THE INFLUENCE OF SUBMERGED AQUATIC VEGETATION ON TROPHIC RELATIONSHIPS OF LARGEMOUTH BASS

by

Scott M. Smith

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APPROVED:

Donald J. Orth, Chairman

Louis A. Helfrich

John J. Ney

Larry A. Nielsen, Department Head

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(ABSTRACT)

Aquatic vegetation is considered a nuisance in many lakes and reservoirs supporting largemouth bass populations, and control (eradication) of vegetation is often undertaken. Yet, the relationship between submerged aquatic vegetation and adult largemouth bass, from a trophic standpoint, is poorly understood. I attempted to quantify this relationship by comparing available prey with consumption from the perspective of individual largemouth bass and the largemouth bass population in Flat Top Lake, West Virginia in 1986 and 1987.

The abundance of largemouth bass ≥200 mm long was positively associated with vegetation density, although no relationship was apparent between the length and relative weight of adult largemouth bass and vegetation. Forage fish abundance was also positively related to vegetation density. Vegetation was heavily utilized by most fish species in the reservoir. Consumption (quantity and diet composition) of individual largemouth bass did not differ among the vegetation densities considered. However, the increased abundance of available prey associated with increased vegetation densities led to increased overall consumption by the largemouth bass population. Thus, largemouth bass production potential was positively related to

vegetation density. Increases in the vegetation/open water interface had no short-term (one month). Evidence from this study indicates that aquatic vegetation could be managed to increase the productivity of largemouth bass in Flat Top Lake. The benefits to largemouth bass provided by aquatic vegetation in Flat Top Lake and similar systems should be considered prior to iniating vegetation control activities.

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INTRODUCTION

The largemouth bass *Micropterus salmoides* is one of the most popular sport fish in North America (Heidinger 1975). In the United States, more sport angling effort is directed toward *Micropterus* spp. than any other fish (USDI, USDC 1982). Submerged vegetation is an important component of aquatic ecosystems inhabited by largemouth bass (Maceina et al. 1984), and there is a great potential for aquatic vegetation and largemouth bass to occur simultaneously. In fact, many studies have examined relationships between aquatic vegetation and largemouth bass from the perspective of predator/prey interactions and largemouth bass productivity (Glass 1971; Savino and Stein 1982; Savitz et al. 1983; Anderson 1984; Durocher et al. 1984; Wiley et al. 1984; Gotceitas and Colgan 1987).

Submerged aquatic vegetation has many impacts on aquatic ecosystems, and these impacts range from beneficial to detrimental from a fisheries management perspective. Submerged vegetation creates habitat for many species of fish and invertebrates. Additionally, vegetation generally increases water clarity by filtering suspended sediments from the water column and by utilizing nutrients there by reducing phytoplankton. Aquatic vegetation also helps to stabilize shorelines by reducing wave action.

On the other hand, excess aquatic vegetation can reduce the accessibility of many aquatic ecosystems to humans. Colle et al. (1987) found that large increases in the amount of submerged vegetation (*Hydrilla* sp.) in Orange Lake, Florida reduced angler efforts by 85% even though harvestable populations of largemouth bass and black crappie *Pomoxis nigromaculatus*were not affected. This reduction in effort was accompanied by a 90% decrease in angler-generated revenue. Thus, the negative impacts of aquatic vegetation can be severe. So severe, in fact, that the control of aquatic vegetation using chemical, mechanical, and biological methods is an important industry.

Adult largemouth bass often use vegetated habitats (Mesing and Wicker 1986; Betsill et al. 1988), but they may avoid areas of extremely dense vegetation (Barnett and Schneider 1974). The relationship between largemouth bass production and vegetation density is inconsistent. Durocher et al. (1984) found a positive correlation between the amount of aquatic vegetation present and the abundance of harvestable largemouth bass in Texas reservoirs with < 20% surface area vegetation coverage. Wiley et al. (1984) described a parabolic relationship between vegetation density and largemouth bass production in small Illinois ponds. Bailey (1978) found no relationship whatsoever between aquatic vegetation and the production of largemouth bass. in 31 Arkansas reservoirs. This relationship (or lack thereof) is further complicated by predator size, as different sizes of largemouth bass may respond to vegetation differently (Ware and Gasaway 1978; Durocher et al. 1984; Wanjala et al. 1986).

Some of the conflicting results in previous studies may relate to an unmeasured factor, i.e., the interface between dense vegetation and open water. Cooper and Crowder (1979) and Savitz et al. (1983) suggested that this interface or "ecotone" was the habitat type utilized most extensively by largemouth bass in systems with aquatic vegetation. Although this interface was important to all sizes of largemouth bass, the foraging opportunities for largemouth bass in this ecotone increased with increasing size of largemouth bass. Thus, it is possible for aquatic vegetation to influence largemouth bass populations, but the relationship may be indeterminate.

The availability of prey is a dominant factor influencing any predator population. In the case of largemouth bass, aquatic vegetation has two principal influences on predator/prey interactions. Theoretical models and empirical data suggest that prey abundance is directly proportional to vegetation density, while predation efficiency is inversely related to vegetation density (Glass 1971; Breck and Kitchell 1979; Crowder and Cooper 1979b; Savino and Stein 1982; Anderson 1984; Wiley et al. 1984; Gotceitas and Colgan 1987). Thus, areas of low vegetation density/abundance have less abundant prey than areas of high vegetation, but that prey is more susceptible to predators. This led Cooper and Crowder (1979) to speculate that the vegetation/open water interface would be the optimal habitat for predators.

The trophic dynamics of largemouth bass in heavily vegetated habitats have not been fully studied. Most of the work involving the distribution of prey and aquatic vegetation has focused on bluegill *Lepomis macrochirus* and other forage fish species. The relationship between vegetation density and crayfish abundance is even more obscure (Camougis and Hichar 1959; Emery 1975; Ricketts 1975; Saiki and Ziebell 1976; Saiki and Tash 1979). In addition, most of the vegetation density/predator efficiency studies have been done in the laboratory with a small number of prey types/densities. Two important questions need to be asked. First, is the foraging ability of largemouth bass inhibited by aquatic vegetation at the levels of prey abundance found in natural situations; and second, does a reduction in foraging efficiency have measurable biological significance to a predator?

This study was undertaken on Flat Top Lake, West Virginia. The impetus behind this investigation was the desire of the Flat Top Lake Owner's Association to control submerged aquatic vegetation in the reservoir with white amur *Ctenopharyngodon idella*. The goals of this work were to provide insight into the relationship between the adult largemouth bass population and the submerged aquatic vegetation of Flat Top Lake, and to further define this relationship for similar aquatic ecosystems. To achieve these aims, I evaluated habitat utilization by and trophic dynamics of adult largemouth bass among different densities of aquatic vegetation in Flat Top Lake. Only adult (≥200 mm in total length) largemouth bass were considered, because Crowder and Cooper (1979a) and Colle and Shireman (1980) suggested that aquatic vegetation has a greater impact on the trophic dynamics of larger predators than on smaller ones.

Primarily, this study evaluated three different but interrelated aspects of the influence of aquatic vegetation on adult largemouth bass. Habitat utilization was compared among various levels of submerged aquatic vegetation coverage. Predator/prey interactions were also compared among various levels of vegetation. Finally, the influence of the vegetation/open water interface on the previously mentioned parameters was evaluated. Specifically, my objectives were to:

1.) evaluate the relative abundance of/habitat utilization by adult largemouth bass among different levels of aquatic vegetation density, and determine the influence of the vegetation/open water ecotone on these variables;

2.) evaluate the trophic ecology/dynamics of adult largemouth bass among different levels of vegetation density, and to determine the influence of the vegetation/open water ecotone based on the following sub-objectives:

a.) evaluate differences in prey abundance among vegetation levels;

b.) evaluate the differences in foraging patterns and prey consumption of largemouth bass among vegetation levels;

c.) evaluate the differences in potential and utilized prey from the predator population standpoint.

METHODS

STUDY SITE

Flat Top Lake was a 94-hectare reservoir in Raleigh County, West Virginia, created in 1953 by impounding Glade Creek. The reservoir was situated approximately 850 m above mean sea level within the Central Appalachians Ecoregion, characterized by high hills and low mountains with a forest/woodland cover (Omernik 1987).

This reservoir was entirely owned by the Flat Top Lake Owners Association, and access was limited to Association members and their guests. The shoreline was divided into 373 residential lots, most of which had houses; residents were both seasonal and permanent. Flat Top Lake was a multiple-use reservoir; water supply, angling, waterskiing, swimming, and pleasure boating were the principal uses.

The impoundment was roughly V-shaped and could be divided into an eastern basin (37 hectares surface area) and a western basin (57 hectares surface area) (Figure 1). Flat Top Lake had a mean depth of 4.37 m and a maximum depth of 9.75 m. The shoreline was relatively steep and had been modified with concrete bulkheads along some lots.

Figure 1. Flat Top Lake, Raleigh Co., West Virginia. Shaded areas are locations of high vegetation density.

Limnological parameters, chlorophyll a (2.87 mg/m ^{3}), Secchi disk (3.31 m), and alkalinity (18.28 mg/l) (D.A. Coahran, unpublished data), suggest that Flat Top Lake was relatively oligotrophic (Taylor 1971). Water temperatures taken at a depth of 1.0 m ranged from 17.0-26.5 °C, with a mean of 23.8 °C (sample dates were 29 May-1 October, 1987) (D.A. Coahran, unpublished data). The nutrient concentrations, high elevation, and latitude gave the reservoir a relatively low level of productivity for warmwater fish (Appendix Table 1). This was substantiated by comparing growth rates of largemouth bass in Flat Top Lake with growth rates for slow, medium, and fast growing populations of largemouth bass from other parts of North America (Zagar and Orth 1986). Largemouth bass in Flat Top Lake grew at a similar rate to the slowest growing largemouth bass population reported.

Flat Top Lake contained several types of submerged aquatic vegetation; *Nitella* sp. and *Najas* sp. were most abundant. *Potamogeton* sp. occurred in small amounts. Due to shoreline development, such as concrete bulkheads, boatslips, etc.; emergent aquatic vegetation was virtually nonexistent. The two dominant vegetation types (*Nitella* sp. and *Najas* sp.) had different patterns of distribution (Table 1). *Nitella* was found at depths of 0.1-6.0 m. This advanced alga typically grew in dense mats that covered large areas of the bottom. However, this was a relatively short plant and rarely grew to a height more than 0.15 m above the substrate. *Najas*, a macrophyte, occurred in shallow coves (< 3 m) at the upper ends of the reservoir (Figure 1) and covered about 13% of the surface area (12.17 ha) of Flat Top Lake. *Najas* often reached the surface of the water by late summer. The growing season began in April/May and peak biomass was reached in August/September. Due to the volume and density of coverage, *Najas* was the vegetation type with the greatest potential to influence the fish community in Flat Top Lake.

Table 1. Biomass/area (g dry wt/m ^{2}) of *Najas* and *Nitella* collected in Flat Top Lake, 20 July 1987 (K.M. Moynan, unpublished data).

Plant Type	Mean Biomass (g dry wt)/m ^{2}	Standard Deviation	n
Najas sp.	113.01^{A}	84.09	60
Nitella sp.	76.91^{B}	43.59	54

^{A} Means with different letters are significantly different with analysis of variance (P = 0.0055).

Fish fauna of Flat Top Lake consisted of 14 fish species (Table 2). Bluegill *Lepomis macrochirus* and largemouth bass *Micropterus salmoides* were the most abundant. Several other species were relatively common, including yellow perch *Perca flavescens*, black crappie *Pomoxis nigromaculatus*, green sunfish *Lepomis cyanellus*, and smallmouth bass *Micropterus dolomieui*. Two species of crayfish (Astacidae) were also found in the reservoir; *Orconectes obscurus* was common and *Cambarus robustus* was rare.

Angling efforts in Flat Top Lake were directed toward several fish species; the most important ones were largemouth bass, yellow perch, bluegill, and smallmouth bass. There was also a substantial put-and-take fishery for rainbow trout *Onchorynchus mykiss*, which were stocked annually (E. Kessler, Flat Top Lake Owners Association, personal communication).

Recent trends of declining alkalinity concentrations and increasing metal (iron and manganese) concentrations (Sheehan and Leonard 1986) suggested that the reservoir was undergoing acidification. In view of this information, a portion of the East arm (25 ha surface area) was treated with 25.4 metric tons of crushed limestone on 13-20 July, 1987. This treatment was done by the Department of Fisheries and Wildlife Sciences, Virginia Polytechnic Institute & State University and Living Lakes, Inc. The effects of this treatment were monitored as a part of a separate study.

Table 2. Fish species occurring in Flat Top Lake, listed in approximate order of abundance.

COMMON NAME	SCIENTIFIC NAME
Bluegill	*Lepomis macrochirus*
Largemouth bass	*Micropterus salmoides*
Yellow perch	*Perca flavescens*
Black crappie	*Pomoxis nigromaculatus*
Green sunfish	*Lepomis cyanellus*
Smallmouth bass	*Micropterus dolomieui*
Rainbow trout	*Oncorhynchus mykiss*
Brown bullhead	*Ictalurus nebulosus*
Black bullhead	*Ictalurus melas*
Channel catfish	*Ictalurus punctatus*
White sucker	*Catastomus commersoni*
Common carp	*Cyprinus carpio*
Creek chub	*Semotilus atromaculatus*
Redhorse	*Moxostoma* sp.

