom sediments with his tail, and then coaxes a female into the nest where she will release the eggs. The male guards the nest before the eggs hatch, actively driving away predators (Pflieger 1975).

Pomoxis nigromaculatus (black crappie) constructs nests in water 3-6 feet deep, sometimes on bottoms that are softer and muddier than those chosen by other centrarchids, but usually on sand and fine gravel (Breder and Rosen 1966, Eddy and Underhill 1974). Spawning occurs from May to early June in most lakes (Eddy and Underhill 1974), at water temperatures of 17.4° to 20°C (Breder and Rosen 1966). Eggs are adhesive and hatch in about 3 days; the larvae remain attached to the substrate for several more days after hatching and then free themselves by vigorous motion. Adults feed primarily on small fish, aquatic insects, and zooplankton; young crappies depend mainly on zooplankton (Hanson and Quadri 1984, Keast and Webb 1966, Pflieger 1975). Larval crappies feed on copepod nauplii and copepodids at the initiation of feeding but, at 7-12 mm, switch to larger Cyclops spp. (Bulkley et al. 1976, Keast 1980). Siefert (1968) noted that 6.0-7.9 mm larvae select Cyclops spp. but, at larval sizes of 10-13.9 mm, they exhibit a significant increase in the selection of Daphnia spp., in contrast to the report of Bulkley et al. (1976) that very few Cladocera or Rotifera were selected by crappies. Adult crappies

are mid-water feeders which inhabit deeper waters and are more mobile than most sunfish (Keast and Webb 1966).

Three species of Lepomis have been reported from Lake Itasca, L. macrochirus, L. cyanellus, and L. gibbosus. Of these species, Lepomis macrochirus, the bluegill, is the more abundant. It spawns from late May to early July in Minnesota (Eddy and Underhill 1974) at water temperatures of 17.2° to 30.5°C (Stevenson et al. 1969). The bluegill is a multiple spawner, producing several cohorts in one summer (Beard 1982). Though fine gravel is preferred, nests may be constructed on a variety of substrates (Carlander 1977, Pflieger 1975). Several females often spawn in the same nest (Pflieger 1975). Bluegill males guard the nest for about 7 days, defending the young against snails, bullheads, adult bluegills, and other predators (Gross and MacMillan 1980). The eggs hatch in 2-3 days and newly hatched larvae are 2.2 - 3.2 mm in length (Heckman 1969, Nakamura et al. 1971). The diets reported for larval bluegills are variable; most authors report a diet consisting mainly of nauplii and small copepodids (Beard 1982, Keast 1980, Lemly and Dimmick 1982, Siefert 1972). Werner (1969), however, notes a conspicuous absence of nauplii from the bluegills in his study, and a preference for cyclopoids and Bosmina spp. An apparent selection of Bosmina spp. and Daphnia spp. has been observed by Werner (1969) and Beard (1982). Siefert (1972) noted that the rotifer, Polyarthra spp., and copepod nauplii were both important at the initiation of feeding at larval lengths of 5.0-5.9 mm, that other rotifers and cyclopoids were incorporated at 7.0 mm, and that cladocerans became the dominant food at 8.0 mm. Adult bluegills are generalist feeders (Keast 1978, Keast and Webb 1966), consuming up to 9 types of prey at or above a 5% volume level (Keast

and Webb 1966), including cladocerans, amphipods, isopods, and insects (Keast 1978). Cladocerans dominated the diet of Year I fish, according to Keast (1978). Werner (1974) determined that the size of prey consumed occurred at a constant prey width to mouth width ratio of 0.59 for bluegill of any length.

Many species of fish, including black crappies and bluegills, are known to migrate into the open water after hatching and, later, to return to the littoral zone (e.g., Beard 1982, Brown and Colgan 1982, Faber 1967, Guma'a 1978, Keast 1980, Peck 1982, Werner 1967, 1969). Whiteside et al. (1985) observed such a littoral-limnetic migration pattern for yellow perch in Lake Itasca. Lepomis macrochirus resides in the limnetic zone of many lakes for about 30-40 days (Beard 1982, Keast 1978, 1980, Werner 1969) before returning to the littoral zone. Werner (1967) reports a longer limnetic residence of 7-8 weeks. Total lengths for fish returning to the littoral zone range from 12-25 mm (Beard 1982, Brown and Colgan 1982, Keast 1980, Werner 1967, 1969).

Adult and juvenile fishes of many species also move diurnally to and from the littoral zone (e.g., Emery 1973, Hall et al. 1979, Keast 1980). In Lake Itasca, Notropis volucellus is found inshore at night and offshore during the day (Hanych et al. 1983). Diel movement patterns in adult bluegills are variable; Baumann and Kitchell (1974) found daylight catches to be greater in open water and night catches greater inshore, but Keast et al. (1978) reports that some bluegills move into the open water after dark. Pomoxis, on the other hand, is thought to feed nocturnally in the open water (Keast et al. 1978), but may show some movement into the shallows at night (Keast and Webb 1966). The larvae of some fish species may undertake diel migrations to and from the littoral zone (Snyder 1983); however, their tendency to rise

to the surface at night is better documented (Snyder 1983, Werner 1967, 1969). This behavior has probably developed in response to the vertical migration of many zooplankton species (Confer et al. 1978, Werner 1967).

The behavioral flexibility of Lepomis macrochirus is well known (Casterlin and Reynolds 1978, Hall and Werner 1977, Mittlebach 1981a, Werner et al. 1981, 1983a). Adults are able to switch back and forth between vegetated and open water habitats. Apparently, individuals tend to specialize on one prey type found in a particular habitat, but are able to learn by sampling of alternate prey types and habitats, switching if necessary. Also, any population of bluegills may contain both specialists and generalists in reference to either prey types or habitat (Werner et al. 1981). Fish may prefer vegetation because, in shady areas, they are simultaneously more difficult for predators to see and better able to see approaching objects themselves (Helfman 1981). An active behavioral response is involved in the selection of habitats (Casterlin and Reynolds 1978); adults may move into the limnetic zone though they prefer vegetation, perhaps because it represents a competitive refuge from more selective sympatric species such as L. cyanellus (Casterlin and Reynolds 1978, Werner and Hall 1977). Mittlebach (1984) noted, however, that larger bluegills prefer the open water plankton.

Small size classes of bluegills (< 100 mm) generally remain in the vegetation (Hall and Werner 1977, Mittlebach 1981a, 1984, Werner et al. 1983a). Structural complexity seems to reduce foraging efficiency because prey are more difficult to locate (Crowder and Cooper 1982, Werner et al. 1983a); bluegills grow best at an intermediate macrophyte density (Crowder and Cooper 1982). Werner et al. (1983a) reports that small sizes prefer open water but

switch to vegetation when predators are introduced. Conflicting demands are presented to a forager by patchy habitats which vary in food abundance and predation risk (Cerri and Fraser 1983). There appears to be less habitat segregation by large and small bluegills when food is abundant in spring and early summer than when food becomes scarce (Hall and Werner 1977). A size-related predation risk forces smaller fish to remain in the vegetation while larger fish are able to maximize their foraging return by switching from the vegetation to the open water (Mittlebach 1981a). According to Werner (1967), juvenile bluegills prefer calm vegetated shallow water several meters from shore.

The early life history of fishes may be divided into three phases. The prolarva or yolk-sac larva is defined as the period from hatching until complete absorption of the yolk (Auer 1982). The larval stage lasts from absorption of the yolk sac until the differentiation or disappearance of the median finfold (Auer 1982, Balon 1975), the ossification of the axial skeleton (Balon 1975), and the appearance of anal fin rays (Auer 1982). The larval period is characterized by the persistence of some embryonic organs and the development of special larval organs (Balon 1975). These are replaced in the juvenile stage, which lasts until the maturation of the gametes (Auer 1982, Balon 1975).

The major causes of larval fish mortality are predation and starvation (Hunter 1976). Predators include conspecifics (cannibalism), other fish species (Hunter 1976), and many invertebrate predators such as odonate nymphs (Werner 1969). Predation on larval fish may directly result not only from active selection by the predator, but also indirectly from higher survivorship of the

predator population, chemical or visual attraction of the predator to the nesting site, and/or a reproductive response by the predator population to the production of eggs and larvae by the prey species (Hunter 1976). In the family Centrarchidae, male fish construct nests and provide protection from predation to the eggs and yolk-sac larvae (Bain and Helfrich 1983, Gross and MacMillan 1980, Siefert 1968). Mortality in bluegills has been found to be much higher in unguarded nests. Also important in predation avoidance is the proportion of coarse substrate from which the nest is constructed; larvae are able to hide in the interstitial spaces (Bain and Helfrich 1983). Small fish may avoid predators by inactivity at twilight. An affinity for schooling and for proximity to vegetation, both of which protect fish from predators, may develop late in larval life (Hunter 1976, Helfman 1979).

Starvation may result from inter- and intra-specific competition and the expansion of the spawning population into areas of low food density (Hunter 1976). However, the highest mortality is associated with the "critical period" which marks the end of yolk absorption and a switch to exogenous feeding (Vladimirov and Eemonov 1959, Li and Mathias 1982). Mass mortality at this time probably results from food limitation, though this has not been fully substantiated (Vladimirov and Eemonov 1959). The main factors involved in mortality during the critical period are food density, the timing of food availability, and fish density (Li and Mathias 1982). The rate of oil globule absorption has been shown to be inversely related to food density, and high mortality is correlated with complete globule absorption; on the other hand, growth and differentiation are directly correlated to food density (Eldridge et al. 1981). The critical period in bluegills begins approximately 4.4 days after

hatching; at about 9 days, starvation is manifested by a cessation of growth and a diminution of feeding activity (Toetz 1966). Larval fish are gape-limited to small-sized prey (Wong and Ward 1972, Zaret 1980), and can only take advantage of a proportion of the total prey available. Furthermore, larval fish have small, poorly developed eyes and may have to feed at higher light intensities than older fish; thus, 0⁺ perch ceased activity earlier in the evening and began later in the morning than did larger fish (Helfman 1979). Retinas grow larger as fish develop, providing the resolution necessary for seeing small objects and in dim light (Hairston et al. 1982).

Mortality has also been correlated with sharp drops in temperature, whereas survival and growth rates are positively correlated to temperature (Clady 1976, Dey 1981). Wind disturbance may kill larval fish, but catastrophic occurrences are probably not a major cause of mortality (Clady 1976).

Selective Predation and Its Impact on the Zooplankton

Studies on prey selection by fish have thus far been concentrated on adult and juvenile fishes, and have generally indicated a preference for the largest prey available (e.g., Brooks and Dodson 1965, Confer and Blades 1974, Irvine and Northcote 1982, Ivlev 1961, Michaletz et al. 1984). Sustained growth in many fishes requires the consumption of progressively larger prey items (Kerr 1971). In adult fish, inter-gillraker spacings may set a minimum prey size that can be retained, forcing a fish to consume larger size classes (Mathias and Li 1982, Wright and O'Brien 1984). Some fish, however, select prey in intermediate size ranges (Mills and Forney 1983, Teska and Behmer 1981). In 0⁺ fishes, gape limitation determines the maximum size of prey that can be

eaten, restricting young fish to smaller size classes of zooplankton (Hansen and Wahl 1981, Wong and Ward 1972, Zaret 1980). Larval fish do not necessarily eat the largest prey items they are capable of consuming; thus, perch fry demonstrated a consistent selection for prey that were smaller than the largest size available to them, possibly resulting from a previously established search image, increased ease of capture, and/or low attack ability (Hansen and Wahl 1981).

Size-selection may be related to the optimal allocation of time spent searching for and handling prey, serving to increase energy intake while conserving energy expenditure (Irvine and Northcote 1982, Werner and Hall 1974, Werner et al. 1983b). Differences in energy content of prey species can be significant; copepods contain from 5400-6800 cal/g (Schindler et al. 1971), whereas cladocerans, e.g., Daphnia sp., contain only 5000 cal/g (Wissing and Hasler 1968). However, copepods are faster swimmers, and may require more energy per capture effort (Zaret 1980). According to Emlen (1966), animals should be more selective when satiated and more indiscriminate when hungry. At low prey density, as wide a range of size classes may be eaten as encountered by the fish, which are dropped sequentially from the diet as abundance increases. In other words, as density increases, so does selection for larger size classes of zooplankton (Bartell 1982, Dodson 1970).

The Apparent Size Hypothesis states that fish will attack what appears to be largest by either actual size or proximity. Thus, at low density, small prey items have a higher probability of appearing large (O'Brien et al. 1976, Wright and O'Brien 1984). Similarly, there may be a differential encounter bias toward larger prey which can be seen at greater distances (Eggers 1977,

Werner and Hall 1977). In the laboratory, fish have been shown to be sensitive even to small differences in apparent size; however, under natural conditions, it is usually rare for two or more prey to be visible to a fish at the same time (Wright and O'Brien 1984).

Confer and Blades (1974) consider visibility and ease of capture to be the major factors in size-selection. Visibility of prey may be influenced by size (Confer et al. 1978, Werner and Hall 1974, Wright and O'Brien 1982), pigmentation, especially of the eye or ephippia (Confer et al. 1978, Tucker 1984, Zaret and Kerfoot 1975), the amount of light and/or turbidity (Confer et al. 1978, Vinyard and O'Brien 1976), and prey motion (Wright and O'Brien 1982, Zaret 1980). The ease of capture is a function of attack ability versus prey evasion (O'Brien 1979) and also predator experience (Brooks 1968, Hansen and Wahl 1981). Drenner et al. (1978) found that, for bluegills, the capture probability was much higher for cladocerans than for copepods, which could result in an apparent selection for cladocerans.

The active selection of larger prey by the fish may be more plausible than either an encounter bias or apparent size selection, which imply a more or less passive role on the part of the fish (Gardner 1981, Werner et al. 1983b). Learning and experience probably take precedence over a perceptual bias for larger sizes, reducing the relative importance of prey visibility. The decision whether or not to bypass a prey item is made on the basis of past encounter rates (Gardner 1981). The establishment of search images may be important in active selection, but is probably flexible (Emlen 1966, Furnass 1979, Werner et al. 1981). Fish may display active selection for one species and then another; i.e., they have search images which are temporally variable, and not

necessarily for species which optimize energy return (Emlen 1966, Furnass 1979). In this way, preferences may change readily and appropriately to the environment, allowing adjustment to prey which are often distributed in patches (Emlen 1966, Werner and Hall 1974). Exactly how prey are distributed naturally is unknown, but there are basically three possibilities: there is a gradual transition between patches such that fish cannot distinguish between them; prey occur in discrete, large patches, appearing to the fish as a "quasi-organism"; prey occur in some combination of the above distributions (Eggers 1977). Feeding selectivity is probably not controlled by a single factor in a dynamic, complex system such as a lake. Prey-specific location, pursuit, attack, and retention success are all involved and may be modified by experience (Wright and O'Brien 1984). From the literature, and in the field, it is difficult to determine whether size-selective predation results from the optimizing of energy intake, differential rates of encounter and capture success, variable prey distribution, or a combination of these and other factors (Eggers 1977).