DATA COLLECTION AND ANALYSES

Preliminary Sampling

In order to determine the feasibility and direction of a predator/prey study on Flat Top Lake, preliminary sampling was initiated in July, 1986. Fish were collected by electrofishing, using a 5500 watt boom-electrofisher mounted on a 5.5 meter boat (Smith-Root Electronics, Inc. Vancouver, WA.). Electrofishing was conducted with pulsed-DC current at output ranges of 250-350 V and 7.0-12.0 A, depending upon water conductivity and transparency. Both day and night electrofishing surveys were conducted, with a minimum of three people (one operating the boat and two netting stunned fish). Typical operational procedure was to proceed parallel to shore (0.3-3.0 m water depth) at the slowest possible speed (3-5 km/hr) for 600 seconds of unit on-time. All captured largemouth bass were measured (total length in mm) and weighed (g) in order to collect information on the relative abundance (based on catch/effort) and size distribution of this population. The stomach contents of the captured largemouth bass were removed by inserting a tube into the stomach through the esophagus, and removing all stomach items via this tube (Van Den Avyle and Roussel 1980). In order to facilitate this process, each fish was first anesthetized using TMS (tricaine-methanesulfanate) (Crescent Research Chemicals, Inc. Phoenix, AZ.), and later returned alive to the reservoir. Different tube sizes were used for different sized fish, with the range of tube diameters being 12-76 mm. A head lamp and a long handled spring-loaded claw device were later incorporated into this procedure to facilitate the removal of the stomach contents. All stomach items were preserved in 95%

ethanol and returned to the lab where individual prey items were wet weighed and measured (total length or standard length for fish, carapace length or chelae length for crayfish, and total length for insects). The live weight of individual prey items was calculated with length/weight regression equations derived from measurements of live organisms (Appendix Table 2). This live weight was used for all analyses of stomach contents (except for the diel sample) in order to correct for different stages of digestion of the various prey items.

After preliminary sampling, a sampling regimen was devised to observe the influence of submerged aquatic vegetation on the distribution and foraging habits of adult largemouth bass ($\geq$ 200 mm total length) as well as the distribution of their prey (fish and crayfish). Three major sampling efforts were conducted, beginning in Fall 1986 and ending in Fall 1987. These included sampling

1) the abundance and size distribution of adult largemouth bass at different vegetation densities (sampling in 1986 and 1987);

2) the abundance and size distribution of crayfish and forage fish at different vegetation densities (sampling in 1987);

3) the foraging patterns of largemouth bass at different vegetation densities (sampling in 1986 and 1987), and comparisons with potential prey abundance (sampling in 1987).

Diel Consumption Patterns

Most of the electrofishing samples in this study were taken after sunset, due to greater capture efficiency at night. *Micropterus* spp. have been shown to feed at all times of the day (Zweiacker and Summerfelt 1974; Reynolds and Casterlin 1976; Stein and Magnuson 1976; Howick and O'Brien 1983; and Wanjala et al. 1986), thus stomach content samples taken at night were assumed to be representative of largemouth bass stomach contents throughout a 24 hr period. To verify this assumption for Flat Top Lake, the stomach contents of largemouth bass were compared for a 24 hr sampling period.

Nine sampling period were chosen beginning at 17:00 hrs on 19 September, 1986 (Table 3). Sampling periods were during, or immediately after, dusk, night, dawn, and daylight time periods. The stomach contents were removed using the methods described previously. Largemouth bass were taken from all areas of the reservoir, and a minimum of 10 fish per sampling time were captured. All largemouth bass were tagged in order to prevent an individual fish from contributing to the sample more than once.

The results from this sampling indicated that there were no differences in stomach contents based on time of day. The percentage of largemouth bass with empty stomachs averaged 44%, and exhibited no trends among the time periods sampled (Figure 2). The data were log transformed (natural logarithms) in order to normalize them for statistical analyses. The wet weights of stomach contents/body weight averaged 0.81% and were not significantly different among time periods (ANOVA; $P = 0.3816$) (Table 3). Thus, there were no diel trends in the amount of prey ingested by a predator. To test for diel differences in the consumption of different prey types, the wet weights of crayfish and fish/largemouth bass weight were compared at the different sampling periods. No significant differences occurred among sampling times for either crayfish ($P = 0.6687$) or fish ($P = 0.3723$) (Table 4). These analyses indicate that the amount of prey in the stomachs of largemouth bass in Flat Top Lake did not

Table 3. Comparisons of mean stomach content weight/largemouth bass weight over a 24hr period in Flat Top Lake (sampled on 19 September 1986).

Hours Sampled	n	Mean Weight of Stomach Contents Per Body Weight (g)
17:00-18:30	10	0.0067
19:00-19:55	10	0.0169
21:30-22:30	10	0.0037
23:00-23:30	11	0.0070
01:30-02:00	11	0.0095
04:15-04:30	11	0.0070
06:00-06:30	11	0.0075
08:30-09:00	11	0.0080
13:40-14:00	11	0.0066

mean = 0.0081

standard deviation = 0.0036

ANOVA P-Value $P = 0.3816$

exhibit diel periodicity in either the total amount or type of prey ingested. Thus, stomach samples obtained from one time period can be assumed to be representative of any time period.

Objective 1 - Relationships of Vegetation Density to Adult Largemouth Bass Abundance and Size Distribution

Data Collection

The abundance and size distribution of largemouth bass was examined at different vegetation densities with two separate comparisons. In 1986, differences in largemouth bass abundance and size structure were evaluated at three classes of vegetation density (high, intermediate, and low) along the entire shoreline of Flat Top Lake. Vegetation classification was based on the following criteria:

high density - areas of abundant *Najas*,

intermediate density - areas of abundant *Nitella*,

low density - areas of sparse or no vegetation.

To compare largemouth bass abundance and length distributions with vegetation density, the distribution pattern of the aquatic vegetation in the reservoir had to be determined. This vegetation mapping was a qualitative effort, in which skin divers swam parallel to the shoreline (water depth 1.0-3.0 m) observing the type and abundance of vegetation. From this information, a map was developed in which shoreline segments were placed into one of three vegetation abundance classes described above (Appendix Figure 1).

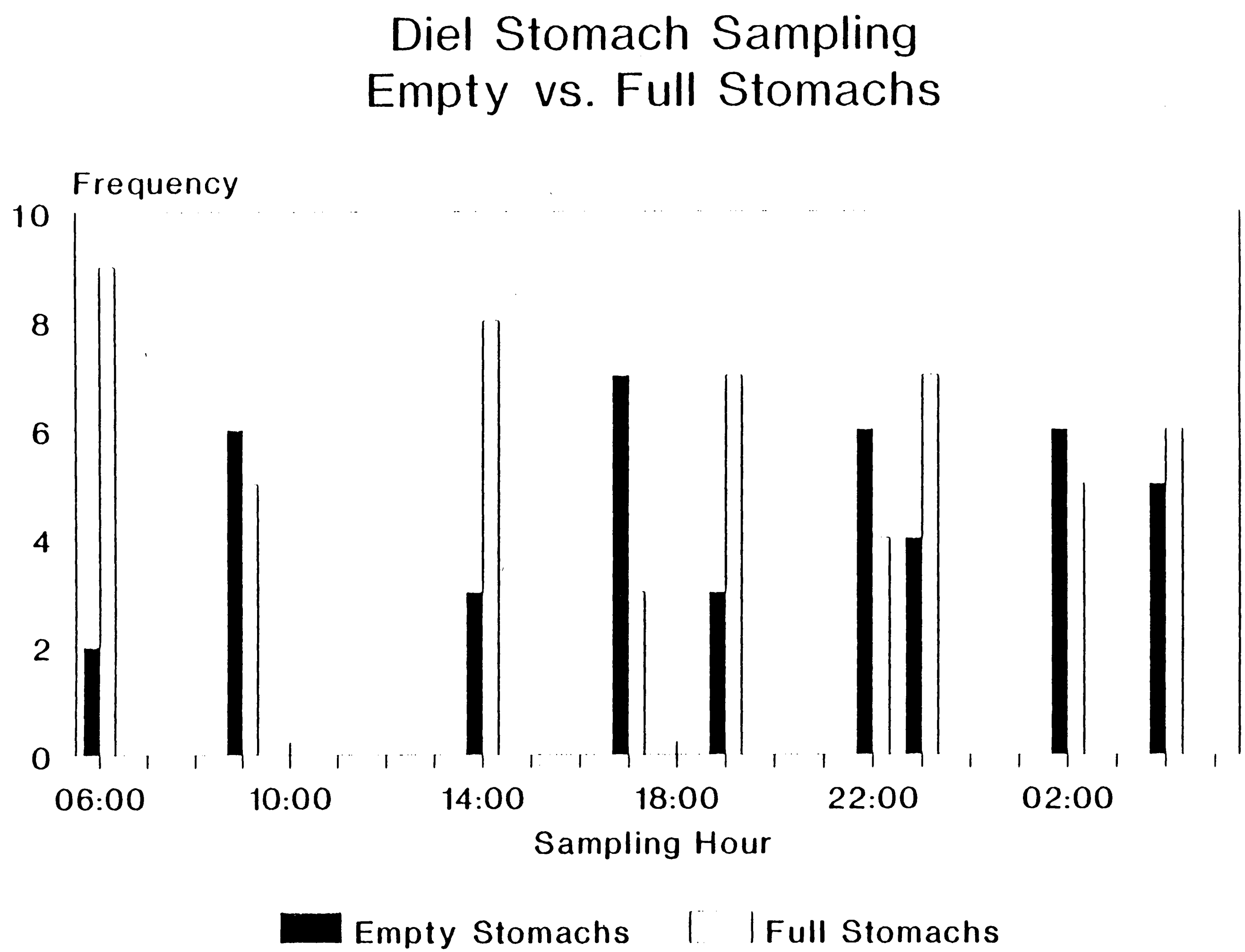


Figure 2. Numbers of empty and full stomachs at different times of the day.

Table 4. Biomass of crayfish and fish consumed/largemouth bass weight over a 24hr period in Flat Top Lake (sampled on 19 September 1986).

Prey Type	Hour Sampled	n	Mean Weight of Stomach Contents Per Body Weight (g)
Crayfish	01:30	11	0.0063
	04:15	11	0.0070
	06:00	11	0.0070
	08:30	11	0.0065
	13:40	11	0.0047
	17:00	10	0.0067
	19:00	10	0.0089
	21:30	10	0.0035
	23:00	11	0.0048
	Mean = 0.0062		Standard Deviation = 0.0016
Fish	01:30	11	0.0029
	04:15	11	0
	06:00	11	0.0004
	08:30	11	0.0015
	13:40	11	0.0019
	17:00	10	0
	19:00	10	0.0080
	21:30	10	0.0002
	23:00	11	0.0020
	Mean = 0.0019		Standard Deviation = 0.0025
	ANOVA P-Values	Crayfish P = 0.6687	Fish P = 0.3723

Largemouth bass at the different vegetation classifications were sampled by electrofishing the entire shoreline. The electrofishing procedure was similar to that described previously. However, rather than operating the boat for a predetermined period of time, the procedure was to separately electrofish each segment of the shoreline (based on vegetation class) and to record the operational time spent on each segment. Electrofishing was begun 1/2 hour after sunset and was concluded approximately 4 hours later. The entire shoreline was sampled on two occasions (3-10 September, 1986 and 1-10 October, 1986); four nights of effort were required for a complete sample.

Only largemouth bass $\geq$200 mm contributed to this data set; all other fish were released. Information obtained from each largemouth bass included length, weight, and stomach contents. After handling, fish were released at the shoreline segment where captured.

In June and August 1987, largemouth bass abundance and size distributions were compared at high and low vegetation densities. This sampling took place at six locations (3 high and 3 low vegetation) in the West arm of the reservoir, in order to avoid the confounding influence of liming in the East arm (see Study Site). Choices of the station locations were limited because areas of high vegetation were clustered in one part of the lake (Appendix Figure 2, Appendix Table 3). High vegetation stations were areas of dense *Najas* coverage, while low vegetation stations had sparse *Nitella* coverage or no vegetation at all.

The influences of changes in the amount of vegetation/open water interface on predator population characteristics were examined in September, 1987. The amount of interface was increased by clearing areas of high vegetation with a large 2.0 m wide "rake" towed behind a boat on 31 August-2 September 1987. This manipulation experiment used the high vegetation sampling stations previously described (Stations 1-3). To maintain equal sample sizes, Station 3 was divided in half (designated Stations 3A and 3B). Two locations were manipulated (Stations 1 and 3B), and two were used as reference locations (Stations 2 and 3A). The pattern of vegetation manipulation varied between Stations 1 and 3B due to differences in the morphometry and size of these locations. In general, this technique removed all vegetation from 2.0 m wide strips in the *Najas* beds. The water depths at the manipulated areas ranged from 0.5-2.5 m, and the *Najas* filled the entire water column. At Station 1, an area approximately 2000 m^2 was cleared of vegetation in 2.0 m wide lanes; and at Station 3B, an area approximately 1500 m^2 was cleared. The actual patterns of vegetation manipulation are illustrated in Appendix Figure 3. In both cases, the amount of open water/vegetation interface was increased, and the total area of vegetation per station was decreased. Obvious regrowth of cleared areas was not observed during the duration of this study (2 September - 1 October). Comparisons were made between reference and experimental sites in September, and between high vegetation-August samples (reference-August) and unmanipulated samples from September (reference-September).

Areas of high and low vegetation density were compared by sampling each station (three stations at high and three at low vegetation) three times in June, 1987 and again three times in August, 1987 (approximately 7-day intervals between samples). Three samples were taken at reference and experimental vegetation locations in September, 1987, at 7-day intervals. This produced three estimates of predator abundance/size for each vegetation level (one estimate per sampling station) in June and August, and two estimates/habitat type in September. The three samples/station obtained each month were used to improve the reliability of the estimates.

All electrofishing was standardized by operational time in order to get variance estimates on catch per unit effort (CPUE). Each station was electrofished for 1000 seconds and all fish were netted. Largemouth bass ≥200 mm were processed as before, while all other fish were placed on ice and and returned to the lab to be measured and weighed. Three stations per night could be electrofished, and the sampling order was randomly chosen.

Data Analyses

Largemouth bass abundance and size structure at high, intermediate, and low vegetation densities (1986) were compared with several methods. Abundance was determined via electrofishing catch/effort (effort = on time of electrofishing unit), and estimates were used to evaluate habitat use by largemouth bass. Comparisons were made between proportions of habitat available (based on the electrofishing effort for each particular habitat type) and habitat used (actual electrofishing catch/effort) for high, intermediate, and low vegetation (Byers et al. 1984). Differences in proportional stock density (PSD) among habitat types were compared by calculating 95% binomial proportion confidence intervals (Zar 1984). Differences in the size distribution of adult largemouth bass were examined by comparing log transformed mean lengths with analysis of variance and by comparing actual length distributions using two-sample Kolmogorov-Smirnov tests (Hollander and Wolfe 1973).

The abundance and size structures of largemouth bass were compared among vegetation densities and months in 1987 with similar techniques, although electrofishing effort was standardized in all samples. Electrofishing catch/effort was used to estimate abundance, and comparisons were made with analysis of variance by time and habitat type. Largemouth bass size distributions were examined by comparing log transformed mean lengths of fish among dates and vegetation densities with analysis of variance. Differences in PSD log transformed values by vegetation and time were compared with ANOVA procedures. The overall distribution of largemouth bass lengths per sample were compared with a two-sample Kolmogorov-Smirnov test. Relative weights of largemouth bass (Wege and Anderson 1978) were compared with ANOVA in order to determine if differences in predator condition were associated with vegetation density or month.

Objective 2 - Trophic Ecology and Predator/Prey Interactions as Related to Vegetation Density

Prey Abundance and Size Distribution

Data Collection

The abundance and size distribution of crayfish and forage fish (all fish < 80 mm defined by the length of 95% of all fish consumed by adult largemouth bass in 1987) were compared among vegetation densities and months in 1987; the same six sampling stations used to estimate predator population characteristics were sampled. Vegetation levels sampled were high and low (June and August) and reference and experimental (September). Crayfish and forage fish were sampled with different techniques, and so analyses of abundance and size distribution were done separately.

The relative abundance and size distributions of crayfish were sampled using two techniques, trapping and SCUBA transects. Five funnel traps baited with cut fish were fished overnight (approximately 12 hours) at each station. Collins et al. (1983) found crayfish to be more active at night, and determined that overnight trapping was an effective method for capturing crayfish. Trapping was conducted three times per month per station in June, August, and September. The traps were placed at approximately equal distances along the shoreline of each sampling station in 0.3-2.0 m of water. Carapace length (cl) and sex were determined for all captured crayfish, and wet weight was determined for selected individuals in order to establish a carapace length/weight relationship. Crayfish were not released at the trap locations, making this procedure sampling without replacement. This was assumed to have no effect on trap success, as Orconectid crayfish have been shown to exhibit no specific home range (Camougis and Hichar 1959; Fielder 1972; Momot and Gowing 1977).

Since crayfish trapping may select for larger individuals (Malley and Reynolds 1979; DiStefano 1987), nocturnal SCUBA diving was used to obtain an additional sample of the population (Davies and Ramsey 1989). Two divers, using submersible flashlights, swam parallel to shore, approximately 5.0-7.5m apart, and attempted to capture all observed crayfish. The effort was standardized by search time, and three 10 min transects were run at each station, with transect locations evenly distributed along the shoreline. All captured crayfish were measured and sexed on board the attending boat. Two stations per night (chosen randomly) could be sampled by this procedure, and all six stations were sampled once in June-July, 1987 and again in August, 1987. SCUBA transects at high-reference and high-experimental vegetation densities were attempted on 22 October, 1987, but were discontinued after three dives due to low crayfish abundance and cold water temperatures.

The abundance and size distribution of forage fish were compared among months (June, August, and September) and vegetation levels (high, low, reference, and experimental). Prey fish were sampled in the electrofishing effort described earlier to estimate predator abundance and size structure. As only two species of forage fish were abundant in electrofishing samples (bluegill and largemouth bass), all other species (black crappie, bullheads, green sunfish, and yellow perch) were grouped together for analyses (group = other prey species), resulting in three fish prey categories.

Data Analyses

The relative abundance of crayfish was determined by catch/effort (number caught/trap or number caught/10 minutes of SCUBA sampling) and comparisons were made with analysis of variance. Size structure differences among samples were analyzed by comparing the mean length of crayfish captured with ANOVA procedures. Length/weight regressions were determined for crayfish and forage fish (Appendix Table 2). For forage fish ($\leq$ 80 mm tl), the catch/effort of each prey group was compared among habitat classes and months with analysis of variance. Habitat related (and monthly) differences in the size structure of prey fish $\leq$ 200 mm tl were examined by comparing log transformed mean lengths of prey groups with analysis of variance.

Predation Patterns - Individual Predators and the Predator Population

Data Collection

The foraging habits of adult largemouth bass in Flat Top Lake were examined in two stages. In September - October, 1986, the numbers, biomass, and size of prey ingested by largemouth bass were compared among high, intermediate, and low vegetation levels throughout the lake. In 1987, these variables were compared between high and low, as well as between reference and experimentally manipulated (experimental) sites in the West Arm of Flat Top Lake. In addition, the numbers, biomass, and size structure of prey ingested per predator were compared with that in the environment. These data were collected in conjunction with sampling for predator and prey abundances. Ingested prey were pooled into one of three categories (crayfish, fish, and insects), because the sample sizes for many individual species were small. These comparisons provided information on the relationship between adult largemouth bass and aquatic vegetation, from the perspective of food acquisition.

Data Analyses

Analyses of largemouth bass food habits were performed using three prey groups (crayfish, fish, and insects). The ratios of different prey types ingested by largemouth bass (based on the numbers of each prey type consumed) were compared among vegetation levels (1986) and vegetation and months (1987) using contingency tables and a G-statistic (Crow 1982). A measure of relative consumption was defined as the live weight of ingested prey/weight of the largemouth bass. Following a log transformation, this variable was compared among vegetation types and months with analysis of variance. The ingested prey size/predator size relationships were compared among vegetation densities and months in order to clarify the influence of vegetation density on patterns of predation exhibited by adult largemouth bass in Flat Top Lake. Correlations between prey length/largemouth bass length were evaluated at the different vegetation densities (in 1986), and the relative size of ingested prey (prey length/predator length) was also compared among vegetation levels and months with analysis of variance. For purposes of comparison with fish, the total length (not carapace length) of crayfish was used; this was obtained by doubling carapace length (Stein 1977).

The potential and actual predation pressures for a given sample were compared among vegetation densities and months (1987 samples). If previously outlined hypotheses are correct, the utilizable prey/consumed prey ratio should be greater at high vegetation than low vegetation density levels. The potential predation was defined as the amount (numbers or biomass) of potentially available prey per sample divided by the number/biomass of largemouth bass sampled in the environment. Actual predation was the number or biomass of prey consumed per sample/number or biomass of largemouth bass captured in the sample. As a wide range of adult largemouth bass were captured in this study (range of lengths = 200-520 mm), a decision was made to focus on a restricted range of predator sizes so that potential prey could be realistically identified. The size range of largemouth bass (predators) in these comparisons was 213-250 mm, which were the 25% and 75% quartiles (based on length) of all largemouth bass sampled in 1987. Potentially available prey was any prey item that could be consumed by a 225 mm largemouth bass (the median length of largemouth bass in 1987 samples). This prey size was chosen, because it represented an approximate maximum size of prey that 213-250 mm largemouth bass consumed in Flat Top Lake. Since the number of predators exactly 225 mm in length was limited, the range of predators examined had to be expanded slightly to obtain useful sample sizes.

The maximum length of a fish that a 225 mm largemouth bass could swallow was determined from the prey depth/largemouth bass mouth gape relationship determined by Lawrence (1957) (Table 5). The largest crayfish ingestible by a 225 mm largemouth bass was determined by examining consumption data from this study. Schramm and Maceina (1986) suggested that the total lengths of fish and crayfish consumed by largemouth bass (of a given size) are similar.

The length frequencies of crayfish and fish ingested by largemouth bass and the length frequencies of crayfish and fish in the environment were compared to examine potential differences in predation patterns of largemouth bass associated with vegetation density. These comparisons were made at high and low vegetation during June and August, and at reference and experimental vegetation during September. Crayfish were sampled with traps and SCUBA in June and August, but with traps only in September. Prey fish were sampled with electrofishing. Insects were consumed, but as no abundance data were available, no food selection comparisons could be made.

Table 5. Maximum total length (mm) of prey species ingestible by a 225 mm largemouth bass.

Prey Species	Maximum Ingestible Prey Total Length (mm) [1]	
Bluegill	73	
Green Sunfish	78	
Largemouth Bass	120	
Black Crappie [2]	73	
Bullheads [3]	106	
Yellow Perch [4]	120	
Crayfish [5]	70	(35 mm carapace length)

[1]From Lawrence (1957)

[2]Used lengths reported for bluegills

[3]Used lengths reported for golden shiners (*Notemigonus crysoleucas*)

[4]Used length reported for largemouth bass

[5]Empirically derived from Flat Top Lake data

RESULTS

The Abundance and Size Distribution of Adult Largemouth Bass

High, Intermediate, and Low Vegetation Comparisons - 1986

Largemouth bass did not use all habitats in proportion to their availability ($P < 0.005$) (Table 6). Proportions of high and intermediate vegetation used were not significantly different from proportions available ($P > 0.05$) (Byers et al. 1984). However, low vegetation habitat was underutilized in proportion to its availability, indicating that largemouth bass may avoid this habitat type.

The size structure of adult largemouth bass was similar among all three vegetation classes (Table 7). There were no significant differences in Proportional Stock Density (PSD), mean length, or the distribution of lengths among high, intermediate, or low vegetation densities.

Table 6. Habitat available and used by largemouth bass at high, intermediate, and low vegetation; as determined by electrofishing catch/effort (effort in seconds) in Flat Top Lake, September-October, 1986 [a]

Vegetation Density	Amount of Available Habitat[b]	Number of LMB[c] Expected	Number of LMB Captured	% Habitat Available	% Habitat Used	95% Bonferroni Confidence Intervals
High	6369	61.19	73	22.2	26.5	20.1-32.8
Intermediate	7462	71.70	87	26.0	31.5	24.8-38.2
Low	14891	143.08	116	51.8	42.0	34.9-49.2
Totals	28722	275.97	276			

$X^2 = 10.67 \quad P < 0.005$

[a] From Byers et al. (1984).

[b] Amount of available habitat = number of seconds spent electrofishing each habaitat type.

[c] LMB = largemouth bass *Micropterus salmoides*

Table 7. Proportional Stock Density and size distribution of largemouth bass at high, intermediate, and low vegetation in Flat Top Lake, September-October, 1986.

95% Binomial Proportion Confidence Intervals Around PSD Values

Vegetation Density	PSD Estimate (%)	95% Confidence Interval	n
High	20.55	11.91-32.05	73
Intermediate	22.99	14.60-33.54	87
Low	28.45	20.01-38.06	116

Analysis of Variance - Mean Length

Vegetation Density	Sample Size	Total Number of Fish	Mean Length (mm)	Standard Deviation
High	9	73	275.22	25.78
Intermediate	14	87	257.04	28.80
Low	25	116	278.56	29.61
		ANOVA P-Value	P=0.0576	

Kolmogorov-Smirnov EDF Tests - Length Distributions

Vegetation Comparison	n_1	n_2	Kolmogorov-Smirnov Statistic
High vs. Int.	73	87	919
	$J^*=0.9117$	P=0.6343	
Int. vs. Low	87	116	1885
	$J^*=1.3170$	P=0.9387	
High vs. Low	73	116	1600
	$J^*=1.2647$	P=0.9206	

High, Low, Reference, and Experimental Vegetation - 1987

Relative abundance of largemouth bass, as determined by electrofishing catch/effort, was influenced by vegetation density, but not by time of year (Table 8). Largemouth bass were significantly more abundant at high vegetation locations in June and August ($P = 0.0007$). However, increasing the amount of vegetation/open water interface had no significant effect on the abundance of largemouth bass ($P = 0.7231$). No significant differences in abundance were observed among months. As effort was identical among all samples, increased abundance of largemouth bass indicates higher densities at that sampling site.

The size structure of adult largemouth bass was not significantly different between the vegetation densities or months tested. The mean length of largemouth bass showed no significant differences among vegetation levels or months (Table 9). Two-sample Kolmogorov-Smirnov tests also revealed no significant differences in length distributions for any comparisons (Table 10). Proportional stock densities (PSD) of the samples were not significantly different between the vegetation levels or the months tested (Table 11). PSD values were lower in the June-September, 1987 samples than in the September-October, 1986 samples, probably due to seasonal changes in the size-selectivity of electrofishing for largemouth bass (Carline et al. 1984). Thus, while the abundance of adult largemouth bass differed among vegetation densities, the size structure did not.