Through selective predation, fish can exert a powerful influence on the zooplankton community. Most studies have concentrated upon the effects of adult and juvenile fishes and have noted their preference for and elimination of larger species and size classes of zooplankton. In addition, large species of zooplankton are replaced by smaller species, leading to a decrease in the mean size of the community (Brooks and Dodson 1965, Hall et al. 1976, Helfman 1979, Hutchinson 1971, Kohler and Ney 1981, Mittlebach 1981b, Wells 1970, Werner and Hall 1974). In a study on predation by fish on odonate nymphs, Morin (1984) observed the dominance of small odonate species due to differential predation upon intermediate sizes, and concluded that fish predators regulate

populations of odonates and other insects. The actual extent to which fish are able to structure zooplankton communities is variable, ranging from no effect attributable to a single fish species (Galbraith 1967, Hunter 1976) to the extinction of large zooplankton species (Brooks and Dodson 1965, Hrbacek et al. 1961). In most lakes, it is probably a combination of fishes which causes changes in the plankton (Galbraith 1967). The effects of predation depend upon whether the prey size range includes both mature and immature individuals, thereby limiting the reproductive capacity for replacement; predation may have to be both age- and size-specific to be effective (Brooks and Dodson 1965, Galbraith 1967, Mills and Forney 1983). No adverse effects upon the population were noted by Galbraith (1967) when fish were eating mostly adults. The intermediate steps as the zooplankton community responds to predation are unclear. Most studies have dealt only with high levels of predation; low and medium predation levels may lead to increased total abundance, perhaps because of nutrient input by fish (Archibald 1975).

In most lakes, the zooplankton community is subject to regular peaks and declines in abundance, usually in the following pattern: spring peak, mid-summer decline, secondary peak in autumn, low numbers through the winter (Allan 1976). The re-occurrence of this basic pattern has been observed for many years in Lake Itasca (Doolittle 1982, Williams 1982, Williams and Whiteside 1978). Several attempts have been made to correlate annual fluctuations in zooplankton abundance with fish predation. Noble (1975) observed that, although perch predation may modify Daphnia populations, variations occur independently and instead control the growth of the fish which is highly correlated with mean annual Daphnia abundance. In this case, the mid-summer decline was

similar in all years, though predation rates varied. Thus, at least in some lakes, fish predation may contribute to the decline, but does not account for it entirely (Hall et al. 1976, Noble 1975). Early spring zooplankton crashes may be caused by older over-wintering fish, but during the summer invertebrate predators may be the more important influence (Bohanan and Johnson 1983). Williams (1984) showed that invertebrate predation could produce the same decline apparent in natural zooplankton assemblages, even when fish were excluded. However, Williams and Whiteside (1978) and Doolittle (1982) demonstrated that no decline in numbers occurred in zooplankton isolated from fish predation but exposed to invertebrate predation. The inshore migration of 0+ yellow perch was found to coincide with declines in the littoral zooplankton by Whiteside et al. (1985). Fairchild (1982) observed that populations of certain prey species with localized littoral distributions may be susceptible to brief episodes of intense predation. Summer fish predation was found to limit zooplankton population growth, thereby playing a large part in the precipitous mid-summer decline noted by Williams (1982), and Keast (1980) noted that a decrease in the numbers of cyclopoids, nauplii, and Bosmina in May and early June coincided with a rise in the number of fish larvae.

III. DESCRIPTION OF AREA

Lake Itasca, the source of the Mississippi River, is located in northwestern Minnesota (47° 14'N, 95° 12'W) within the boundaries of Itasca State Park (Figure 1). Formed by glacial retreat during the Wisconsin Period (Megard 1968), this wishbone-shaped lake covers an area of 436 hectares. It is relatively shallow, with a maximum depth of 14 meters and a mean depth of 5.2 meters (Megard 1968), and is classified as eutrophic (Cole and Underhill 1965); the hypolimnion often becomes anaerobic in late summer. Lake Itasca possesses an extensive littoral zone made up of the aquatic macrophytes Nuphar, Nymphaea, Potamogeton, Scirpus, Typha, Zizania and others, and submerged mats of the macro-alga, Chara. The dominant phytoplankton species are members of the Cyanophyta and the Chlorophyta (Megard 1968) which help to support a diverse zooplankton fauna (Williams and Whiteside 1978, Pittinger 1978). Twenty-six species of fish have been recorded from Lake Itasca including yellow perch, the numerically dominant fish, mimic shiners, johnny darters, pumpkinseeds, green sunfish, black crappie and bluegill.

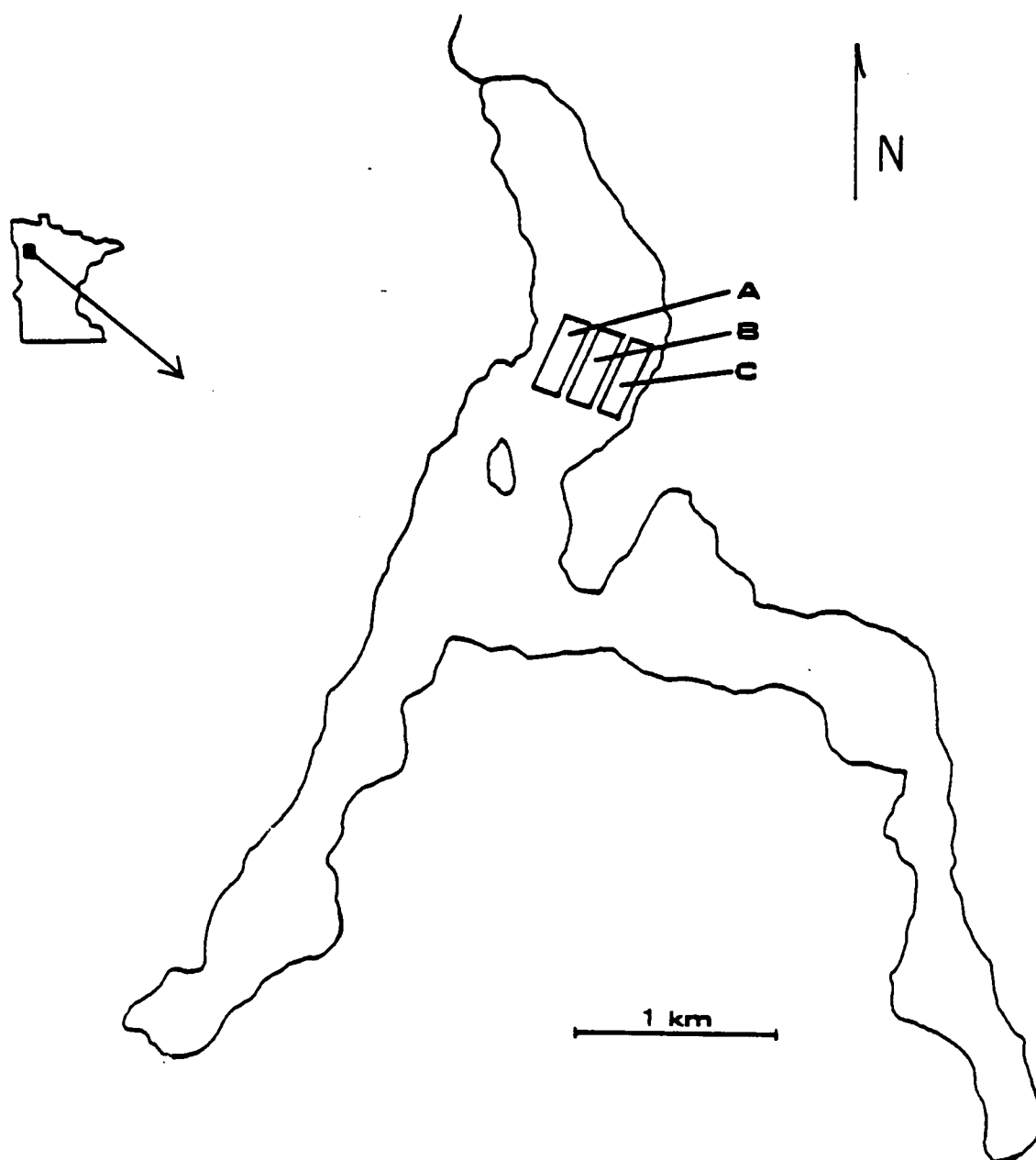


Figure 1. The Study Site, Lake Itasca, Minnesota. The limnetic, sublittoral, and littoral zones are represented by the letters A, B, and C, respectively.

IV. MATERIALS AND METHODS

Sampling for larval fish was conducted from May 25 to August 15 during the summer of 1984. Collections were made from three habitats: the open-water, limnetic zone; a zone of submersed vegetation, the sublittoral; and the littoral zone, characterized by submergent, floating-leaved and emergent vegetation. Sampling was restricted to the north arm of the lake (Figure 1). For all samples, a 706 μ m, 1-meter diameter plankton net was towed behind a motor-driven pontoon boat to which the net was attached by cable. Three 1-minute tows were made in each zone during each sampling period. Only the surface waters were sampled in the littoral and sublittoral zones; in the limnetic, 3 additional oblique tows were made in which the net was dropped to a depth of approximately 5 meters and pulled to the surface. This was done to increase the chances of capturing fish in the deeper water. Sampling was conducted from 1700 to 2300 hours every 2 to 5 days. Sampling was conducted every 5 hours over a 24-hour period on June 28-29. The first sample was taken at 1200 hours on June 28; the last was taken at 1300 hours on June 29.

Larval fish were killed immediately with formalin and then sorted and identified in the laboratory. Fish were identified to genus with the help of the keys in Auer (1982). Only the centrarchids, Pomoxis nigromaculatus and Lepomis spp. were analyzed for feeding selectivity and distribution. Because identification was unreliable, it was not attempted to distinguish among the species of Lepomis.

For the subsamples of 10-15 fish from which gut analyses would be made, total length was measured with a calipers and a ruler. The entire intestinal

tract was removed with a probe and/or a razor blade and the contents identified and counted under a dissecting microscope. Copepods and Cladocera were identified to genus; except for Asplanchna spp., rotifers were counted simply as Rotifera. Total length of prey items was measured with an optic micrometer. All data were entered into an Apple II-E computer. A program obtained from Ed Mills (Cornell University Field Station) was used to summarize data and generate electivity indices from comparative fish gut and environmental samples. Prey selection was estimated by Strauss's Linear Index, $E = r_i - p_i$, where r_i equals the relative abundance of a prey item in the stomach and p_i equals the relative abundance in the environment (Strauss 1979). The index ranges from -1 to +1, with a positive value indicating active selection of a prey item by the fish, a negative value indicating avoidance, and a 0 value indicating random selection.

Zooplankton was sampled concurrently with the larval fish using a 64 μ m, 30-cm diameter plankton net which was lowered to a depth of 4 meters in the limnetic zone, 3-4 meters in the sublittoral zone, and 1.5-2 meters in the littoral zone and pulled to the surface. One sample per zone per sampling period was collected; all samples were preserved in ethanol and formalin.

Aliquots of 5 ml were drawn from each zooplankton sample with a Hensen-Stempel pipette and placed in a counting dish. Samples were diluted or concentrated as necessary to obtain 50-100 animals per subsample. Five subsamples from each sample were counted, identified, and measured with an optic micrometer, and all counts and measurements were entered into the computer. Zooplankton was identified with the help of keys in Pennak (1978).

To calculate the volume of lake water filtered, the following formula was used: $V = \pi r^2 h$, where r equals the radius of the mouth of the net and h equals the depth to which the net was lowered. The number of animals per liter was calculated by the following formula: $n = \frac{N/5 (Vs)}{Vf}$, where n equals the number of organisms per liter, $N/5$ equals the number of organisms per subsample divided by 5 subsamples, Vs equals the subsample volume, and Vf equals the volume of lake water filtered. Calculations were carried out by the computer. All statistics were carried out by programs created by Sokal and Rohlf (1969).

V. RESULTS

Fish

Over the course of the summer, a total of five genera of fish were collected, including Perca flavescens, Notropis spp., Etheostoma spp., Pomoxis nigromaculatus, and Lepomis spp. However, I confined this study to the Centrarchidae, represented by Pomoxis nigromaculatus and Lepomis spp. The bluegill, L. macrochirus occurs sympatrically with the pumpkinseed, L. gibbosus, and the green sunfish, L. cyanellus, in Lake Itasca. Because the bluegill is the dominant sunfish in Lake Itasca (J. Hatch, pers. comm.), it is assumed that most if not all of the larvae collected were L. macrochirus. There is currently no reliable method for distinguishing the species of Lepomis at the larval stage (Keast 1978). Therefore, no attempt was made to identify the young Lepomis spp. beyond the generic level.

Yellow perch are among the first fish to spawn in Lake Itasca and were thus the first to appear in the samples (Whiteside et al. 1985). Following the perch the order of appearance in the samples was Pomoxis - Etheostoma - Lepomis - Notropis. This sequence of appearance has been observed by other investigators in other lakes (e.g., Faber 1963, Keast 1980), presumably following the spawn/hatch timing of these fish. A total of 1398 Lepomis spp. were collected, but only 283 Pomoxis nigromaculatus were taken (Table A1).