The relative weight of largemouth bass was compared among vegetation levels and months in order to determine the relationships between habitat/month and the

Table 8. Relative abundance of largemouth bass at high, low, reference, and experimental vegetation in Flat Top Lake, 1987. Mean number of adult largemouth bass captured per sample (1000 sec of electrofishing) with standard deviations in parentheses.*

	Number of Adult Largemouth Bass / Sample	
Month	High Vegetation	Low Vegetation
June	19.44	12.89
	(1.58)	(9.05)
August	19.56	9.78
	(2.99)	(4.11)
	ANOVA P-Values	Vegetation P=0.0007 Month P=0.4057 Interaction P=0.3802

	Number of Adult Largemouth Bass / Sample	
Month	Reference Vegetation	Experimental Vegetation
August	19.56	--
	(2.99)	
September	15.67	15.50
	(0.94)	(1.18)
	ANOVA P-Values	Month P=0.1266 Vegetation P=0.7231

* n=3 for samples in June and August, n=2 for samples in September

Table 9. Mean length (mm) of largemouth bass at high, low, reference, and experimental vegetation in Flat Top Lake, 1987 (standard deviation in parentheses).*

	Mean Lengths (mm) of Adult Largemouth Bass	
Month	High Vegetation	Low Vegetation
June	232.99	257.00
	(1.4837)	(26.3082)
August	236.48	249.87
	(14.0162)	(10.2468)
	ANOVA P-Values	Vegetation P=0.0536 Month P=0.9832 Interaction P=0.6360

	Mean Lengths (mm) of Adult Largemouth Bass	
Month	Reference Vegetation	Experimental Vegetation
August	236.48	--
	(14.0162)	
September	241.58	240.54
	(4.7493)	(0.0954)
	ANOVA P-Values	Month P=0.7242 Vegetation P=0.7102

* n=3 for samples in June and August, n=2 for samples in September

Table 10. Largemouth bass length distributions at high, low, reference, and experimental vegetation in Flat Top Lake, 1987. Two-sample Kolmogorov-Smirnov EDF tests.

High Vegetation vs. Low Vegetation (June)		
$n_1=175$	K-S Statistic=3487	P=0.9684
$n_2=116$	$J^*=1.4347$	
High Vegetation vs. Low Vegetation (August)		
$n_1=176$	K-S Statistic=3520	P=0.9956
$n_2=88$	$J^*=1.7408$	
June vs. August (High Vegetation)		
$n_1=175$	K-S Statistic=3905	P=0.8823
$n_2=176$	$J^*=1.1877$	
June vs. August (Low Vegetation)		
$n_1=116$	K-S Statistic=1248	P=0.5645
$n_2=88$	$J^*=0.8648$	
August vs. September (Reference Vegetation)		
$n_1=176$	K-S Statistic=1736	P=0.5038
$n_2=94$	$J^*=0.8214$	
Reference vs. Experimental Vegetation (September)		
$n_1=94$	K-S Statistic=1547	P=0.8903
$n_2=93$	$J^*=1.2099$	

Table 11. Mean proportional stock density (PSD) of largemouth bass at high, low, reference, and experimental vegetation in Flat Top Lake, 1987 (Means with standard deviations in parentheses).*

	Mean PSD Value (%) / Sample	
Month	High Vegetation	Low Vegetation
June	6.12	18.38
	(1.76)	(16.52)
August	5.87	21.65
	(7.59)	(26.12)
	ANOVA P-Values	Vegetation P=0.5917 Month P=0.5160 Interaction P=0.7891

	Mean PSD Value (%) / Sample	
Month	Reference Vegetation	Experimental Vegetation
August	5.87	--
	(7.59)	
September	8.11	4.15
	(0.93)	(0.44)
	ANOVA P-Values	Month P=0.5238 Vegetation P=0.3223

* n=3 for samples in June and August, n=2 for samples in September

condition of predators. No significant differences were found at any level tested (Table 12).

Characteristics of the Prey Base at High, Low, Reference, and Experimental Vegetation

Crayfish

The relative abundance of crayfish differed between vegetation densities in June and August, and between months (August and September) at high vegetation. Trap data suggested that crayfish were significantly more abundant (based on the number of crayfish captured/trap) at low vegetation than at high vegetation in both June and August ($P=0.0023$) (Table 13), with no significant differences in abundance between the two months ($P=0.1882$). Relative abundance information collected by SCUBA transects also showed crayfish to be significantly more abundant at low vegetation levels ($P=0.0013$), with no difference between months ($P=0.1983$) (Table 14). Crayfish abundance (based on trapping) did decline significantly between August and September at high vegetation densities ($P=0.0073$) (Table 13). The manipulation of vegetation density did not appear to influence crayfish abundance ($P=0.9033$).

The mean carapace lengths of crayfish were generally similar among months and vegetation densities. Mean carapace lengths of crayfish captured in traps in June and August were not different between vegetation densities ($P=0.9242$) (Table 15), al-

Table 12. Relative weight (W_r) of largemouth bass at high, low, reference, and experimental vegetation in Flat Top Lake, 1987 (Means with standard deviations in parentheses).

	Mean W_r of Adult Largemouth Bass / Sample	
Month	High Vegetation	Low Vegetation
June	96.76	95.69
	(4.52)	(5.64)
August	93.67	93.93
	(1.99)	(1.33)
	ANOVA P-Values	Vegetation P=0.8572 Month P=0.3016 Interaction P=0.7700

	Mean W_r of Adult Largemouth Bass / Sample	
Month	Reference Vegetation	Experimental Vegetation
August	93.67	--
	(1.99)	
September	92.80	96.75
	(1.74)	(4.19)
	ANOVA P-Values	Month P=0.6525 Vegetation P=0.3440

* n=3 for samples in June and August, n=2 for samples in September

Table 13. Relative abundance (catch/effort)[a] of crayfish captured by trapping in Flat Top Lake, 1987; means, with standard deviation in parentheses.[b]

	Mean Number of Crayfish Captured / Trap Night	
Month	High Vegetation	Low Vegetation
June	6.31	11.89
	(0.67)	(2.89)
August	7.33	15.29
	(1.19)	(4.26)
	ANOVA P-Values	Vegetation P=0.0023 Month P=0.1882 Interaction P=0.4614

	Mean Number of Crayfish Captured / Trap Night	
Month	Reference Vegetation	Experimental Vegetation
August	7.33	--
	(1.19)	
September	1.53	1.60
	(0.19)	(0.66)
	ANOVA P-Values	Month P=0.0073 Vegetation P=0.9033

[a] Catch effort = number crayfish captured/trap night.

[b] n=3 for samples in June and August, n=2 for samples in September

Table 14. Relative abundance (catch/effort)* of crayfish as determined by SCUBA transect at high and low vegetation in Flat Top Lake, 1987. Means, with standard deviation in parentheses (n=3 for all samples).

	Mean Number of Crayfish Captured / 10 Min SCUBA Transect	
Month	High Vegetation	Low Vegetation
June	17.89	27.56
	(4.55)	(8.06)
August	7.89	28.67
	(4.29)	(4.06)
	ANOVA P-Values	Vegetation P=0.0013 Month P=0.1983 Interaction P=0.1176

* catch effort = number crayfish captured/10 min SCUBA transect

though larger crayfish were captured in August ($P = 0.0257$). SCUBA transect data from June and August revealed no significant differences in the mean carapace length of crayfish captured between either vegetation density ($P = 0.0704$) or month ($P = 0.2926$) (Table 16). In September, the size of crayfish captured in traps, at high vegetation was not different from those captured in August ($P = 0.3378$), nor were there any differences between manipulated and reference vegetation densities ($P = 0.2655$) (Table 15).

Fish

The relative abundance of forage fish $\leq$ 80 mm in length (determined by the catch/1000 seconds of electrofishing) differed between vegetation densities and months. The abundance of bluegill in June and August was significantly greater at high vegetation than low vegetation ($P = 0.0002$) (Table 17). Bluegill abundance also changed significantly between June and August, although these changes were not consistent at the two vegetation levels. Bluegill increased abundance at the high vegetation sites, and decreased at the low vegetation sites (interaction $P = 0.0002$). Juvenile largemouth bass were also more abundant at high vegetation ($P = 0.0015$), and they were significantly more abundant in June than August at high vegetation (interaction $P = 0.0001$). The abundance of other forage species was also greatest at the high vegetation-August samples (interaction $P = 0.0085$). or month ($P = 0.1142$) in the June and August samples.

The relative abundance of bluegill, largemouth bass, and other species $\leq$ 80 mm in length showed no responses to the vegetation manipulation (Table 18). The abun-

Table 15. Mean carapace length (mm) of crayfish captured by trapping at high, low, reference, and experimental vegetation in Flat Top Lake, 1987 (standard deviation in parentheses)*.

	Mean Carapace Length of Crayfish (mm)	
Month	High Vegetation	Low Vegetation
June	38.21	37.80
	(0.94)	(0.39)
August	38.65	39.13
	(0.15)	(0.45)
	ANOVA P-Values	Vegetation P=0.9242 Month P=0.0257 Interaction P=0.2084

	Mean Carapace Length of Crayfish (mm)	
Month	Reference Vegetation	Experimental Vegetation
August	38.65	--
	(0.15)	
September	40.21	38.21
	(2.15)	(0.67)
	ANOVA P-Values	Month P=0.2655 Vegetation P=0.3378

* n=3 for samples in June and August, n=2 for samples in September

Table 16. Mean carapace length (mm) of crayfish captured by 10 minute SCUBA transect at high and low vegetation in Flat Top Lake, 1987 (standard deviation in parentheses)*.

	Mean Carapace Length of Crayfish (mm)	
Month	High Vegetation	Low Vegetation
June	34.06	33.16
	(0.68)	(2.08)
August	36.57	33.20
	(1.48)	(2.05)
	ANOVA P-Values	Vegetation P=0.0704 Month P=0.2926 Interaction P=0.3092

* n=2 for samples in June, n=3 for samples in August

Table 17. Relative abundance (catch/1000 sec electrofishing) of forage species ≤ 80 mm in length at high and low vegetation in Flat Top Lake, 1987. Means with standard deviations in parentheses (n=3 for all samples).

		Mean Number of Fish Captured / 1000 Sec of Electrofishing	
Species	Month	High Vegetation	Low Vegetation
Bluegill	June	1.00	0.89
		(0.33)	(0.69)
	August	39.22	1.22
		(9.96)	(0.77)
		ANOVA P-Values	Vegetation P=0.0002 Month P=0.0002 Interaction P=0.0002
Largemouth Bass	June	0	0.11
		(0)	(0.19)
	August	11.33	2.67
		(1.15)	(2.91)
		ANOVA P-Values	Vegetation P=0.0015 Month P=0.0001 Interaction P=0.0013
Other Species	June	0	0.11
		(0)	(0.19)
	August	0.78	0.22
		(0.19)	(0.19)
		ANOVA P-Values	Vegetation P=0.0497 Month P=0.0017 Interaction P=0.0085

dance of bluegill increased significantly from August to September at reference sites ($P = 0.0339$), but there were no significant differences in abundance between the reference and experimental sites in September ($P = 0.1062$). The abundance of juvenile largemouth bass did not differ significantly between August and September at reference sites ($P = 0.9554$), or between reference and experimental sites in September ($P = 0.1348$). The abundance of other prey species was significantly greater in September than August at reference sites ($P = 0.0237$), but abundance was not significantly different at experimental sites when compared with reference sites in September ($P = 0.2011$).

The mean length of all forage fish < 200 mm in length, as captured by electrofishing showed significant relationships to time of year and vegetation density. The mean length of prey fish in the samples declined between June and August (Table 19). This was expected due to recruitment of age-0 fish. The mean lengths of bluegill and juvenile largemouth bass were similar at high and low vegetation in June, but by August, the mean lengths of these species were significantly smaller at high vegetation than low in August (bluegill $P = 0.0001$; largemouth bass $P = 0.0172$). The mean lengths of other prey species was not significantly different between vegetation densities ($P = 0.8382$).

Comparisons in mean length of prey fish between August and September (at high vegetation densities), and reference and experimental vegetation (September) revealed mean length/month and mean length/vegetation relationships (Table 20). The mean length of bluegill decreased from August to September ($P = 0.0004$), and the mean length of bluegill sampled in the experimental vegetation was smaller than those sampled in the reference vegetation ($P = 0.0393$). The mean length of juvenile

Table 18. Relative abundance (catch/1000 sec electrofishing) of forage fish ≤ 80 mm in length at reference and experimental vegetation in Flat Top Lake, 1987. Means with standard deviations in parentheses.*

		Mean Number of Fish Captured / 1000 Sec of Electrofishing	
Species	Month	Reference Vegetation	Experimental Vegetation
Bluegill	August	39.22	--
		(9.96)	
	September	97.00	160.33
		(25.93)	(18.38)
		ANOVA P-Values	Vegetation P=0.1062 Month P=0.0339
Largemouth Bass	August	11.33	--
		(1.15)	
	September	11.17	23.83
		(4.95)	(5.42)
		ANOVA P-Values	Vegetation P=0.1348 Month P=0.9554
Other Species	August	0.78	--
		(0.19)	
	September	2.00	5.50
		(0.47)	(2.59)
		ANOVA P-Values	Vegetation P=0.2011 Month P=0.0237

*n=3 for samples in August, n=2 for samples in September

Table 19. Mean length (mm) of forage fish < 200 mm in length at high and low vegetation in Flat Top Lake, 1987. Means with standard deviations in parentheses (n=3 for all samples).

Species	Month	High Vegetation	Low Vegetation
		Mean Lengths (mm) of Forage Fish Captured by Electrofishing	
Bluegill	June	138.78	132.61
		(8.40)	(2.90)
	August	78.74	133.94
		(1.48)	(14.29)
		ANOVA P-Values	Vegetation P=0.0001 Month P=0.0001 Interaction P=0.0001
Largemouth Bass	June	162.34	161.01
		(5.65)	(4.99)
	August	108.95	138.22
		(6.30)	(13.86)
		ANOVA P-Values	Vegetation P=0.0172 Month P=0.0001 Interaction P=0.0120
Other Species	June	160.87	169.38
		(17.98)	(6.98)
	August	149.21	137.15
		(13.12)	(10.61)
		ANOVA P-Values	Vegetation P=0.8382 Month P=0.0197 Interaction P=0.2950

largemouth bass was not significantly different between August and September ($P=0.7751$), but mean lengths were significantly smaller at the experimental vegetation densities ($P=0.0463$). The mean length of other prey species did not differ between August and September at reference vegetation ($P=0.1357$), or between reference and experimental vegetation in September ($P=0.6023$).

Vegetation Density and the Foraging Patterns of Largemouth Bass

Food Habits of Largemouth Bass at High, Intermediate, and Low Vegetation Densities - 1986

Largemouth bass consumed crayfish, fish, and insects in equal proportions at all vegetation densities in September-October 1986 ($P>0.95$) (Table 21). A G-statistic was used in these analyses to compare the ratios of different prey types consumed among the three levels of vegetation density (Crow 1982). No significant differences were found in the relative weight of stomach contents (back-calculated live weight of prey/weight of individual predator) of largemouth bass among the three vegetation densities (Table 22). This trend was observed for all prey types combined, as well as for each prey type analyzed separately.

Table 20. Mean length (mm) of forage fish < 200 mm in length at reference and experimental vegetation in Flat Top Lake, Means with standard deviations in parentheses.*

		Mean Lengths (mm) of Forage Fish Captured by Electrofishing	
Species	Month	Reference Vegetation	Experimental Vegetation
Bluegill	August	78.74	–
		(1.48)	
	September	61.27	48.18
		(2.46)	(2.83)
		ANOVA P-Values	Vegetation P=0.0393 Month P=0.0004
Largemouth Bass	August	108.95	–
		(6.30)	
	September	108.88	79.97
		(9.39)	(1.25)
		ANOVA P-Values	Vegetation P=0.0463 Month P=0.7751
Other Species	August	149.21	–
		(13.12)	
	September	113.54	96.65
		(32.68)	(11.39)
		ANOVA P-Values	Vegetation P=0.6023 Month P=0.1357

*n=3 for samples in August, n=2 for samples in September

Table 21. Total numbers and percentages of prey consumed by largemouth bass at high, intermediate, and low vegetation in Flat Top Lake, September-October, 1986 (percentages by vegetation density in parentheses). Contingency table analysis.*

Numbers and Percentages of Prey Consumed by Largemouth Bass

	Vegetation Density				
Prey Type	High	Intermediate	Low	Totals	G-Statistic
Crayfish	45 (80%)	83 (84%)	91 (81%)	219 (82%)	0.043
Fish	9 (16%)	12 (12%)	19 (17%)	40 (15%)	0.434
Insects	2 (4%)	4 (4%)	3 (2%)	9 (3%)	0.158
Totals	56 (100%)	99 (100%)	113 (100%)	268 (100%)	
G-Statistic	0.068	0.372	0.229		0.635
		X^2 P>0.95			
No. of LMB per Sample	73	87	116		

*From Crow (1982), statistical tests conducted on actual numbers, not percentages.

Table 22. Mean biomass (g) of prey consumed by largemouth bass/biomass (g) of largemouth bass* at high, intermediate, and low vegetation densities in Flat Top Lake, September-October, 1986.

Mean Biomass Ingested Prey (g) / Biomass Largemouth Bass (g)

ALL PREY TYPES

Vegetation	n	Mean Biomass (g)	Standard Deviation
High	9	0.0202	0.0089
Intermediate	14	0.0198	0.0081
Low	25	0.0199	0.0115
ANOVA P-Value	P=0.9206		

CRAYFISH

Vegetation	n	Mean Biomass (g)	Standard Deviation
High	9	0.0176	0.0099
Intermediate	14	0.0173	0.0065
Low	25	0.0136	0.0099
ANOVA P-Value	P=0.8642		

FISH

Vegetation	n	Mean Biomass (g)	Standard Deviation
High	9	0.0025	0.0032
Intermediate	14	0.0023	0.0037
Low	25	0.0063	0.0091
ANOVA P-Value	P=0.2058		

INSECTS

Vegetation	n	Mean Biomass (g)	Standard Deviation
High	9	0.0001	0.0001
Intermediate	14	0.0001	0.0002
Low	25	0.0001	0.0001
ANOVA P-Value	P=0.5164		

*Biomass of consumed prey in back-calculated live weight.

The size of ingested prey was positively correlated, to some extent, with the size of the predator for most prey types and at most vegetation levels (Table 23). When all prey types were combined, prey length/predator length correlations were statistically significant at all vegetation levels. Crayfish and fish lengths were significantly correlated with predator size, with the exception of crayfish consumed in high vegetation. The length of insects consumed was not related to the length of the predator. There were no significant differences in the relative prey size (prey length/largemouth bass length) of consumed crayfish or insects among vegetation densities (Table 24). Significantly larger fish were consumed at low vegetation than at either high or intermediate vegetation. In general, foraging patterns were similar among high, intermediate, and low vegetation in 1986.

Largemouth Bass Food Habits and Potential Prey Abundance at High, Low, Reference, and Experimental Vegetation Densities - 1987

In 1987, the diet composition (comparing the numbers of each prey type consumed between vegetation densities and months) of largemouth bass differed between high and low vegetation and between June and August (Table 25). Crayfish were consumed in similar proportions in all samples. In the low vegetation-August sample, proportional consumption of fish was significantly greater than expected, while proportional consumption of insects was less than expected. An opposite trend existed in the high vegetation-June sample, in which proportional fish consumption was reduced while proportional consumption of insects was greater than expected. Comparing August and September samples at high vegetation revealed an increase in the proportion of fish in the diet from August to September with a corresponding de-

Table 23. Consumed prey length/predator length (mm) correlations at high, intermediate, and low vegetation in Flat Top Lake, September-October, 1986.

			Correlation Coefficient	
Vegetation Density	Prey Type	n	Kendall's τ	P-Value
High	All	56	0.1852	0.0460
Intermediate	All	99	0.3406	0.0001
Low	All	113	0.3155	0.0001
All	Crayfish	219	0.2475	0.0001
All	Fish	40	0.6118	0.0001
All	Insects	9	0.0572	0.8330
High	Crayfish	45	0.0928	0.3729
Intermediate	Crayfish	83	0.2406	0.0014
Low	Crayfish	91	0.3151	0.0001
High	Fish	9	0.8061	0.0037
Intermediate	Fish	12	0.7385	0.0009
Low	Fish	19	0.5374	0.0015

Table 24. Mean relative prey size (prey length in mm/predator length in mm) at high, intermediate, and low vegetation in Flat Top Lake, September-October, 1986.

Prey Type	Vegetation Density	n	Mean Relative Prey Size	Standard Deviation
Crayfish	High	9	0.1942	0.0244
	Intermediate	14	0.1860	0.0334
	Low	22	0.1773	0.0290
Fish	High	5	0.2623[A]	0.0559
	Intermediate	8	0.2054[A]	0.0977
	Low	11	0.3721[B]	0.0822
Insects	High	1	0.0548	–
	Intermediate	4	0.0582	0.0045
	Low	3	0.0799	0.0382
	ANOVA P-Values		Crayfish	P=0.3357
			Fish	P=0.0011
			Insects	P=0.5006

[A] Means with different letters are siginificantly different at the $\alpha=0.05$ level with an LSD test.

crease in the proportion of insects consumed (Table 26). The diet composition at reference and experimental vegetation densities in September were not statistically different (Table 26).

Prey consumption by largemouth bass in Flat Top Lake was similar between the vegetation densities and months examined. The mean relative biomass consumed (live weight of prey in stomach/weight of individual predator) was not significantly different between vegetation densities and months (Table 27, Table 28, Table 29). The relative size of ingested prey (prey length/largemouth bass length) was not significantly different between vegetation densities or months for any of the prey types tested (crayfish, fish, insects) (Table 30, Table 31, Table 32).

Although few differences in diet composition were detected, prey/predator ratios were spatially and temporally variable. The numbers of prey in the environment/predator (as determined by trapping for crayfish and electrofishing for forage fish) were significantly different between vegetation densities (crayfish), and between vegetation densities and months (forage fish). The numbers of crayfish captured in the environment that could be ingested by a 225mm largemouth bass (crayfish $<$ 35 mm carapace length = potentially available)/213-250 mm largemouth bass were greater at low vegetation than at high vegetation in June and August ($P = 0.0019$) (Table 33). No differences in numbers of potentially available crayfish/largemouth bass were noted between June and August at either vegetation density ($P = 0.9443$), between August and September at high vegetation ($P = 0.1677$), or between reference and experimentally manipulated vegetation levels in September ($P = 0.5666$). More potentially available forage fish/predator were present at high vegetation than low ($P = 0.0094$), and in August than in June ($P = 0.0024$), with

Table 25. Total numbers and percentages of prey consumed by largemouth bass at high and low vegetation in Flat Top Lake, 1987 (percentages by vegetation density in parentheses). Contingency table analysis.[a]

	Numbers and Percentages of Prey Consumed by Largemouth Bass					
	Vegetation Density and Month					
Prey Type	High-June	Low-June	High-August	Low-August	Totals	G-Statistic
Crayfish	133 (32%)	121 (38%)	130 (39%)	97 (39%)	481 (37%)	3.22
Fish	61 (15%)	83 (26%)	46 (14%)	85 (34%)	275 (21%)	37.85 [b]
Insects	216 (53%)	117 (36%)	154 (47%)	66 (27%)	553 (42%)	30.49 [b]
Totals	410 (100%)	321 (100%)	330 (100%)	248 (100%)	1309 (100%)	
G-Statistic	20.13 [b]	6.10	11.01	34.32 [b]		71.56 [b]
No. of LMB per Sample	175	116	176	88		

$$X^2_{6,0.05} = 12.59$$

$$X^2_{6,0.01} = 16.81$$

[a] From Crow (1982), statistics conducted on actual numbers, not percentages.

[b] G-values significantly different at the $\alpha = 0.01$ level with a X^2 test.

Table 26. Total numbers and percentages of prey consumed by largemouth bass at reference and experimental vegetation in Flat Top Lake, 1987 (percentages by vegetation density/month in parentheses). Contingency table analysis.[a]

Numbers and Percentages of Prey Consumed by Largemouth Bass

	Vegetation and Month			
Prey Type	Reference-Aug	Reference-Sep	Totals	G-Statistic
Crayfish	130 (39%)	66 (48%)	196 (42%)	1.73
Fish	46 (14%)	29 (21%)	75 (16%)	2.99
Insects	154 (47%)	42 (31%)	196 (42%)	6.29 [b]
Totals	330 (100%)	137 (100%)	467 (100%)	
G-Statistic	3.17	7.83 [b]		11.01 [c]
No. of LMB per Sample	176	94		

	Vegetation and Month			
Prey Type	Reference-Sep	Experimental-Sep	Totals	G-Statistic
Crayfish	66 (48%)	64 (50%)	130 (49%)	0.03
Fish	29 (21%)	26 (20%)	55 (21%)	0.03
Insects	42 (31%)	39 (30%)	81 (30%)	0.004
Totals	137 (100%)	129 (100%)	266 (100%)	
G-Statisitic	0.03	0.03		0.06
No. of LMB per Sample	94	93		

$X^2_{2,0.05} = 5.99$ $X^2_{2,0.01} = 9.21$

[a] From Crow (1982) statistics conducted on actual numbers, not percentages.

[b] G-values significantly different at the $\alpha = 0.05$ level with a X^2 test.

[c] G-values significantly different at the $\alpha = 0.01$ level with a X^2 test.

Table 27. Mean biomass of all prey consumed by largemouth bass at high, low, reference, and experimental vegetation in Flat Top Lake, 1987. Biomass consumed = back-calculated live weight of prey (g)/weight of predator (g) (Means with standard deviations in parentheses).

Mean Biomass of Prey Consumed (g) / Mean Biomass of Largemouth Bass (g)

Month	High Vegetation	Low Vegetation
June	0.0234	0.0226
	(0.0035)	(0.0043)
August	0.0198	0.0196
	(0.0022)	(0.0048)
	ANOVA P-Values	Vegetation P=0.0970 Month P=0.6700 Interaction P=0.9416

Month	Reference Vegetation	Experimental Vegetation
August	0.0198	--
	(0.0022)	
September	0.0150	0.0153
	(0.0006)	(0.0050)
	ANOVA P-Values	Month P=0.4017 Vegetation P=0.9775

* n=3 for samples in June and August, n=2 for samples in September

Table 28. Mean biomass of crayfish consumed by largemouth bass at high, low, reference, and experimental vegetation in Flat Top Lake, 1987. Biomass consumed = back-calculated live weight of crayfish (g)/weight of largemouth bass (g) (Means with standard deviations in parentheses).