Pomoxis nigromaculatus and Lepomis spp. both demonstrated migrations into the limnetic zone shortly after hatching followed by a second migration back to the littoral zone after about a month (Figures 2 and 3). These migrations were incomplete because fish were never entirely restricted to the

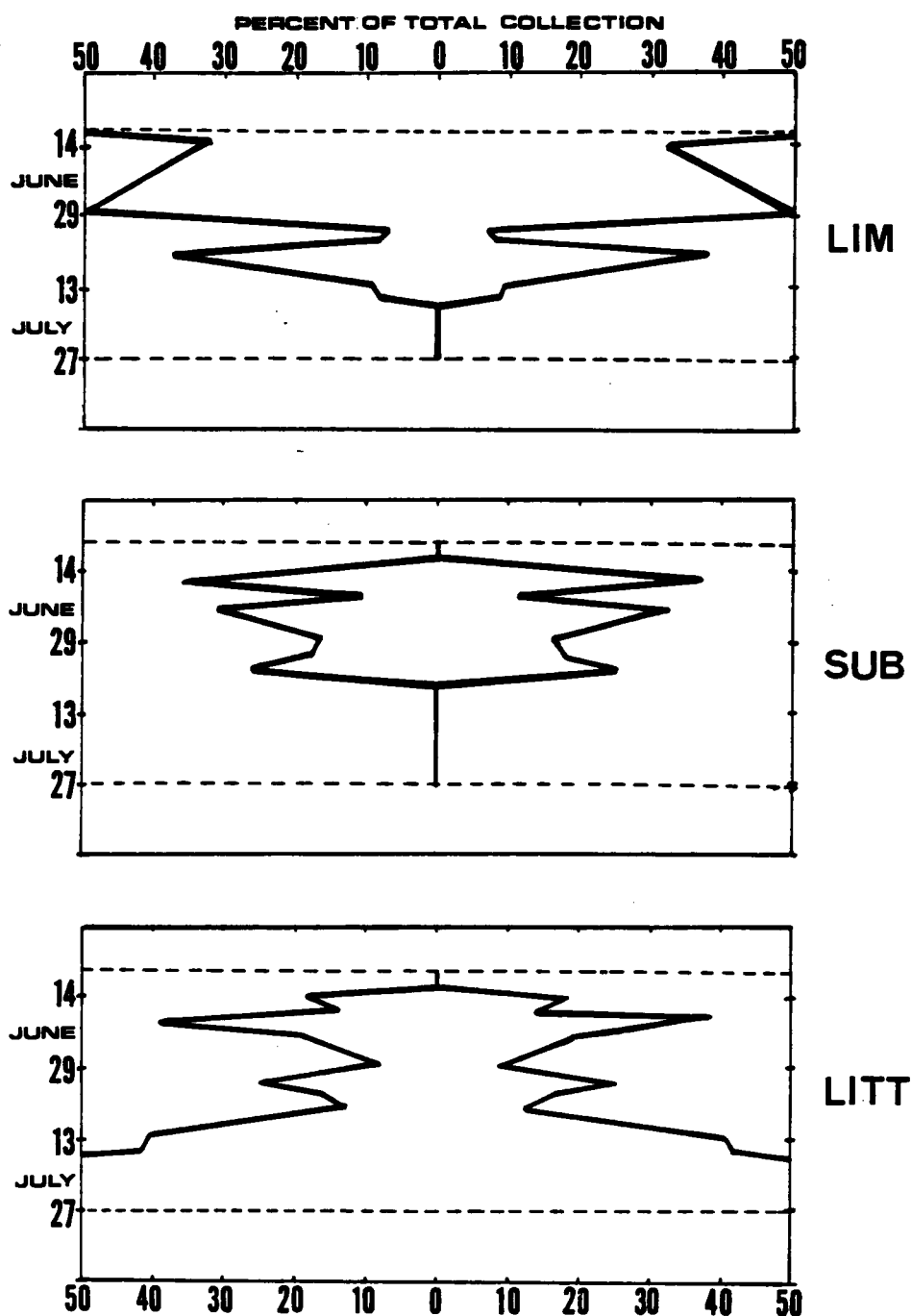


Figure 2. The Percent of Total Collection of *Pomoxis nigromaculatus* in Each Zone for Each Sampling Date. Thus, on June 14, for example, 64% of the crappie larvae were collected in the limnetic zone, 0% were collected in the sublittoral zone, and 36% were collected in the littoral zone. See Appendix 2 for data.

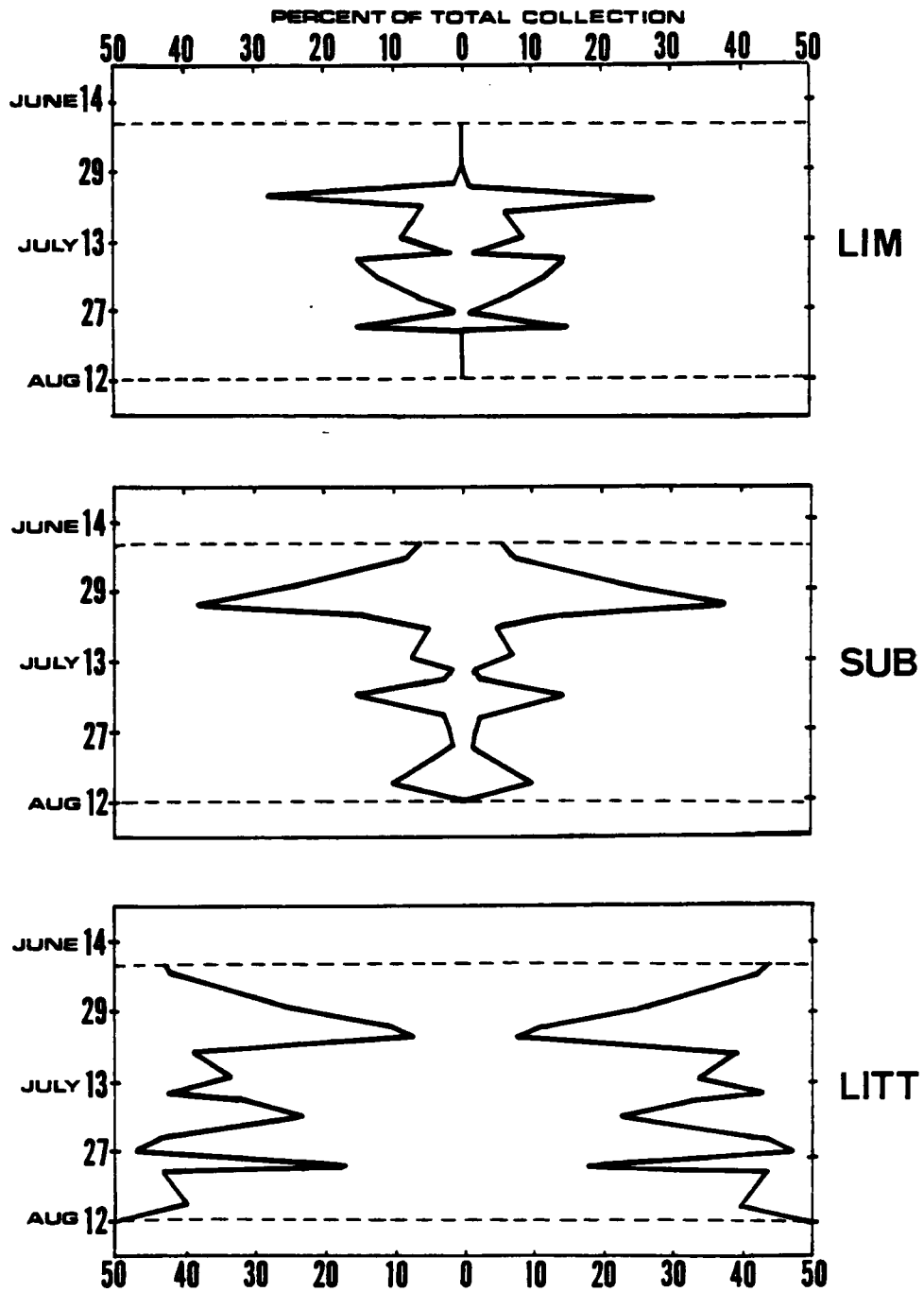


Figure 3. The Percent of Total Collection of *Lepomis* spp. in Each Zone for Each Sampling Date. Interpretation as in Figure 2. See Appendix 3 for data.

limnetic zone. Prior to July 6, most of the young Pomoxis were less than 12 mm ($\bar{x}$ = 9.98 mm) in total length and were collected in the limnetic zone. After July 15 no Pomoxis were collected in the limnetic at all (Figure 2). On the other hand, Pomoxis showed a steady increase in abundance in the littoral zone, especially those at lengths greater than 13 mm. The mean length of fish collected in the limnetic over the course of the entire study was 11.04 ± 2.85 mm; in the sublittoral, 9.42 ± 1.99 mm; and in the littoral, 12.96 ± 6.0 mm. However, after July 6 the mean length of fish collected in the littoral zone was 16.6 mm. Pomoxis cohorts move inshore as they become older.

Lepomis spp. present a more complex picture because their members are multiple spawners, whereas crappies are not (Scott and Crossman, 1973). Whether or not different cohorts actually reside in the limnetic zone or move back and forth between the littoral and limnetic is not known. Most of the sunfish larvae were collected in the littoral zone on all but one sampling date (Figure 3). It is clear, however, that only smaller fish (6.5 - 11.6 mm total length) were collected in the limnetic and sublittoral zones while fish of increasingly larger sizes (6.6 - 19.1 mm) were collected in the littoral zone (Table A3). The mean length of fish collected in the limnetic over the course of the entire study was 7.72 ± 1.03 mm; in the sublittoral, 8.04 ± 1.56 mm; and in the littoral, 11.09 ± 4.36 mm. Werner (1969) reports a limnetic residence in bluegills from 6-22 mm; Keast (1980) found that it took about 4 weeks for bluegills to reach 10-12 mm at which time they migrated inshore. Brown and Colgan (1982) first observed bluegills inshore at 21 mm on August 4 in Lake Opinicon, Ontario.

The mean total length for catches of Pomoxis and Lepomis spp. increased with time as did the mean number of prey items per stomach. The greatest

increase in total length for Pomoxis occurred after July 15 when the fish had moved inshore (Table A2). Lepomis showed a general increase in total length in the littoral and sublittoral zones although means were calculated from a mixture of size classes. In the limnetic zone there was an apparent restriction of both Pomoxis and Lepomis to smaller sizes (Tables A2 and A3). For both Pomoxis and Lepomis, differences in the numbers collected and in the mean number of prey items per stomach were insignificant over a 24-hour period (t-test, $P > .05$).

Zooplankton

The dominant taxa of zooplankton in the net collections were Cyclops spp., Diaptomus spp., copepod nauplii, rotifers, Chydorus sphaericus, Bosmina spp., Daphnia spp., and Ceriodaphnia spp. Plots of the total zooplankton numbers per liter over time show high numbers until the first half of July when a precipitous decline occurred (Figure 4). Numbers remained low until mid-August when a secondary increase took place. An examination of changes in the density of major groups and various genera reveal similar patterns (Figures 5-9). Among sublittoral Cyclops spp., the major decline apparently occurred early in June (Figure 7); limnetic nauplii were found in low numbers, so that it is difficult to distinguish a clear period of decline (Figure 9). In a comparison of the littoral, sublittoral, and limnetic regions, the pelagic rotifers and Cladocera were more abundant in the limnetic zone (Figures 5 and 9). Total copepods and nauplii, however, were somewhat more abundant inshore (Figures 6 and 8).

The mean size of zooplankton in the water column tended to increase over a portion of the summer, mirroring the decline in numbers observed during

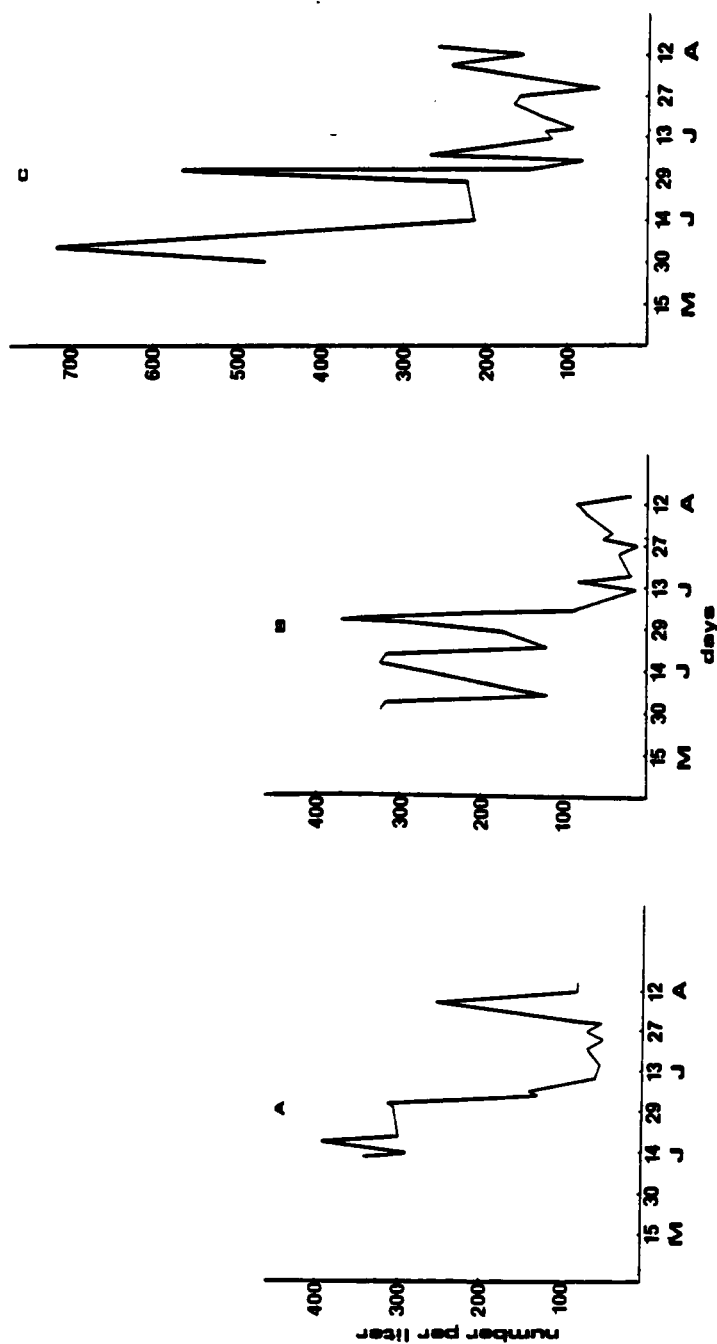


Figure 4. Changes in Total Zooplankton Density (Numbers Per Liter) Over Time (Days) for the Summer of 1984. Plots for the littoral, sublittoral, and limnetic collections are represented by the letters A, B, and C, respectively. The letters M, J, J, and A represent May, June, July, and August, respectively. See Appendix 4 for data.

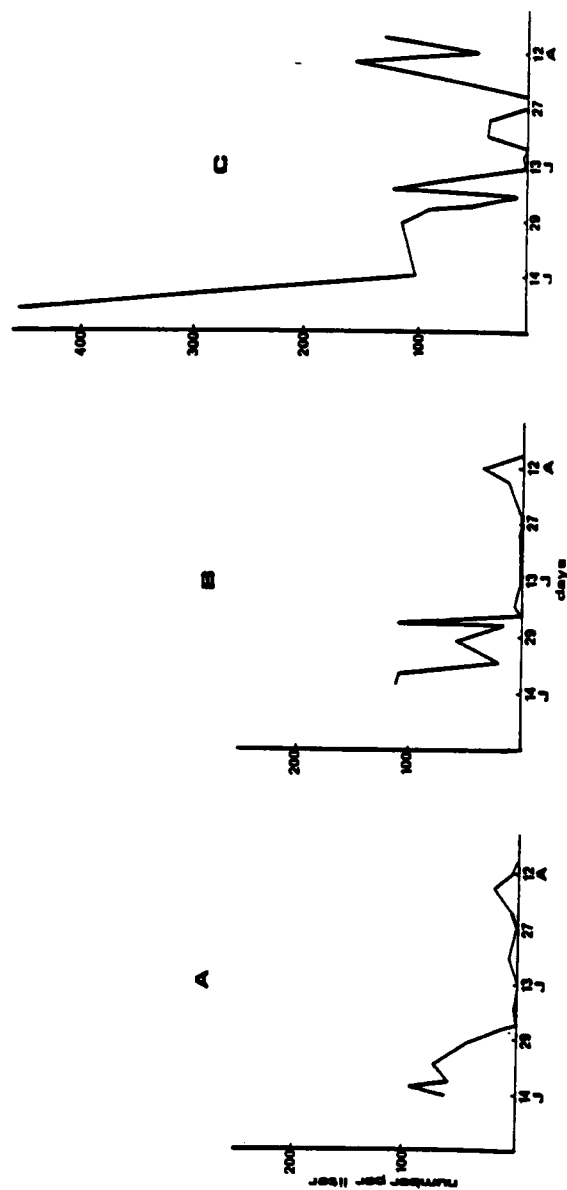


Figure 5. Changes in the Density (Numbers Per Liter) of Rotifers Over Time (Days) for the Summer of 1984. Interpretation as in Figure 4. See Appendix 4 for data.