Mean Biomass of Crayfish Consumed (g) / Mean Biomass of Largemouth Bass (g)

Month	High Vegetation	Low Vegetation
June	0.0210	0.0196
	(0.0033)	(0.0066)
August	0.0149	0.0159
	(0.0018)	(0.0056)
	ANOVA P-Values	Vegetation P=0.0535 Month P=0.2060 Interaction P=0.9063

Month	Reference Vegetation	Experimental Vegetation
August	0.0149	–
	(0.0018)	
September	0.0123	0.0124
	(0.0011)	(0.0038)
	ANOVA P-Values	Month P=0.4580 Vegetation P=0.9119

* n=3 for samples in June and August, n=2 for samples in September

Table 29. Mean biomass of fish consumed by largemouth bass at high, low, reference, and experimental vegetation in Flat Top Lake, 1987. Biomass consumed = back-calculated live weight of fish (g)/weight of largemouth bass (g) (Means with standard deviations in parentheses).

Mean Biomass of Fish Consumed (g) / Mean Biomass of Largemouth Bass (g)

Month	High Vegetation	Low Vegetation
June	0.0020	0.0029
	(0.0007)	(0.0025)
August	0.0043	0.0033
	(0.0032)	(0.0034)
	ANOVA P-Values	Vegetation P=0.6907 Month P=0.4329 Interaction P=0.7891

Month	Reference Vegetation	Experimental Vegetation
August	0.0043	--
	(0.0032)	
September	0.0025	0.0027
	(0.0002)	(0.0011)
	ANOVA P-Values	Month P=0.8119 Vegetation P=0.9542

* n=3 for samples in June and August, n=2 for samples in September

Table 30. Relative size of crayfish consumed by largemouth bass at high, low, reference, and experimental vegetation in Flat Top Lake, 1987. Relative size = total length of crayfish (mm)/total length of largemouth bass (mm). (Means with standard deviations in parentheses).

Mean Total Lengths of Crayfish (mm)/Total Lengths of Largemouth Bass (mm)

Month	High Vegetation	Low Vegetation
June	0.1970	0.1770
	(0.0100)	(0.0165)
August	0.1788	0.1565
	(0.0260)	(0.0142)
	ANOVA P-Values	Vegetation P=0.0719 Month P=0.0945 Interaction P=0.9155

Month	Reference Vegetation	Experimental Vegetation
August	0.1788	--
	(0.0260)	
September	0.1744	0.1799
	(0.0017)	(0.0075)
	ANOVA P-Values	Month P=0.8358 Vegetation P=0.4176

* n=3 for samples in June and August, n=2 for samples in September

Table 31. Relative size of fish consumed by largemouth bass at high, low, reference, and experimental vegetation in Flat Top Lake, 1987. Relative size = total length of fish (mm)/total length of largemouth bass (mm). (Means with standard deviations in parentheses).

	Mean Lengths of Fish (mm)/Lengths of Largemouth Bass (mm)	
Month	High Vegetation	Low Vegetation
June	0.1235	0.1457
	(0.0399)	(0.1403)
August	0.1944	0.1335
	(0.0324)	(0.1057)
	ANOVA P-Values	Vegetation P=0.7237 Month P=0.5940 Interaction P=0.4538

Month	Reference Vegetation	Experimental Vegetation
August	0.1944	--
	(0.0324)	
September	0.1749	0.1778
	(0.0449)	(0.0240)
	ANOVA P-Values	Month P=0.6040 Vegetation P=0.9436

* n=3 for samples in June and August, n=2 for samples in September

Table 32. Relative size of insects consumed by largemouth bass at high, low, reference, and experimental vegetation in Flat Top Lake, 1987. Relative size = total length of insects (mm)/total length of largemouth bass (mm). (Means with standard deviations in parentheses).

Mean Total Lengths of Insects (mm)/Total Lengths of Largemouth Bass (mm)

Month	High Vegetation	Low Vegetation
June	0.0948	0.0959
	(0.0143)	(0.0028)
August	0.1120	0.1042
	(0.0214)	(0.0265)
	ANOVA P-Values	Vegetation P=0.7663 Month P=0.2671 Interaction P=0.6890

Month	Reference Vegetation	Experimental Vegetation
August	0.1120	--
	(0.0214)	
September	0.0634	0.0768
	(0.0078)	(0.0037)
	ANOVA P-Values	Month P=0.0603 Vegetation P=0.1602

* n=3 for samples in June and August, n=2 for samples in September

temporal changes primarily due to an increased abundance of prey in the high vegetation (August) samples. Prey fish were also more abundant in September than August at high vegetation ($P=0.0172$). No significant differences in numbers of potentially available forage fish/predator were found between reference and experimental samples in September ($P=0.0607$).

When the numbers of prey ingested by 213-250 mm largemouth bass/numbers of 213-250 mm largemouth bass in the environment were compared between vegetation densities and months, no significant differences were found (Table 34). Thus, the number of prey consumed/predator did not parallel the number of potentially available prey/predator, with respect to vegetation density and sampling month.

Analyses of utilizable prey biomass/predator biomass revealed fewer differences between habitat types and months for this parameter than those found for numbers of potentially available prey/predator. The biomass of ingestible crayfish/biomass of 213-250 mm largemouth bass was significantly greater at low vegetation than high vegetation in June and August ($P=0.0038$) (Table 35). Biomass differences between June and August (high and low vegetation), between August and September (high vegetation), and between reference and experimental vegetation densities (September) were not statistically significant. There were no significant differences in the biomass of potentially available fish/biomass of 213-250 mm largemouth bass associated with vegetation density. There was also no difference in potentially available forage fish biomass/predator biomass between June and August. However, this ratio was significantly greater in September than August at high vegetation ($P=0.0458$).

Table 33. Numbers of crayfish and fish potentially available to 225mm largemouth bass by habitat type in Flat Top Lake, 1987. Mean number of prey in the environment/mean number of largemouth bass 213-250mm in length. Standard deviations in parentheses.* Crayfish captured by trapping, fish captured by electrofishing.

Mean Number of Prey/Number of 213-250 mm Largemouth Bass

	CRAYFISH			FISH	
Month	High Veg.	Low Veg.	Month	High Veg.	Low Veg.
June	0.6296	3.6219	June	0.4759	0.6869
	(0.2555)	(1.7299)		(0.3980)	(0.3515)
August	0.4985	3.6551	August	5.2666	1.0255
	(0.2425)	(1.5513)		(1.8151)	(0.7848)
	ANOVA P-Values	Vegetation P=0.0019 Month P=0.9443 Interaction P=0.9066		ANOVA P-Values	Vegetation P=0.0094 Month P=0.0024 Interaction P=0.0054
Month	Reference Veg.	Experimental Veg.	Month	Reference Veg.	Experimental Veg.
August	0.4985	--	August	5.2666	--
	(0.2425)			(1.8151)	
September	0.1516	0.2124	September	13.5950	24.3259
	(0.1201)	(0.0400)		(2.0603)	(3.3351)
	ANOVA P-Values	Month P=0.1677 Vegetation P=0.5666		ANOVA P-Values	Month P=0.0172 Vegetation P=0.0607

*n=3 for samples in June and August, n=2 for samples in September

Table 34. Numbers of crayfish and fish actually ingested per 213-250mm largemouth bass in Flat Top Lake, 1987. Mean number of prey in stomachs/mean number of 213-250 mm largemouth bass in each sample. Standard deviations in parentheses.* Crayfish captured by trapping, fish captured by electrofishing.

Mean Number of Prey Consumed/Number of 213-250 mm Largemouth Bass

	CRAYFISH			FISH	
Month	High Veg.	Low Veg.	Month	High Veg.	Low Veg.
June	0.7847	1.3433	June	0.1563	0.1791
	(0.2703)	(0.8603)		(0.0285)	(0.1619)
August	0.7166	1.5185	August	0.2562	1.2778
	(0.2284)	(0.7507)		(0.0868)	(1.1260)
	ANOVA P-Values	Vegetation P=0.0842 Month P=0.8805 Interaction P=0.7335		ANOVA P-Values	Vegetation P=0.1516 Month P=0.1064 Interaction P=0.1681
Month	Reference Veg.	Experimental Veg.	Month	Reference Veg.	Experimental Veg.
August	0.7166	--	August	0.2562	--
	(0.2284)			(0.0868)	
September	0.7338	0.5922	September	0.2326	0.3596
	(0.2299)	(0.2220)		(0.0357)	(0.0437)
	ANOVA P-Values	Month P=0.9397 Vegetation P=0.5950		ANOVA P-Values	Month P=0.7492 Vegetation P=0.0861

*n=3 for samples in June and August, n=2 for samples in September

Table 35. Biomass of crayfish and fish potentially available to 225 mm largemouth bass by habitat type in Flat Top Lake, 1987. Mean biomass of prey in the environment (g)/mean biomass of 213-250 mm largemouth bass (g). Standard deviations in parentheses.[a] Crayfish captured by trapping, fish captured by electrofishing.

Mean Biomass of Prey (g)/Biomass of 213-250 mm Largemouth Bass (g)					
	CRAYFISH[b]			*FISH*[c]	
Month	High Veg.	Low Veg.	Month	High Veg.	Low Veg.
June	0.0349	0.2030	June	0.0379	0.0472
	(0.0147)	(0.0809)		(0.0395)	(0.0322)
August	0.0329	0.2162	August	0.1091	0.0415
	(0.0195)	(0.1254)		(0.0515)	(0.0081)
	ANOVA P-Values	Vegetation P=0.0038 Month P=0.9013 Interaction P=0.8664		ANOVA P-Values	Vegetation P=0.3672 Month P=0.3161 Interaction P=0.2518
Month	Reference Veg.	Experimental Veg.	Month	Reference Veg.	Experimental Veg.
August	0.0329	–	August	0.1091	–
	(0.0195)			(0.0515)	
September	0.0073	0.0089	September	0.1675	0.2796
	(0.0051)	(0.0037)		(0.0260)	(0.0719)
	ANOVA P-Values	Month P=0.1815 Vegetation P=0.7560		ANOVA P-Values	Month P=0.0458 Vegetation P=0.1705

[a] n=3 for samples in June and August, n=2 for samples in September

[b] ANOVA for crayfish conducted on normal data.

[c] ANOVA for fish conducted on log transformed data.

The biomass of crayfish consumed by 213-250 mm largemouth bass/biomass of 213-250 mm largemouth bass was not statistically different between vegetation densities (high, low, reference, and experimental) or between months (June, August, and September) using the same comparisons as described previously (Table 36). There were no significant differences in the biomass of ingested forage fish/biomass of 213-250 mm largemouth bass associated with vegetation density. However, the biomass of ingested forage fish/biomass predators was greater in August than in June ($P = 0.0029$), although no differences were noted between August and September (at high vegetation).

The sizes of prey potentially available to and selected by largemouth bass varied with vegetation density and month. In general, adult largemouth bass (200-520 mm in length) consumed smaller crayfish than were sampled by either trapping or SCUBA transect. Length frequency comparisons of potentially available and ingested crayfish at low and high vegetation in June and August indicated similar prey bases and consumption patterns (with respect to crayfish carapace length) between vegetation densities (Figure 3 and Figure 4). In addition, length frequencies of potentially available and ingested crayfish were similar between reference and experimental vegetation in September (Figure 5). This agrees with the the lack of significant differences in the size of consumed crayfish between vegetation levels (Table 30). While differences in the mean length of ingested crayfish were not statistically significant between months, there was a general trend toward consumption of smaller crayfish in August than in either June or September at all vegetation levels. This may coincide with the growth of age 0 and age 1 crayfish (as determined by length-frequency) throughout the summer and fall. Age 1 crayfish may be heavily utilized in June, with

Table 36. Biomass of crayfish and fish actually ingested per predator for 213-250mm largemouth bass in Flat Top Lake, 1987. Mean biomass of prey in stomachs (g)/mean biomass of 213-250 mm largemouth bass (g). Standard deviations in parentheses.[a] Crayfish captured by trapping, fish captured by electrofishing.

Mean Biomass of Prey Ingested (g)/Biomass of 213-250 mm Largemouth Bass (g)					
	CRAYFISH [b]			**FISH** [c]	
Month	High Veg.	Low Veg.	Month	High Veg.	Low Veg.
June	0.0204	0.0248	June	0.0015	0.0016
	(0.0092)	(0.0109)		(0.0003)	(0.0026)
August	0.0149	0.0151	August	0.0066	0.0015
	(0.0046)	(0.0037)		(0.0074)	(0.0011)
	ANOVA P-Values	Vegetation $P=0.6189$ Month $P=0.1259$ Interaction $P=0.6582$		ANOVA P-Values	Vegetation $P=0.0957$ Month $P=0.0029$ Interaction $P=0.8599$
Month	Reference Veg.	Experimental Veg.	Month	Reference Veg.	Experimental Veg.
August	0.0149	–	August	0.0066	--
	(0.0046)			(0.0074)	
September	0.0137	0.0116	September	0.0019	0.0034
	(0.0046)	(0.0006)		(0.0012)	(0.0007)
	ANOVA P-Values	Month $P=0.7960$ Vegetation $P=0.5926$		ANOVA P-Values	Month $P=0.1393$ Vegetation $P=0.6434$

[a] n=3 for samples in June and August, n=2 for samples in September

[b] ANOVA for crayfish conducted on normal data.

[c] ANOVA for fish conducted on log transformed data.

age 0 crayfish contributing heavily to the diet of largemouth bass in August and September.

The length-frequency distributions of potentially available and actually ingested forage fish differed between months and vegetation densities. In June, the forage fish consumed by largemouth bass were generally smaller than those sampled by electrofishing (Figure 6), although vegetation density did not appear to influence either. However, by August, there was a marked difference in the length-frequencies of ingested and potentially available forage fish between high and low vegetation densities (Figure 7). Consumption at low vegetation densities was directed toward smaller forage fish than at high vegetation, possibly due to differences in the sizes of forage fish present at high and low vegetation sites. Manipulating the vegetation did not appear to influence the length-frequencies of potentially available or ingested forage fish (Figure 8). Therefore, vegetation density was related to differences in the sizes of forage fish potentially available to largemouth bass, as well as the sizes of forage fish ingested by largemouth bass.

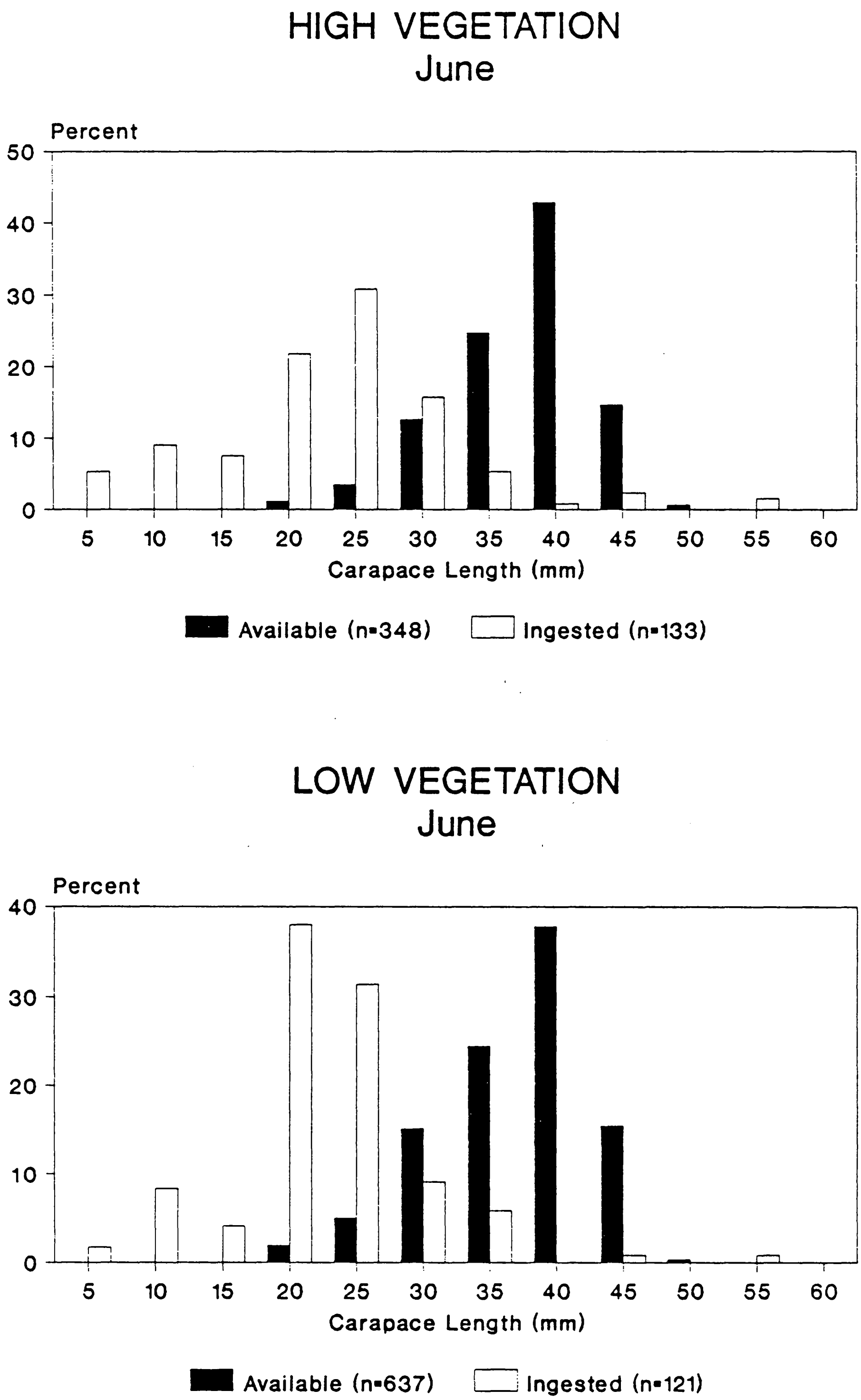
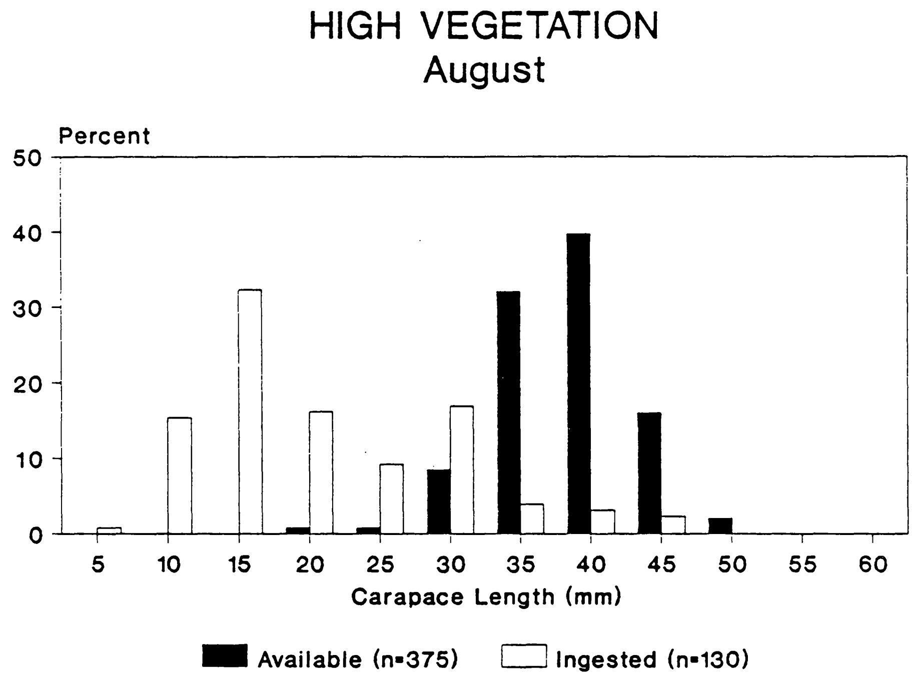


Figure 3. Length frequencies of potentially available and ingested crayfish, June, 1987. Crayfish from LMB stomachs, traps, and SCUBA.



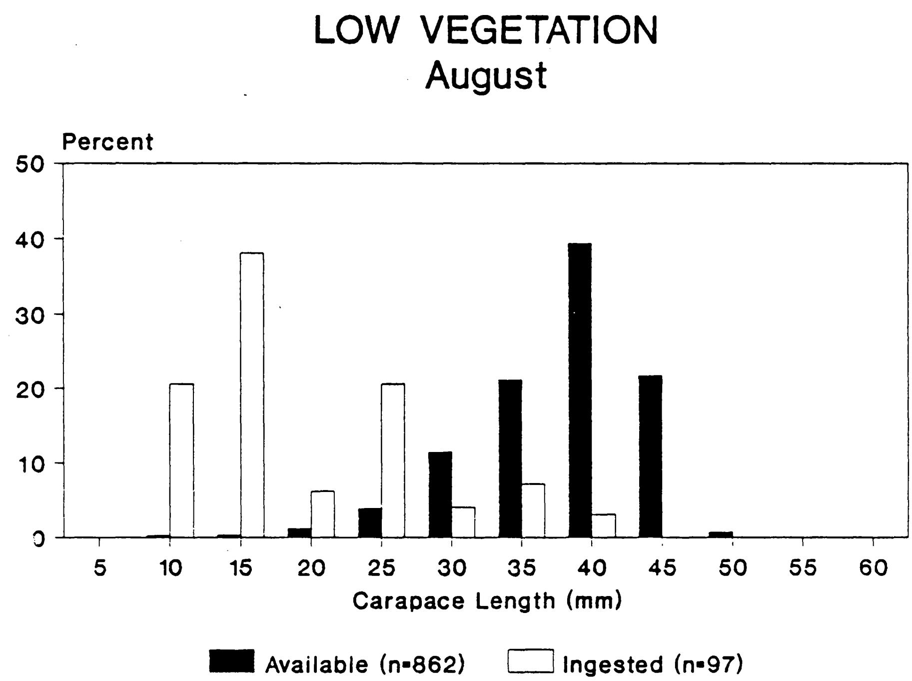
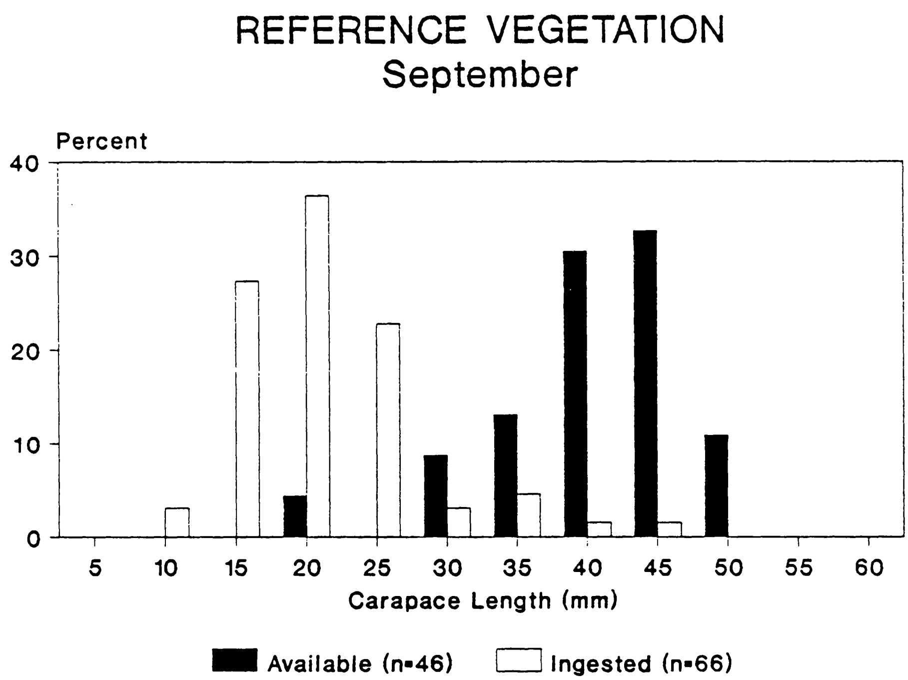


Figure 4. Length frequencies of potentially available and ingested crayfish, Aug., 1987. Crayfish from LMB stomachs, traps, and SCUBA.



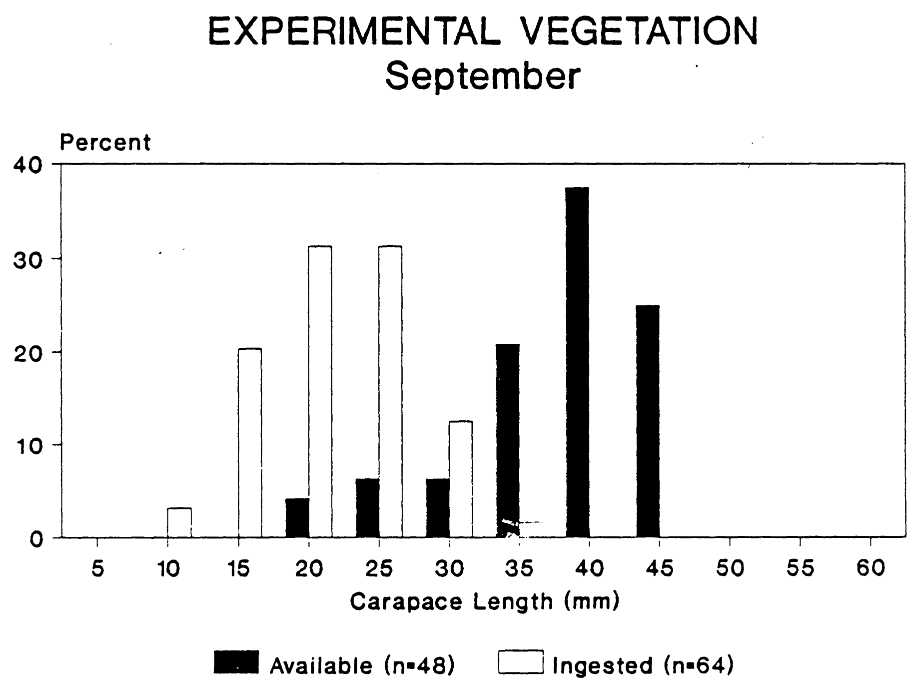


Figure 5. Length frequencies of potentially available and ingested crayfish, Sept., 1987. Crayfish from LMB stomachs and traps.