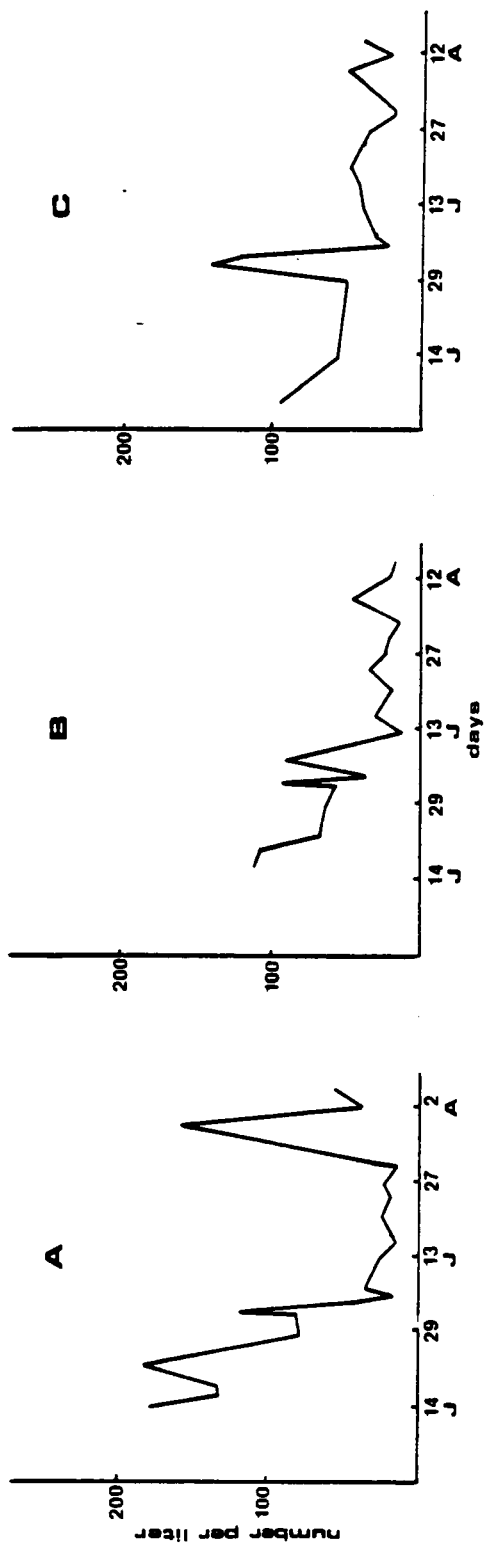


Figure 6. Changes in the Density (Numbers Per Liter) of Total Copepods Over Time (Days) for the Summer of 1984. Interpretation as in Figure 4. See Appendix 4 for data.

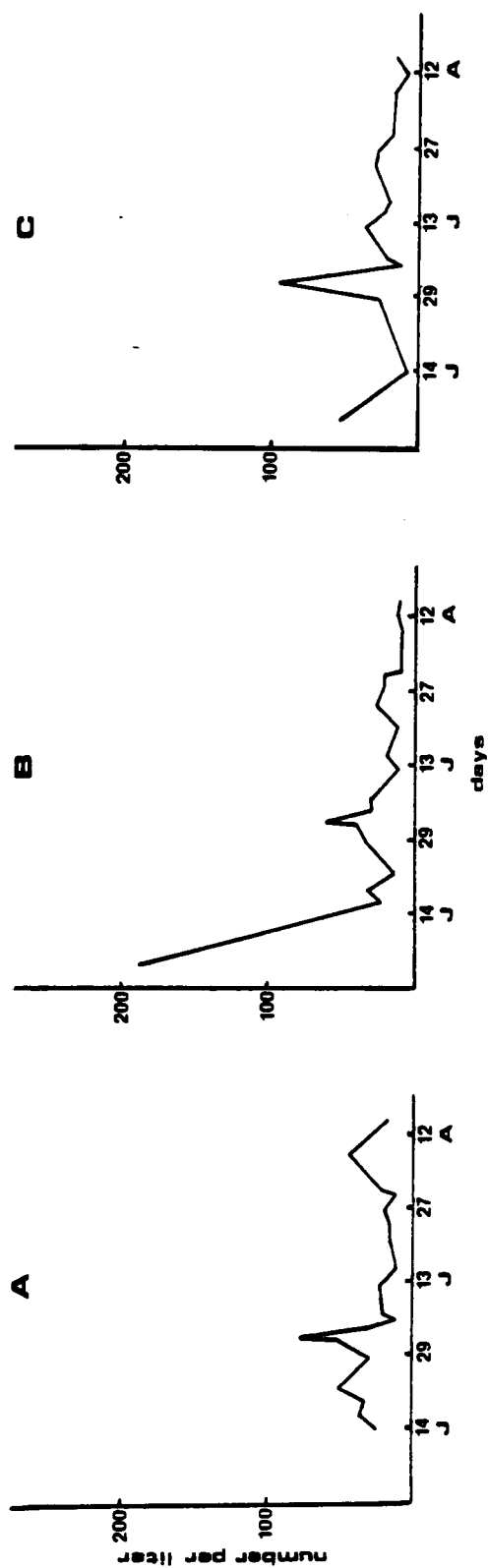


Figure 7. Changes in the Density (Numbers Per Liter) of *Cyclops* spp. Over Time (Days) for the Summer of 1984. Interpretation as in Figure 4. See Appendix 4 for data.

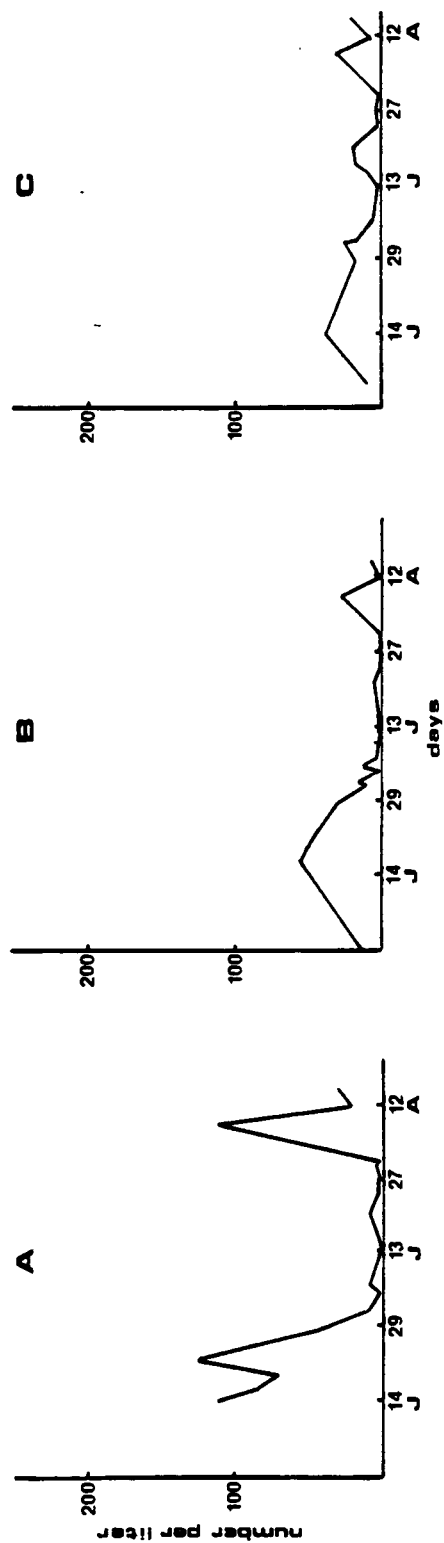


Figure 8. Changes in the Density (Numbers Per Liter) of Copepod Nauplii Over Time (Days) for the Summer of 1984. Interpretation as in Figure 4. See Appendix 4 for data.

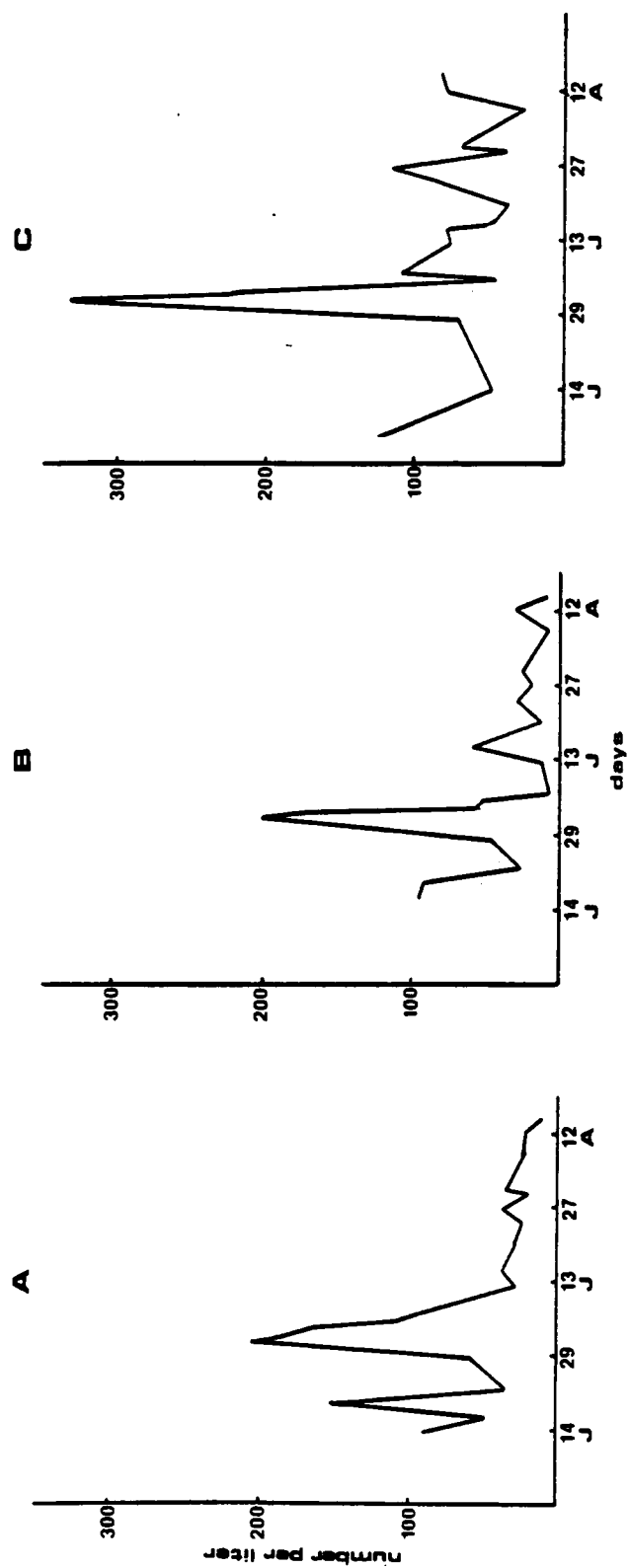


Figure 9. Changes in the Density (Numbers Per Liter) of Total Cladocera Over Time (Days) for the Summer of 1984. Interpretation as in Figure 4. See Appendix 4 for data.

the first half of July (Table A4). A t-test comparison of mean sizes before and after July 1, 6, and 12 shows a significant increase in all zones ($P > .05$, see Table 1). After July 30, there was a decrease in the mean size of the zooplankton community (see Table 2). Over a 24-hour period, differences in the abundance of zooplankton were insignificant (t-test, $P > .05$).

Electivities

Electivity indices were calculated separately for each zone. Cyclops spp. were positively selected by Pomoxis in all three zones (Figure 10). Negative to random values were calculated for Diaptomus spp. in the littoral and sublittoral zones, and random to slightly positive values were recorded in the limnetic. Diaptomus spp. is more difficult for fish to locate (Wright and O'Brien 1984) and was not actively selected by P. annularis in studies by Siefert (1968) and Bulkley et al. (1976). Except for initial positive selection of nauplii in the sublittoral and limnetic zones, Pomoxis demonstrated negative to random selection of nauplii. Siefert (1968) noted that nauplii are most important at the initiation of feeding by P. annularis, but that a sharp increase in selection of Cyclops spp. occurs when the fish reach the 6.0-7.9 mm size class; Keast (1980) reports a switch to Cyclops spp. at 7-12 mm. Negative to random selection of Ceriodaphnia spp. took place in all zones. Selection for Bosmina spp. was negative to random in the limnetic and sublittoral zones; selection was also negative in the littoral zone until July 15 when selection grew strongly positive, probably as a result of the influx of larger fish (Figure 11). A similar increase in selection of Daphnia spp. by white crappie was reported for fish 10.0-13.9 mm (Siefert 1968), although in this study negative selection was constant for Daphnia spp., rotifers, and Chydorus sphaericus.

Table 1. Changes in Mean Size of Total Zooplankton Over the Summer of 1984. Results of a t-Test Comparison of Means for Sizes (mm) of Total Environmental Zooplankton Before and After July 1, 6, and 12.

		Littoral		Sublittoral		Limnetic	
		mean size (mm)	t-test	mean size (mm)	t-test	mean size (mm)	t-test
before July	1	.24	5.03 $\geq$ 2.07* df=23	.26	4.43 $\geq$ 2.07* df=23	.31	2.73 $\geq$ 2.06* df=23
after July	1	.35		.39		.43	
before July	6	.27	3.73 $\geq$ 2.07* df=23	.29	3.58 $\geq$ 2.07* df=23	.33	2.82 $\geq$ 2.07* df=23
after July	6	.36		.40		.46	
before July	12	.27	4.16 $\geq$ 2.07* df=23	.29	3.75 $\geq$ 2.07* df=23	.33	3.39 $\geq$ 2.07* df=23
after July	12	.36		.41		.47	

*All tests significant at $P > .05$.

Table 2. Mean Size (mm) of Total Zooplankton During the Summer of 1984.

	ZOOPLANKTON MEAN SIZE (mm)		
	Litt	Sub	Lim
June 4-28	.24	.29	.24
July 1-6	.33	.35	.37
July 12-30	.39	.45	.53
Aug. 1-15	.34	.36	.39

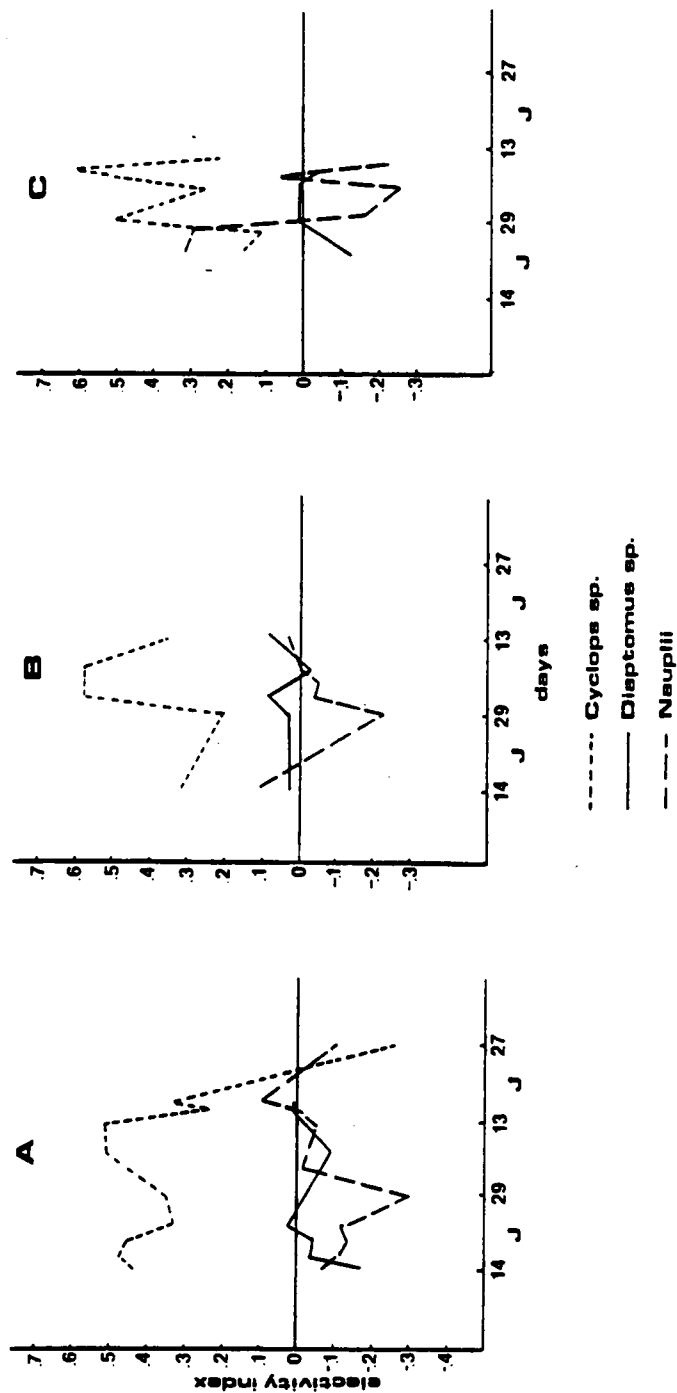


Figure 10. Electivity Indices for Predation Upon the Copepods *Cyclops* spp., *Diaptomus* spp. and Copepod Nauplii by *Pomoxis nigromaculatus* for the Summer of 1984. Electivity values were calculated with the formula $E = r_j - p_j$ (Strauss 1979); the index ranges from -1 to +1 with positive values indicating active selection, negative values indicating avoidance, and 0 values indicating random selection. The littoral, sublittoral, and limnetic zones are represented by the letters A, B, and C, respectively. Time is measured in days; the letters J and J represent June and July.

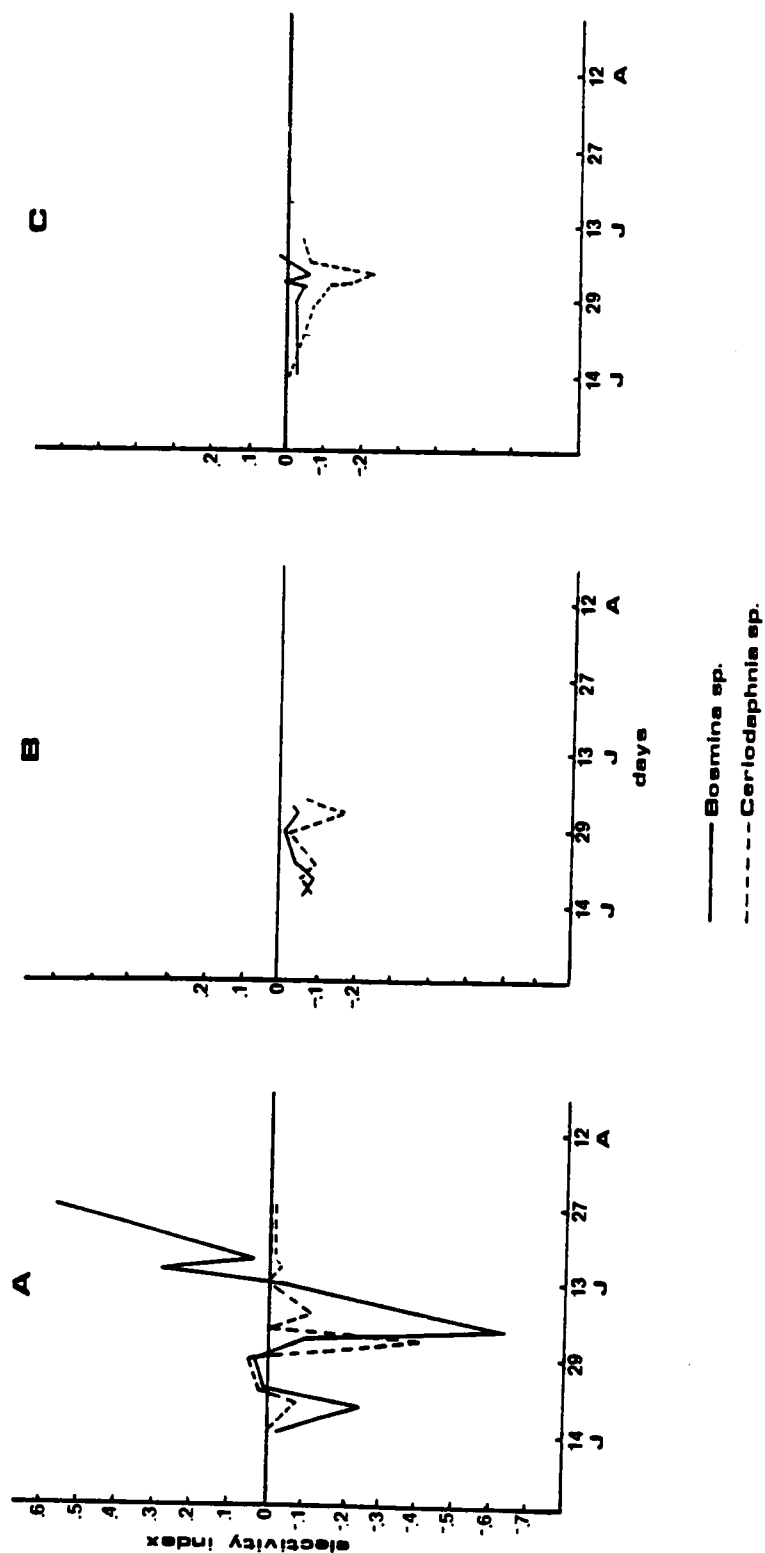


Figure 11. Electivity Indices for Predation Upon the Cladocerans, *Bosmina* spp. and *Ceriodaphnia* spp. by *Pomoxis nigromaculatus* for the Summer of 1984. Interpretation as in Figure 10.

Mathur and Robbins (1971) consider Daphnia spp. and Cyclops spp. to be the most important food items in juvenile and adult white crappies. Perhaps the selection for or against Daphnia spp. represents a species-specific difference in the feeding habits of P. annularis and P. nigromaculatus.

Electivities for Lepomis spp. contrast with those for Pomoxis in that there was strong positive selection for rotifers over all three zones (Figure 12) and fairly strong selection for nauplii, especially in the limnetic (Figure 13). Selection for Cyclops spp. was negative in the limnetic and sublittoral zones and variable in the littoral. In all zones, selection for Ceriodaphnia spp. was initially negative to random, becoming positive toward the end of July (Figure 14). Lepomis spp. showed consistent negative selection for Bosmina spp., Daphnia spp., and Chydorus sphaericus. Keast (1980) reports that all larvae 4-7 mm fed on nauplii and small cyclopoids, while older fish preferred Sida spp. and Diaphanosoma spp.; Chydorus spp. were of little significance in all cases (see Table A6).

Electivity values were not calculated for insect larvae, mostly Chironomidae, which appeared in the guts of larger Lepomis spp. (> 15 mm) late in the summer, as did the large zooplankter, Sida crystallina. Fairchild (1982) has observed heavy predation upon Sida by the centrarchid, Micropterus salmoides. Over a 24-hour period, changes in the electivities were insignificant (t-test, $P > .05$).

Size Selection

Young crappies consumed prey items with a mean size of 0.34 mm. The mean size consumed in the littoral was 0.31 mm, in the sublittoral 0.32 mm,

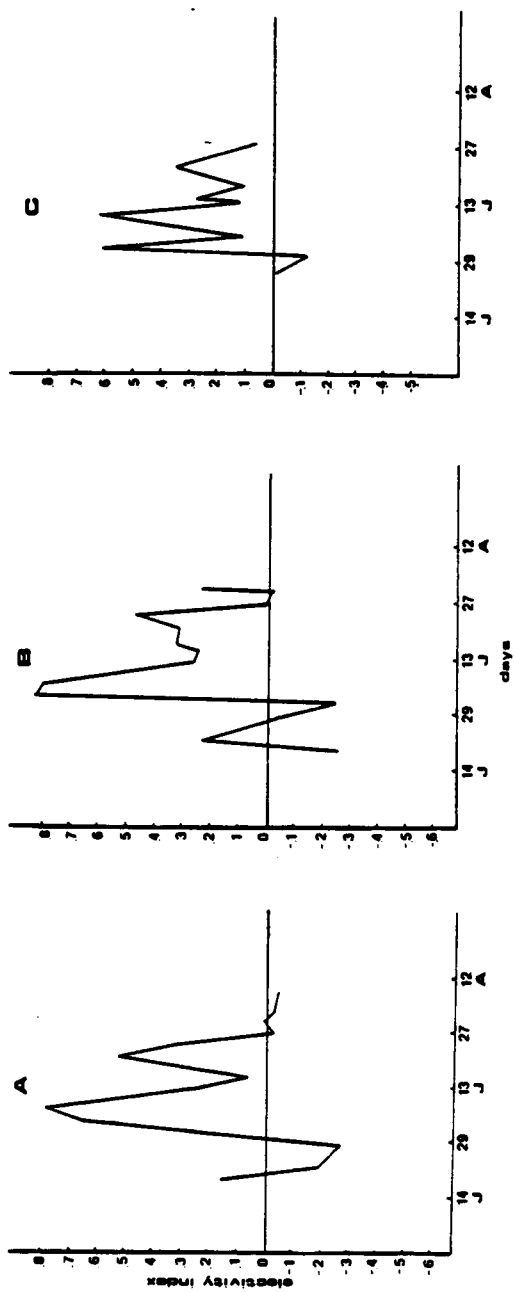


Figure 12. Electivity Indices for Predation Upon Rotifers by Lepomis spp. During the Summer of 1984. Interpretation as in Figure 10.

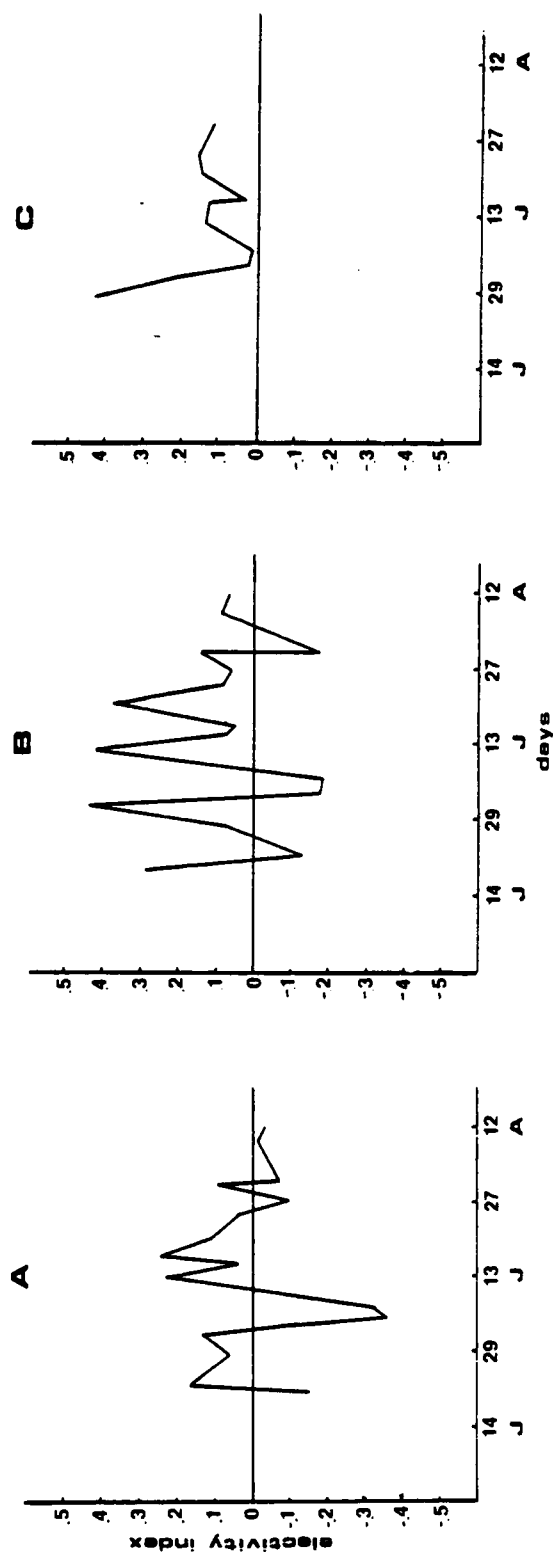


Figure 13. Electivity Indices for Predation Upon Copepod Nauplii by Lepomis spp. During the Summer of 1984. Interpretation as in Figure 10.

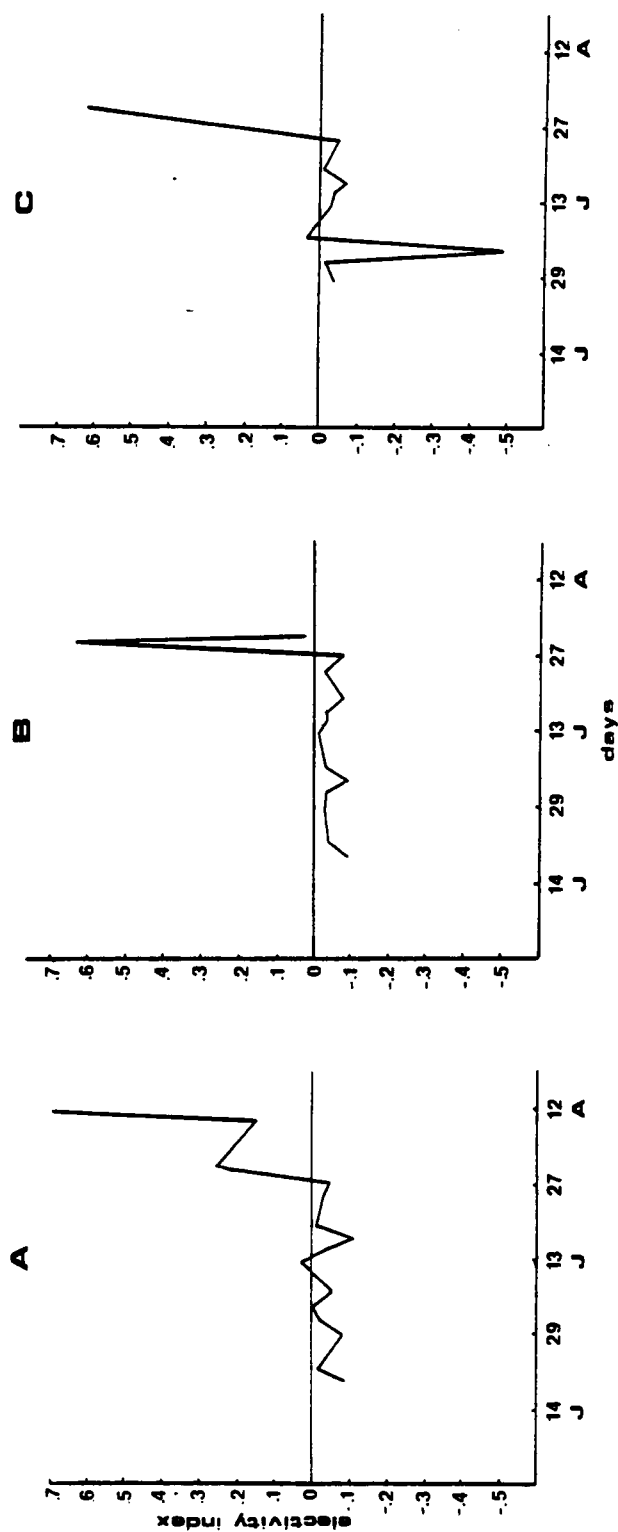


Figure 14. Electivity Indices for Predation Upon *Ceriodaphnia* spp. by *Lepomis* spp. During the Summer of 1984. Interpretation as in Figure 10.

and in the limnetic 0.39 mm. Over the summer there was little increase in the sizes selected by Pomoxis nigromaculatus (Range = .19-.47, Table A7), although sizes in the environment did increase somewhat. A trend toward selecting larger sizes of prey after July 6 was insignificant (t-test, $0.33 \leq 0.68$, $P > .5$). These numbers reflect continued selective predation primarily upon Cyclops spp.

The mean size of prey items consumed by Lepomis spp. was 0.22 mm (Table A8). In the littoral zone the mean was 0.27 mm, in the sublittoral, 0.21 mm and in the limnetic, 0.21 mm. There was a significant trend toward consumption of larger prey in a comparison of means before and after July 6 (t-test, $3.30 > 2.70$, $P > .01$), and before and after July 30 (t-test, $6.19 > 2.70$, $P > .01$). The range of sizes consumed was 0.10 - 0.42 mm.

VI. DISCUSSION

Fish Distributions

One of the adaptive strategies of young fish is to undertake a pelagic migration shortly after hatching and remain in the limnetic zone for a period of time before returning to the littoral zone (e.g., Faber 1963, Keast 1980, Whiteside et al. 1985, Werner 1967, 1969). Thus, for both crappies and sunfish, the observed limnetic/littoral distributions are not unusual. The black crappie, which has one major spawning period each year (Scott and Crossman 1973), shows a fairly well-defined period of limnetic residence (Figure 2, p. 20) in which most of the fish collected prior to July 15 were located in the limnetic zone, and after this date most were collected in the littoral zone. There was a direct relationship between the size of the fish and their respective location within the lake; i.e., smaller fish (7.0-11.6 mm TL) predominated in the limnetic and larger fish (13.4-29.6 mm TL) were most abundant in the littoral (Table A2). The inshore migration for Pomoxis probably occurs when the fish reach 15 to 20 mm TL, approximately 1 month after hatching.

Lepomis macrochirus is a multiple spawner (Beard 1982). Evidence that multiple spawning occurs in Lake Itasca is provided by the mixture of sizes in later littoral collections of Lepomis. Also, 0+ Lepomis were well-represented in collections from June 19 to August 12. Werner (1969) and Faber (1963) have noted that young Lepomis spp. reside in the limnetic zone during their first 4-5 weeks and then return to the littoral; other studies have indicated a longer period of residence (Werner 1967). It is unclear from these data whether or not young Lepomis spp. reside exclusively in the limnetic zone during their

first month. In all but one sample, fish of all sizes were most abundant in the littoral collections (Figure 3, p. 21). Werner (1967) reported a broad range of sizes (10-55 mm) in his littoral collections. Only small fish (6.5-11.6 mm TL) were collected in the limnetic and sublittoral open-water zones (Table A3). This indicates that at least some Lepomis spp. move into the limnetic region. Eventually, all cohorts of 0+ Lepomis migrate inshore, so that after July 30 bluegills were no longer collected in the limnetic (Figure 3, p. 21).

In neither fish species does there appear to be a complete shift into the limnetic zone after hatching. It is thought that larval fish migrate into the limnetic zone primarily to escape heavy predation by vertebrate and invertebrate predators in the littoral region (Casterlin and Reynolds 1978, Werner 1969, Werner et al. 1983a, Whiteside et al. 1985). Rotifers, the preferred prey of young Lepomis spp., are most abundant in the limnetic zone throughout the summer (Figure 5, p. 25). A period of residence in the limnetic region would assure the fish of both an adequate food supply and a lower probability of being eaten. Taking only these points into account, the limnetic zone would appear to be the logical choice of habitats for larval centrarchids. However, "limnetic"-sized larvae were collected repeatedly in littoral samples. Their presence may be explained by any of the following factors:

1. Lake Itasca has an extensive littoral zone, comprising 55% of its area (Cole and Underhill 1965), and the east side of the lake, where sampling was conducted, has a greater extent of littoral zone than do other shores. Lake Itasca is also relatively narrow. It is possible that the littoral zone remains more or less accessible to the young fish, precluding a prolonged residence in the limnetic zone. Furthermore, the lake is highly productive

(Cole and Underhill 1965), and subject to mixing by wind and storms. The pelagic zooplankton species on which larval centrarchids depend are probably available throughout the lake most of the time.

2. The ichthyoplankton are subject to translocation by wind, storms, or currents; since larval fish are not strong swimmers, they may have been moved inshore by external factors.

3. Young fish are not evenly distributed in the lake. External factors, schooling tendencies and other causes may result in spatial variation for which sampling methods cannot correct. Quantitative sampling of larval fish is therefore difficult to impossible, at least by the methods used in this study. The actual percentage of small fish in the limnetic zone may actually have been much higher.

4. The small sizes of fish (6-11 mm TL) collected in the littoral zone may have been in transit to the limnetic (Werner 1969).

5. Larval fish undertake diurnal offshore-inshore migrations (Werner 1967).

6. Some individuals do not participate in the migration to the limnetic zone but remain in shallow water (Werner 1967).

7. The different species of Lepomis have different migration patterns and/or timing of littoral-limnetic movements.

8. It is possible that there are mechanisms of predation avoidance in larval fish other than refuge in the open-water. The behavioral plasticity of bluegills has been observed by several investigators (Keast 1980, Casterlin and Reynolds 1978, Werner and Hall 1977); this characteristic may extend to larval bluegills as well.

After reaching approximately 20 mm in length, both Pomoxis nigromaculatus and Lepomis spp. clearly prefer the littoral zone. This inshore migration is thought to be in response to an inadequate food supply in the limnetic zone and to the greater diversity and abundance of littoral prey items (Werner 1969, Whiteside et al. 1984, 1985). Cyclops spp., the preferred prey of Pomoxis, was found to be most abundant in the littoral, as were insects and large substrate-bound zooplankton utilized by older sunfish. Food availability may not be the only factor influencing this change of habitats. Werner et al. (1983a) reports that small size classes of larger bluegills may prefer open water where foraging is more profitable, but switch to the vegetated littoral to find refuge from predators, presumably different ones than prompted their initial move into the limnetic.

The Relationship of Larval Fish, Zooplankton Abundance and Size

If it is assumed that larval centrarchids are gape-limited (Zaret 1980), then young fish are obligate planktivores for at least their first few weeks. The extent to which any particular fish species is able to structure the zooplankton community through predation is dependent on fish and zooplankton density, temporal and spatial variation among fish or plankton, the relative abundance of other fish species and other factors. A problem that cannot be addressed here, but may be essential to understanding declines in zooplankton populations, is whether or not changes in the phytoplankton, e.g., the predominance of blue-greens in late summer or the production of toxins, induce corresponding changes in the zooplankton (Brown 1984). Williams and Whiteside (1978) deduced that zooplankton were not food-limited because birth rates did not decline throughout the season. Because sampling of both the fish and

zooplankton populations did not necessarily provide accurate estimates of their numbers, these data cannot be used to generate causal relationships for the effect of larval fish predation on zooplankton in Lake Itasca. Only general patterns and apparent correlations are reported here.

The electivity index from which feeding preferences are determined is subject to several errors of interpretation. First, although zooplankton and fish collections in this study were made at the same time, zooplankton was sampled vertically whereas fish were collected in an integrated horizontal tow. For any single index value, there is some doubt as to whether the environmental sample actually represented what was available to the fish. Strauss's Linear Index has the advantage of taking on extreme values only when an item is abundant in the environment but occurs very rarely in the fish stomachs, or is rare and consumed almost exclusively. However, significant sources of error in its interpretation may result from inadequate habitat sampling, differential availability of prey (patchiness), and differential digestion rates (Strauss 1979). Gannon (1976) found that Daphnia spp. were digested more rapidly and were thus under-represented in fish stomach samples. Also, there may be substantial within sample (Layzer 1982) and day-to-day variation in food consumption (Smagula and Adelman 1982). "Caution should be exercised when observed differences in food consumption measured at discrete points in time are attributed to abiotic or biotic environmental factors such as ... prey density" (Smagula and Adelman 1982).

In the limnetic, sublittoral, and littoral zones, the major food item for young Pomoxis nigromaculatus was Cyclops spp. (Figure 10, p. 33). If the fish had significant impact on the Cyclops spp. population in the lake, one would

expect a decline in the density of Cyclops concurrent with predation by crappies. Figures 6 and 7 (pp. 26 and 27) show that a major decline in numbers of both total copepods and Cyclops spp. occurred during the first half of July in most zones; in the sublittoral, numbers of Cyclops dropped most sharply early in June. During the first two weeks of July, crappie larvae spent most of their time in the limnetic and sublittoral zones (Figure 2, p. 20) where they actively selected Cyclops spp. While they may have contributed to the mid-summer decline in numbers of Cyclops spp., young crappies were probably not abundant enough to be a significant factor (Table A1).

In Lepomis spp., the preferred prey items for fish until the end of July were rotifers and nauplii (Figures 12 and 13, pp. 36 and 37). Bluegills first spawned in mid-June and then contributed several more cohorts through July. The mid-summer decline in total zooplankton density (Figure 4, p. 24) occurred during the time that many Lepomis began intensive feeding, i.e., the first week of July. Since the main component of the pelagic zooplankton appears to be rotifers (Figure 5, p. 25), and Lepomis spp. are abundant in the lake (Table A1), it is possible that Lepomis spp. has a significant role in the initial drop in numbers of rotifers. These numbers remain low until mid-August when a secondary increase coincides with the selection of a more diverse array of prey items by Lepomis spp. Noble (1975) also reports a mid-July maximum intensity of predation. Thus, Lepomis spp. may not only contribute to the decline in rotifers, but may also keep these numbers low as long as rotifers are a preferred prey item. Nauplii occurred in much lower numbers than did rotifers in environmental samples, but showed a similar decline and secondary peak; the same reasoning may apply to the predation of Lepomis upon nauplii

as well. Bluegills in the littoral and sublittoral zones showed some positive selection for Cyclops spp. and may act along with Pomoxis to keep the numbers of Cyclops low until mid-August (Figure 7, p. 27). Keast (1980) noted a decrease in the numbers of cyclopoids, nauplii, and Bosmina coincident with the rise in numbers of fish larvae which included both Pomoxis and Lepomis.

The Size Efficiency Hypothesis (Brooks and Dodson 1965) states that fish will consume the largest available prey items that they are able to ingest. If this is true, then an increase in the mean size of prey items in the fish guts would be expected as the fish grow. For Pomoxis, there is a slight increase with time in the mean size of prey consumed in all three zones (Table A7). The mean size of Cyclops spp. available in the environment (0.49 mm) was significantly greater than that of those eaten by the fish (0.45 mm), (t-test, $2.39 > 2.00$, $P > .05$). It is possible that the higher average size for Cyclops spp. in the environment is a product of predation by small fish, including Pomoxis nigromaculatus, upon smaller size classes of Cyclops spp. Wright and O'Brien (1984) noted, however, that adult white crappies have gill rakers which cannot retain prey less than 3.5 mm, which leads to increased predation upon larger size classes. It would be interesting to determine whether it is the young fish or the adults which have a more profound influence on the size structure of the zooplankton community.

The mean size of prey consumed by young Lepomis spp. does not change significantly (t-test, $P > .05$) except in the littoral zone, when fish begin to consume larger prey items such as Ceriodaphnia spp. and insect larvae. Until July 30, relatively small sizes of prey (range = 0.10-0.35 mm, $\bar{x}$ = 0.22 mm), i.e., rotifers and nauplii, were consumed in the littoral (see Table A8). Though

the sizes of rotifers and nauplii in the environment remained constant throughout the summer (0.10-0.25 mm), the mean size of total zooplankton in the environment (0.37 mm) was generally higher than the sizes consumed by Lepomis spp. (0.22 mm) and tended to increase over a portion of the summer (Tables 1 and 2, pp. 31 and 32). Perhaps heavy predation upon small zooplankters such as rotifers and nauplii drives the average size of the total zooplankton up. In late summer, as fish switch to a more diverse array of prey items, small zooplankton taxa may experience a release from predation, and the mean size of the total zooplankton may thus decrease. Size-selective predation upon small and intermediate size classes of zooplankton may be more important in structuring the pelagic zooplankton community than predation upon large size classes (Archibald 1975), at least over short periods of time.

VII. CONCLUSIONS

To summarize the major points of this study:

1. Both Pomoxis nigromaculatus and Lepomis spp. undertake early migrations into the limnetic zone, where food is plentiful and predation levels are low.
2. As older larvae, both crappies and sunfish become more visible to limnetic predators. They return to the littoral zone where there are aquatic plants that provide structure for refugia from predation (Helfman 1981a). In addition, they find a greater diversity and abundance of food organisms (Whiteside et al. 1984).
3. Pomoxis nigromaculatus feeds preferentially upon copepod nauplii at the initiation of feeding, soon switching to Cyclops spp. Cladocerans are incorporated into the diet following the return to the littoral zone.
4. Lepomis spp. feed upon rotifers and copepod nauplii and some Cyclops spp. until they reach a length of 15-20 mm and begin to feed on a wider array of invertebrates in the littoral zone.
5. Pomoxis nigromaculatus is probably not abundant enough in Lake Itasca to account for major changes in the zooplankton community.
6. A positive correlation exists between predation intensity by bluegills and the mid-summer decline in numbers of rotifers and nauplii. Predation by a combination of larval fish species may be able to induce annual declines in the numbers of zooplankton.
7. In general, the mean sizes of prey consumed by both Pomoxis and Lepomis were lower than the mean sizes available in the environment.

8. A positive correlation exists between the mean size of environmental zooplankton and predation upon small size classes by larval Lepomis spp. It is possible that the increase in the mean size of the total zooplankton up to the end of July is due to predation upon small zooplankton taxa by a combination of larval fish species.

Suggestions For Future Study

The goal of any pilot study is to provide information which can be used to refine research methods and to ask better questions. The most difficult problems in larval fish research lie, first, in carrying out reliable identification to the species level and, second, in obtaining quantitative samples of the fish and their zooplankton prey. Without accurate population estimates, one can draw only tenuous conclusions from observed patterns. In the meantime, until sampling techniques improve, comparative field and laboratory studies may provide a means of double-checking the information from either source.

Following is a list of questions generated by this project, but beyond its scope:

1. Are there differences in the diets and distribution of larval bluegills, pumpkinseeds, and green sunfish? What are the relative abundances of larval species of Lepomis in Lake Itasca, and are they the same as those of the adults?
2. Under controlled conditions, how do larval fish affect zooplankton densities?
3. Are these patterns (e.g., electivities, migrations, zooplankton densities) constant for other parts of the lake? For other years?

4. How do Notropis spp. and Etheostoma spp. differ? In the few stomachs I examined, there appeared to be a very different array of prey items. Notropis spp. contained predominantly Chydorus sphaericus, and Etheostoma spp. contained many littoral and benthic forms.

5. Where are the larvae of the other fish species known to occur in the lake? Are they in water as yet too shallow to sample and/or in discrete nesting sites in other parts of the lake? Or in deep water?

6. Why do Pomoxis prefer Cyclops? Are electivity values inflated due to differential digestion rates, or does selection of Cyclops spp. result from higher energy return per effort, the formation of a search image, or some other factor?

7. How do fish change search images as they grow?

8. Do larval Lepomis spp. demonstrate the same behavioral flexibility as adults? If given a choice, do larvae always choose the open-water? Do they act differently when predators are not present?

9. How different is the complement of predators for larval and juvenile fishes? It is likely that invertebrate predators in the littoral zone are not as important to larger juveniles as they are to larval fish, and may prompt the initial pelagic migration.

10. How do young-of-the-year and adult fishes interact to affect the zooplankton community?

11. What is the role and relative importance of the phytoplankton in structuring the zooplankton community?

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APPENDIX

Table A1. The Number of Fish Collected in Each Zone on Each Sampling Date. 24-Hour Samples Are Not Included.

Date	Zone	Black Crappie	Sunfish	Yellow Perch	Shiners	Darters
May 25	Litt	-	-	-	-	-
	Sub	-	-	-	-	-
	Lim Total	0 0	0 0	152 152	0 0	0 0
May 30	Litt	-	-	-	-	-
	Sub	-	-	-	-	-
	Lim Total	0 0	0 0	36 36	0 0	0 0
June 7	Litt	-	-	-	-	-
	Sub	-	-	-	-	-
	Lim Total	0 0	0 0	4 4	0 0	0 0
June 8	Litt	-	-	-	-	-
	Sub	-	-	-	-	-
	Lim Total	2 2	0 0	8 8	0 0	0 0
June 12	Litt	-	-	-	-	-
	Sub	-	-	-	-	-
	Lim Total	6 6	0 0	7 7	0 0	9 9
June 14	Litt	8	0	19	0	0
	Sub	-	-	-	-	-
	Lim Total	14 22	0 0	0 19	0 0	0 0
June 16	Litt	21	0	12	0	0
	Sub	54	0	0	0	0
	Lim Total	75	0	12	0	0

Table A1 (Continued)

Date	Zone	Black Crapple	Sunfish	Yellow Perch	Shiners	Darters
June 19	Litt Sub Lim Total	14 4 <u>18</u>	30 4 <u>34</u>	0 0 <u>0</u>	0 0 <u>0</u>	0 0 <u>0</u>
June 22	Litt Sub Lim Total	12 20 <u>32</u>	36 7 <u>43</u>	0 0 <u>0</u>	0 0 <u>0</u>	0 0 <u>0</u>
June 28	Litt Sub Lim Total	1 2 3 <u>6</u>	10 10 0 <u>20</u>	2 0 0 <u>2</u>	5 0 1 <u>6</u>	0 0 0 <u>0</u>
July 1	Litt Sub Lim Total	22 16 6 <u>44</u>	62 214 6 <u>282</u>	0 0 0 <u>0</u>	16 46 3 <u>65</u>	1 0 7 <u>8</u>
July 3	Litt Sub Lim Total	2 3 1 <u>6</u>	13 24 49 <u>86</u>	0 0 0 <u>0</u>	22 70 32 <u>124</u>	3 1 0 <u>4</u>
July 6	Litt Sub Lim Total	2 0 6 <u>8</u>	33 4 5 <u>42</u>	0 0 0 <u>0</u>	15 1 0 <u>16</u>	2 0 0 <u>2</u>
July 12	Litt Sub Lim Total	13 0 3 <u>16</u>	172 39 44 <u>255</u>	0 0 0 <u>0</u>	20 66 20 <u>106</u>	2 0 0 <u>2</u>

Table A1 (Continued)

Date	Zone	Black Crappie	Sunfish	Yellow Perch	Shiners	Darters
July 15	Litt	5	128	0	3	0
	Sub	0	4	0	1	0
	Lim	1	5	0	6	0
	Total	6	137	0	10	0
July 17	Litt	27	86	0	4	0
	Sub	0	7	0	3	0
	Lim	0	39	0	7	0
	Total	27	132	0	14	0
July 20	Litt	0	25	0	4	0
	Sub	0	16	0	9	0
	Lim	0	13	0	1	0
	Total	0	54	0	14	0
July 24	Litt	3	56	0	0	1
	Sub	0	3	0	3	0
	Lim	0	8	0	51	0
	Total	3	67	0	54	1
July 27	Litt	4	52	0	1	0
	Sub	0	2	0	22	0
	Lim	0	1	0	16	0
	Total	4	55	0	39	0
July 30	Litt	0	25	0	3	0
	Sub	0	25	0	72	0
	Lim	0	21	0	140	0
	Total	0	71	0	215	0
August 1	Litt	0	66	0	0	0
	Sub	0	2	0	0	0
	Lim	0	0	0	1	0
	Total	0	68	0	1	0

Table A1 (Continued)

Date	Zone	Black Crappie	Sunfish	Yellow Perch	Shiners	Darters
August 8	Litt	0	4	0	0	1
	Sub	0	1	0	1	0
	Lim	0	0	0	12	0
	Total	0	5	0	13	1
August 12	Litt	0	21	0	0	3
	Sub	0	0	0	2	0
	Lim	0	0	0	9	0
	Total	0	21	0	11	3
TOTAL		283	1398	248	668	70

Table A2. The Number and Relative Percentage of Pomoxis nigromaculatus Collected in Each Zone.

Date	Zone	Number collected	% of Total	$\bar{X}$ Total Length (mm)
June 8	Litt	-	-	-
	Sub	-	-	-
	Lim	2	1.00	6.0
	Total	2		
June 12	Litt	-	-	-
	Sub	-	-	-
	Lim	6	1.00	6.6
	Total	6		
June 14	Litt	8	.36	7.4
	Sub	-	-	-
	Lim	14	.64	7.9
	Total	22		
June 16	Litt	21	.28	7.7
	Sub	54	.72	6.4
	Lim	-	-	-
	Total	75		
June 19	Litt	14	.78	9.8
	Sub	4	.22	7.5
	Lim	-	-	-
	Total	18		
June 22	Litt	12	.38	9.3
	Sub	20	.62	10.2
	Lim	-	-	-
	Total	32		
June 28	Litt	1	.17	10.8
	Sub	2	.33	11.5
	Lim	3	.50	12.5
	Total	6		
July 1	Litt	22	.50	11.0
	Sub	16	.36	10.4
	Lim	6	.14	11.8
	Total	44		

Table A2 (Continued)

Date	Zone	Number collected	% of Total	$\bar{X}$ Total Length (mm)
July 3	Litt	2	.33	10.2
	Sub	3	.50	9.2
	Lim	1	.17	12.0
	<u>Total</u>	<u>6</u>		
July 6	Litt	2	.25	12.3
	Sub	0	-	-
	Lim	6	.75	11.6
	<u>Total</u>	<u>8</u>		
July 12	Litt	13	.81	13.3
	Sub	0	-	-
	Lim	3	.19	15.5
	<u>Total</u>	<u>16</u>		
July 15	Litt	5	.83	15.6
	Sub	0	-	-
	Lim	1	.17	13.0
	<u>Total</u>	<u>6</u>		
July 17	Litt	27	1.00	17.3
	Sub	0	-	-
	Lim	0	-	-
	<u>Total</u>	<u>27</u>		
July 20	Litt	0	-	-
	Sub	0	-	-
	Lim	0	-	-
	<u>Total</u>	<u>0</u>		
July 24	Litt	3	1.00	17.5
	Sub	0	-	-
	Lim	0	-	-
	<u>Total</u>	<u>3</u>		
July 27	Litt	4	1.00	29.6
	Sub	0	-	-
	Lim	0	-	-
	<u>Total</u>	<u>4</u>		

Table A3. The Number and Relative Percentage of Lepomis spp. Collected in Each Zone.

Date	Zone	Number collected	% of Total	$\bar{X}$ Total Length (mm)
June 19	Litt	30	.88	6.6
	Sub	4	.12	6.9
	Lim	-	-	-
	Total	34		
June 22	Litt	36	.84	6.9
	Sub	7	.16	5.9
	Lim	-	-	-
	Total	43		
June 28	Litt	10	.50	6.9
	Sub	10	.50	6.3
	Lim	0	-	-
	Total	20		
July 1	Litt	62	.22	8.0
	Sub	214	.76	8.4
	Lim	6	.02	8.2
	Total	282		
July 3	Litt	13	.15	7.7
	Sub	24	.28	7.1
	Lim	49	.57	6.7
	Total	86		
July 6	Litt	33	.78	9.2
	Sub	4	.10	8.9
	Lim	5	.12	8.0
	Total	42		
July 12	Litt	172	.67	8.7
	Sub	39	.15	8.3
	Lim	44	.17	7.8
	Total	255		
July 15	Litt	128	.85	9.7
	Sub	4	.03	8.7
	Lim	5	.03	8.0
	Total	137		

Table A3 (Continued)

Date	Zone	Number collected	% of Total	$\bar{X}$ Total Length (mm)
July 17	Litt	86	.65	10.8
	Sub	7	.05	7.1
	Lim	39	.30	7.4
	<u>Total</u>	<u>132</u>		
July 20	Litt	25	.46	7.1
	Sub	16	.30	7.2
	Lim	13	.24	6.9
	<u>Total</u>	<u>54</u>		
July 24	Litt	56	.87	11.1
	Sub	3	.05	7.5
	Lim	8	.13	7.1
	<u>Total</u>	<u>67</u>		
July 27	Litt	52	.94	19.2
	Sub	2	.04	10.5
	Lim	1	.02	6.5
	<u>Total</u>	<u>55</u>		
July 30	Litt	25	.35	11.6
	Sub	25	.35	11.6
	Lim	21	.30	10.2
	<u>Total</u>	<u>71</u>		
August 1	Litt	66	.97	16.4
	Sub	2	.03	8.0
	Lim	0	0	-
	<u>Total</u>	<u>68</u>		
August 8	Litt	4	.80	19.1
	Sub	1	.20	10.0
	Lim	0	-	-
	<u>Total</u>	<u>5</u>		
August 12	Litt	21	1.00	15.1
	Sub	0	-	-
	Lim	0	-	-
	<u>Total</u>	<u>21</u>		

Table A4 (Continued)

Date	Zone	Total	Copepods	Cladocera	Rotifers	Nauplii	Cyclops	Bosmina	Rotifers (excluding Asplanchna)			Daphnia	Total X Size
									Ceriodaphnia				
July 6	Litt	135.8	34.5	93.7	6.8	7.7	20.2	15.4	3.5	8.9	3.7	.28	
	Sub	150.9	87.1	7.0	7.1	4.8	28.3	10.5	6.5	7.1	14.1	.33	
	Lim	266.9	30.7	108.7	125.6	4.4	19.6	10.4	124.7	24.2	48.1	.29	
July 12	Litt	56.4	24.7	28.3	0.9	1.0	22.3	2.6	0	0.2	7.7	.41	
	Sub	24.7	13.7	10.6	0.7	0.3	11.9	0.6	0.1	0.4	1.7	.50	
	Lim	115.5	39.2	75.3	1.8	0.7	35.7	0.4	0.4	0.7	41.7	.59	
July 15	Litt	53.1	15.1	36.3	1.9	4.5	10.4	7.1	0	1.6	3.4	.45	
	Sub	88.6	28.6	58.3	1.1	3.8	17.6	2.1	0.2	1.5	33.9	.51	
	Lim	126.5	43.1	78.1	12.4	8.5	24.4	1.1	4.2	6.0	47.3	.51	
July 20	Litt	69.3	22.1	28.9	15.9	7.2	14.8	18.4	0.8	3.1	2.1	.33	
	Sub	33.9	18.9	12.5	1.4	6.4	10.8	0.6	0.9	1.4	5.0	.38	
	Lim	125.4	48.0	37.1	38.9	18.4	20.8	.7	38.9	1.4	27.2	.39	
July 24	Litt	49.8	18.5	23.4	6.8	3.0	15.1	5.3	0.4	3.0	5.7	.37	
	Sub	67.5	34.6	28.1	4.6	3.4	27.4	0.5	3.9	2.7	10.6	.38	
	Lim	163.9	42.1	84.4	36.4	2.8	29.3	1.4	36.4	11.7	61.1	.49	
July 27	Litt	69.2	20.9	35.8	2.8	3.0	17.9	0.4	0.2	1.9	2.5	.35	
	Sub	-	23.4	19.1	1.1	0.7	20.1	0.1	0.5	3.5	11.9	.41	
	Lim	155.5	37.1	114.8	2.7	2.2	28.3	0	1.1	8.1	93.9	.60	
July 30	Litt	50.0	13.9	21.3	0.9	0.6	13.2	0.2	0.4	0.8	11.9	.41	
	Sub	58.3	21.2	24.4	1.1	0.7	20.1	0.5	1.1	0.7	13.8	.49	
	Lim	61.8	22.4	38.0	1.4	1.7	18.7	0.6	0.6	1.6	28.4	.58	
August 1	Litt	75.0	23.9	33.7	2.1	1.0	18.9	0	0.5	6.9	12.3	.41	
	Sub	43.1	15.4	23.8	4.1	2.5	10.3	0	2.8	0.6	18.8	.49	
	Lim	91.1	19.8	67.9	4.7	2.1	10.6	0.4	2.1	1.4	63.6	.60	
August 8	Litt	256.4	158.6	22.6	37.9	112.5	43.9	0.2	22.7	15.1	1.1	.26	
	Sub	70.7	43.6	8.8	13.9	33.4	9.3	0.6	13.5	5.1	1.7	.21	
	Lim	240.6	51.9	28.9	159.7	31.1	16.6	0	159.7	1.8	25.4	.19	

Table A4 (Continued)

Date	Zone	Total	Copepods	Cladocera	Rotifers	Nauplii	Cyclops	Bosmina	Rotifers (excluding Asplanchna)	Ceriodaphnia	Daphnia	Total X Size
August 12	Litt	81.7	36.4	20.6	6.6	6.1	28.1	0.2	5.5	13.2	1.5	.34
	Sub	85.7	18.8	28.2	38.7	3.2	11.2	0	36.6	1.9	18.6	.32
	Lim	154.8	23.7	78.8	51.6	7.1	7.3	0	48.7	6.0	69.9	.45
August 15	Litt	81.1	53.4	11.5	4.3	29.4	18.7	1.5	2.6	5.5	1.3	.33
	Sub	37.0	17.8	9.5	3.4	6.3	10.6	0	0.9	0.8	5.7	.43
	Lim	257.9	40.6	83.0	132.5	18.4	13.8	0	129.3	3.2	74.9	.32

Table A5. *Pomoxis nigromaculatus* Electivity Indices. In This Table, N = Number of Fish in Subsample, TL = Total Length of Fish, S = Number of Prey in Stomach Sample, E = Number of Prey in Environmental Sample, and I = Linear Electivity Index ($E = r_1 - p_1$).

Date	Zone	N	TL (mm)	Nauplii			Cyclops			Diaptomus			Rotifers			Bosmina			Ceriodaphnia			Chydorus		
				S	E	I	S	E	I	S	E	I	S	E	I	S	E	I	S	E	I	S	E	I
June 14	Litt	7	7.4	15	31	-.063	17	3	.438	2	14	-.165	1	15	-.210	0	15	-.160	0	1	-.010	0	5	-.030
	Sub	11	7.9	20	18	.105	29	6	.321	7	7	.031	13	69	-.413	9	19	-.044	0	3	-.020	0	2	-.020
June 16	Litt	12	7.7	39	25	-.106	93	10	.467	2	3	-.030	14	19	-.183	2	8	-.103	1	3	-.037	0	4	-.050
	Sub	10	6.4	82	28	.308	42	15	.153	3	20	-.129	32	72	-.382	0	5	-.040	0	10	-.090	0	6	-.010
June 19	Litt	14	9.8	23	22	-.130	94	13	.456	8	7	-.037	16	12	-.048	10	24	-.241	0	8	-.090	0	7	-.030
	Sub	4	7.5	25	24	.295	8	6	.115	0	13	-.060	8	41	-.322	1	9	-.089	0	16	-.060	0	1	-.020
June 22	Litt	9	9.3	17	34	-.121	29	11	.328	2	1	.020	6	30	-.247	8	10	.011	2	2	.009	0	3	-.030
	Sub	10	10.2	8	22	-.158	76	9	.500	4	2	-.001	6	11	-.144	3	3	-.027	1	6	-.098	0	3	-.010
June 28	Litt	3	10.8	2	25	-.314	10	16	.344	0	1	-	1	0	.063	2	5	.037	0	4	-.090	0	13	-.150
	Sub	2	11.5	1	13	.250	7	18	.278	0	2	-	0	0	-	0	5	-.120	0	5	-.030	1	5	-.028
July 1	Litt	9	11.0	7	11	-.101	217	25	.581	3	2	-.011	4	0	.019	6	3	-.091	8	35	-.414	2	8	-.086
	Sub	9	10.4	11	10	-.060	83	40	.612	1	7	-.022	2	0	-.266	5	31	-.051	1	35	-.393	0	5	-.050
July 2	Litt	5	12.7	3	5	.025	29	26	.515	0	11	-.120	0	0	-.010	1	16	-.164	2	97	-.187	0	35	-.100
	Sub	8	13.3	0	11	-.040	54	48	.592	1	9	-.031	0	0	-	5	23	-.042	2	34	-.147	1	29	-.136
July 3	Litt	2	10.2	1	8	-.092	49	11	.790	1	0	.019	0	0	-	1	53	-.717	0	2	-.020	0	5	-.050
	Sub	2	9.2	0	3	-.020	44	21	0	0	8	-.060	0	0	-	0	11	-.080	0	7	-.050	0	12	-.090
July 6	Litt	2	12.3	0	7	-.060	73	15	.506	1	4	-.093	5	0	.062	1	14	-.356	1	5	-.119	0	58	-.410
	Sub	6	11.6	3	3	-.005	118	13	.579	3	5	-.020	36	71	-.316	4	3	.001	4	12	-.065	0	7	-.120

Table A6. *Lepomis* spp. Electivity Indices. In This Table, N = Number of Fish in Subsample, TL = Mean Total Length of Fish, S = Number of Prey in Stomach Sample, E = Number of Prey in Environmental Sample, and I = Linear Electivity Index ($E = r_1 - p_1$).

Date	Zone	N	TL (mm)	Nauplii S E I	Cyclops S E I	Rotifers S E I	Bosmina S E I	Ceriodaphnia S E I	Chydorus S E I
June 19	Litt	12	6.6	23 22	0 13	23 12	0 24	0 8	0 7
	Sub	3	6.9	15 24	7 6	8 41	1 9	0 16	0 1
	Lim	-	-	-	-	-	-	-	-
June 22	Litt	11	7.0	18 34	5 11	6 30	0 10	0 2	0 3
	Sub	5	5.9	3 22	0 9	5 11	1 3	1 6	0 3
	Lim	-	-	-	-	-	-	-	-
June 28	Litt	4	7.6	1 15	1 6	0 0	3 2	1 6	1 6
	Sub	9	7.7	7 20	8 10	8 0	0 9	0 6	0 6
	Lim	4	6.3	2 23	0 22	5 0	0 15	0 16	0 6
July 1	Litt	12	8.0	23 11	17 25	13 0	0 3	0 35	0 8
	Sub	9	8.4	14 10	13 40	5 0	2 31	0 97	0 35
	Lim	8	8.2	16 13	21 64	19 61	0 21	0 44	0 40
July 2	Litt	3	7.7	3 5	1 26	1 0	1 16	0 35	0 5
	Sub	4	8.5	0 11	2 48	3 0	0 23	0 34	0 29
	Lim	3	9.0	0 13	2 38	0 35	0 21	0 42	0 16
July 3	Litt	10	7.4	3 8	15 11	32 0	0 53	0 2	0 5
	Sub	10	7.5	7 3	14 21	35 0	0 11	0 7	0 12
	Lim	10	7.6	6 1	31 13	68 1	0 4	1 15	0 11
July 6	Litt	10	9.3	7 7	71 15	304 0	0 14	0 5	0 58
	Sub	4	8.9	2 8	25 19	100 0	0 6	0 7	0 33
	Lim	5	8.0	6 3	2 13	128 71	0 3	0 12	0 7
July 12	Litt	10	8.8	19 4	21 17	15 0	0 3	2 0	1 17
	Sub	10	8.3	13 0	12 15	11 0	1 1	2 2	2 14
	Lim	10	7.9	8 0	10 21	34 0	0 0	1 2	3 25
July 15	Litt	12	9.7	5 1	109 6	13 0	69 6	2 2	6 8
	Sub	3	8.7	0 10	4 20	2 1	1 4	0 2	0 21
	Lim	4	8.0	5 5	4 15	9 12	0 1	0 3	0 8

Table A7. Mean Size (mm) of Prey Items in Black Crappie Stomachs (S) and in Environmental Samples (E).

Date	Zone	N	TL (mm)	Nauplii S E	Cyclops S E	Rotifers S E	Diaptomus S E	Bosmina S E	Ceriodaphnia S E	Daphnia S E	Chydorus S E	Total X S E
June 14	Litt	7	7.4	.19	.39	.10	.60	.71	-	-	-	.32
	Sub	-	-	-	-	-	-	-	-	-	-	-
	Lim	11	7.9	.15	.39	.10	.59	.81	.20	.24	-	.28
												.21
June 16	Litt	12	7.7	.17	.36	.11	.50	.77	.20	.19	.20	.25
	Sub	10	6.4	.17	.34	.10	.63	.93	-	-	-	.31
	Lim	-	-	-	-	-	-	-	-	-	-	.35
												-
June 19	Litt	14	9.8	.20	.43	.10	.78	.86	.23	.22	-	.35
	Sub	4	7.5	.17	.33	.10	-	-	.20	.23	-	.30
	Lim	-	-	-	-	-	-	-	-	-	-	.20
												.31
June 22	Litt	9	9.3	.17	.38	.10	.55	.60	.19	.20	-	.26
	Sub	10	10.3	.19	.42	.10	.70	.70	.20	.20	-	.20
	Lim	-	-	-	-	-	-	-	.30	.35	-	.32
									-	-	-	.25
June 28	Litt	3	10.8	.20	.43	.10	-	-	.15	.20	-	.24
	Sub	2	11.5	.20	.50	-	-	-	-	.20	.23	.27
	Lim	2	12.5	.20	.54	-	-	-	.32	-	.20	.23
									-	-	.17	.37
July 1	Litt	9	11.1	.20	.52	.10	.63	.55	.33	.29	.25	.30
	Sub	9	10.4	.18	.47	.10	.70	.79	.22	.23	-	.27
	Lim	5	11.8	.10	.51	.10	.82	.53	.35	.29	-	.47
									-	.60	-	.38
July 2	Litt	5	12.7	.17	.48	-	-	-	.20	.21	-	.29
	Sub	8	13.3	-	.51	-	.60	.61	.20	.22	.20	.39
	Lim	5	9.5	-	.46	.10	.80	.63	.40	.393	-	.46
									-	-	-	.40
July 3	Litt	2	10.3	.10	.46	-	-	-	.20	.21	-	.44
	Sub	2	9.3	.15	.41	-	-	-	-	-	-	.49
	Lim	2	9.0	-	.44	.10	.70	.48	-	-	-	.41
									-	-	-	.41
July 6	Litt	2	12.3	-	.50	.10	-	-	.20	.20	-	.28
	Sub	-	-	-	.53	-	-	-	.30	.34	-	.33
	Lim	6	11.6	.17	.52	.10	.87	.70	.40	.40	.63	.41
									-	-	-	.29

Table A8. Mean Size (mm) of Prey Items in Sunfish Stomachs (S) and in Environmental Samples (E).

Date	Zone	N	TL (mm)	Nauplii	Cyclops	Rotifers	Bosmina	Ceriodaphnia	Chydorus	Daphnia	Total X Size
				S	S	S	S	S	S	S	S
				E	E	E	E	E	E	E	E
June 19	Litt	12	6.6	.16	.17	.10	.10	-	-	-	.13
	Sub	3	6.9	.19	.15	.10	.20	.23	-	-	.19
	Lim	-	-	-	-	-	-	-	-	-	-
June 22	Litt	11	6.9	.16	.16	.10	.10	-	-	-	.19
	Sub	5	5.9	.13	.17	.10	.10	.35	-	-	.13
	Lim	-	-	-	-	-	-	-	-	-	.25
June 28	Litt	4	7.6	.20	.20	.10	.20	.28	.16	-	.21
	Sub	9	7.7	.13	.17	.10	-	-	-	-	.16
	Lim	4	6.3	.10	.18	.10	-	-	-	-	.23
July 1	Litt	12	8.0	-	.37	.10	.20	.19	-	-	.24
	Sub	9	8.4	.19	.22	.10	.20	.19	-	-	.21
	Lim	8	8.2	.19	.22	.10	.20	.23	-	-	.22
July 2	Litt	3	7.7	.13	.22	.10	.10	.21	-	-	.16
	Sub	3	8.5	-	.30	.10	.10	-	-	-	.20
	Lim	4	9.0	-	.30	.10	-	.30	.34	.54	.22
July 3	Litt	10	7.4	.20	.37	.10	-	-	-	-	.22
	Sub	10	7.4	.16	.38	.10	-	-	-	.50	.29
	Lim	10	7.5	.15	.37	.10	-	.20	.32	-	.20
July 6	Litt	10	9.3	.19	.38	.10	-	-	-	-	.22
	Sub	4	9.9	.20	.40	.11	-	-	-	-	.24
	Lim	5	8.0	.20	.30	.10	-	-	-	-	.20
July 12	Litt	10	8.8	.19	.38	.10	-	.15	.18	-	.23
	Sub	10	8.3	.18	.31	.10	.20	.30	.20	-	.21
	Lim	10	7.9	.19	.35	.10	-	.20	.40	-	.19
July 15	Litt	12	9.7	.18	.38	.10	-	.35	.20	.83	.28
	Sub	3	8.7	-	.38	-	.20	-	.21	.50	.23
	Lim	4	8.0	.18	.40	-	-	-	-	-	.23

Table A9. Sample Electivity Print-Out Calculated for Predation Upon Cyclops spp. by Lepomis spp.

ELECTIVITY AND LINEAR INDICES

CALC SPECIES 4/11/84

VAR 272084 DF 2

DATE: 272034

TRIAL #: 2

SAMPLE STATION: LIM VL

DEPTH OF COLLECTION:

NUMBER OF FISH COLLECTED: 13

TEMPERATURE:

CLOUD COVER:

PREY DENSITY:

COLLECTIONS GEAR:

REMARKS: LEPOMIS

VARIABLE EVALUATED: DENSITY

FIELD EXPERIMENT

TIME OF COLLECTION

START: 1000

END

WIND DIRECTION:

WIND SPEED:

MEAN SIZE OF PREY IN FISH SAMPLE: .33333333 MM

MEAN SIZE OF PREY IN ENVIRONMENT SAMPLE: .560526316 MM

MEAN FISH SIZE : 6.9 MM

NUMBER OF FISH EXAMINED: 10

TOTAL # PREY: FISH SAMPLE - 92

ENVIRONMENT SAMPLE - 86

AVE # PREY: 9.2

VARIANCE: 14.6222222

CYCLOPS VERNALIS

FISH		ENVIRONMENT								
SIZE	#	R*	#	P	E	L	VAR(P)	WITHIN	AMONG	
VAR(R)	VAR(R*)		VAR(L)	HET	CONF	INT				
0-3 MM	18	0.20	38	0.44	-0.386	-0.246	0.0028677	0.0056263	0.0505310	0.
0561573	0.0091902		0.0120578	3.6399	-0.4614	TO	-0.0310	*NEG*		
TOTALS	18		38							

VITA

Catherine Ann Justis was born in Memphis, Tennessee, on June 27, 1959. She attended several universities and graduated from Tennessee Technological University with a Bachelor of Science degree in 1981. From August 1981 until May 1983, she worked for the Kentucky Nature Preserves Commission and the Division of Water Quality in Frankfort, Kentucky. In September of 1983 she began work toward a Master of Science degree in Zoology at The University of Tennessee, and received her degree in August 1985.