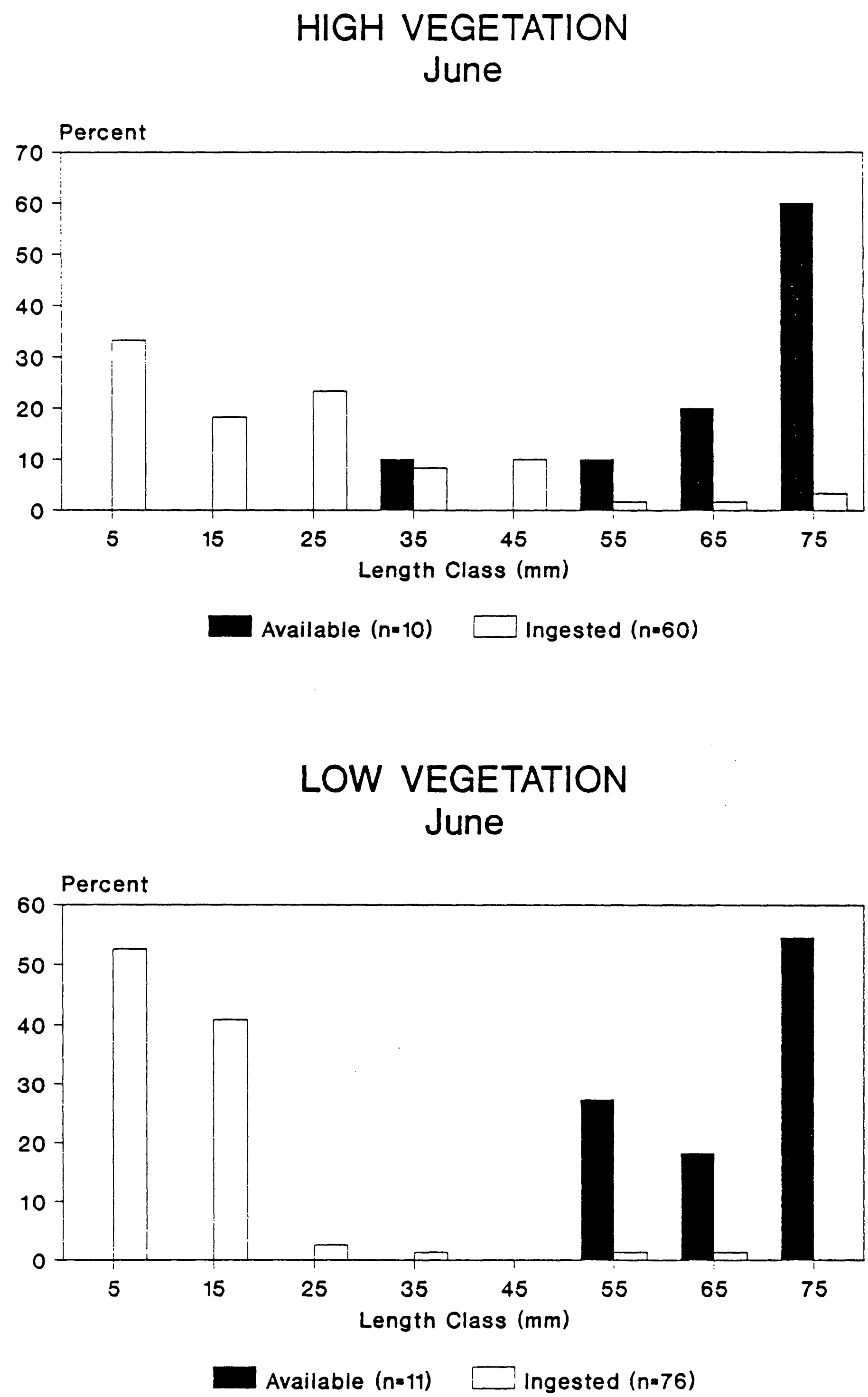
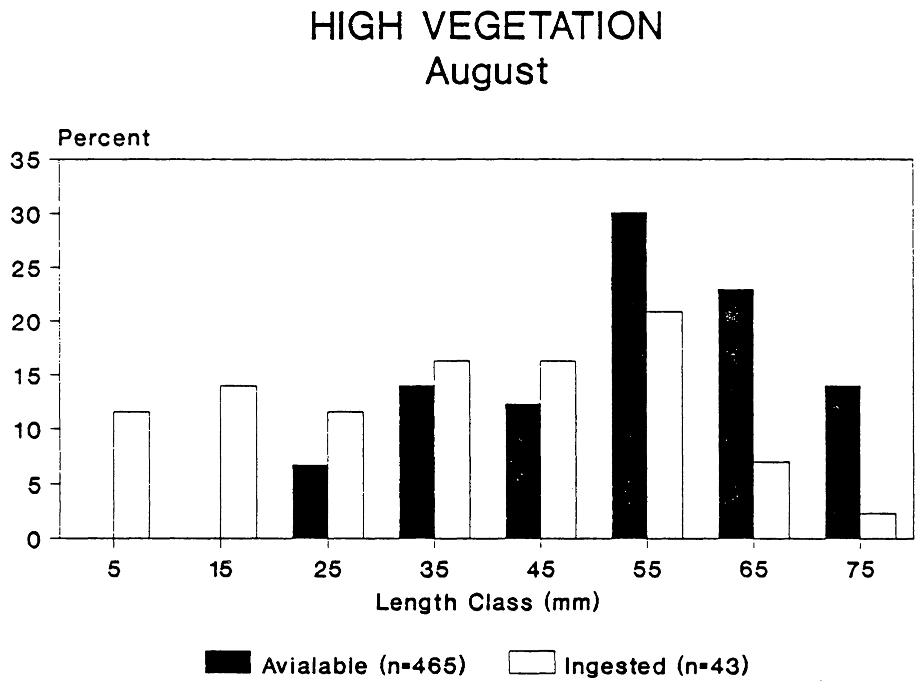


Figure 6. Length frequencies of potentially available and ingested forage fish, June, 1987. Fish from LMB stomachs and electrofishing.



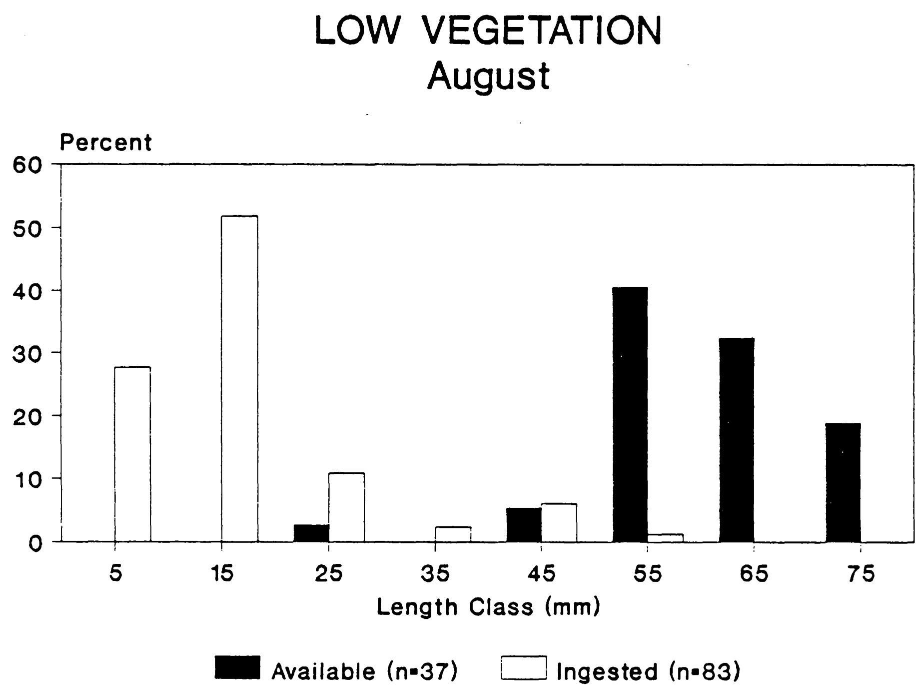
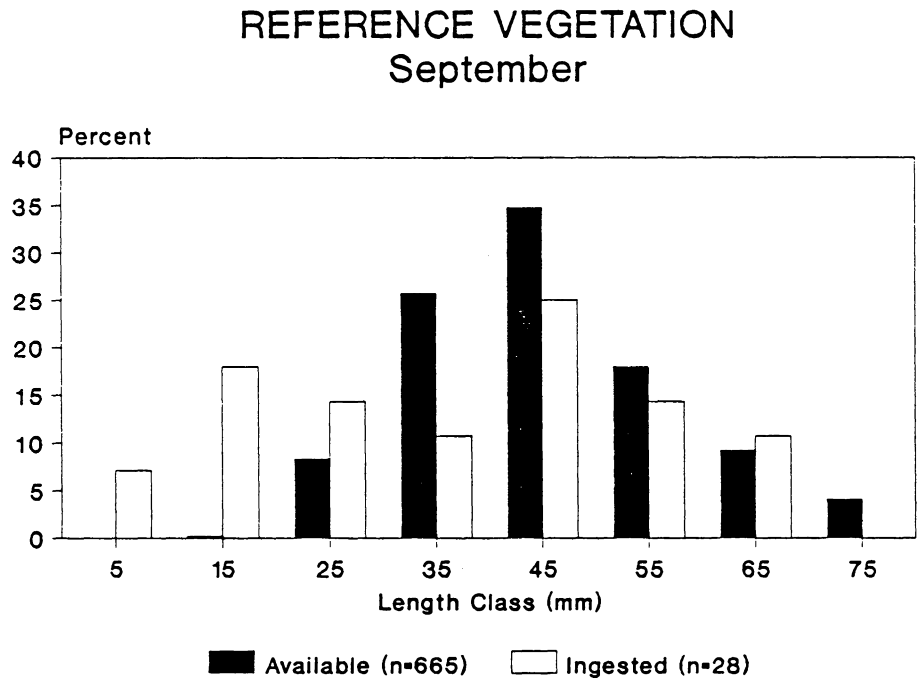


Figure 7. Length frequencies of potentially available and ingested forage fish, Aug., 1987. Fish from LMB stomachs and electrofishing.



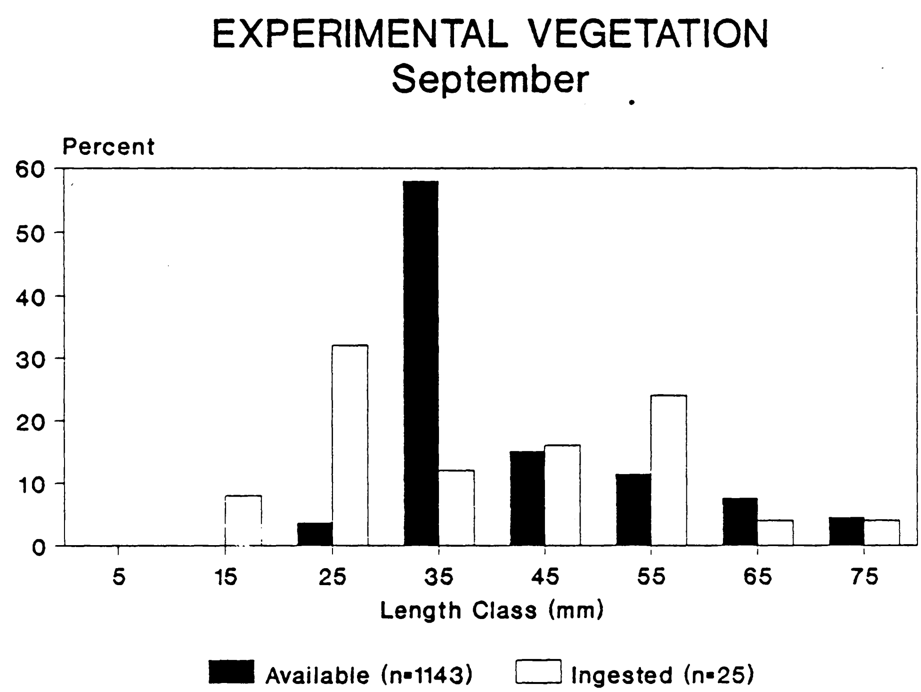


Figure 8. Length frequencies of potentially available and ingested forage fish, Sep., 1987. Fish from LMB stomachs and electrofishing.

DISCUSSION

Predator Population Characteristics and Vegetation Density Relationships

Adult largemouth bass in Flat Top Lake were more abundant in high (and intermediate) vegetation habitats than in low vegetation, but the size distributions were not influenced by vegetation density. The manipulative experiment did not show any short term effects of increasing the amount of vegetation/open water interface on largemouth bass abundance or size structure. Previous studies document an association between aquatic vegetation and largemouth bass abundance or production. In a comparison among 30 Texas reservoirs, Durocher et al. (1984) found significant positive correlations between the standing crop of largemouth bass (and the number of largemouth bass ≥254 mm) and the percent area covered by submerged aquatic vegetation (species not reported, maximum coverage = 20%). In Illinois ponds, Wiley et al. (1984) indicated that a parabolic relationship exists between largemouth bass production and the density on *Najas flexilis* and *Potamogeton crispus*, with production greatest at an intermediate level of vegetation density of 36% surface area coverage (52 g dry wt/m^3 for a 0.2 ha pond). Mesing and Wicker (1986) indicated that largemouth bass (40 - 410 g in weight) selected vegetated habitat (*Panicum* spp., *Typha* sp., and *Nuphar* sp.) over open water habitat in two Florida lakes. Betsill et al. (1988) found both subspecies of largemouth bass (northern largemouth bass *Micropterus salmoides salmoides* and Florida largemouth bass *M. s. floridanus*) used cover extensively, particularly aquatic vegetation (*Chara* sp.) in two Texas impoundments. However, densely vegetated habitat may not be used by largemouth bass in all situations. Barnett and Schneider (1974), examining 9 lakes and rivers in Florida, found an inverse relationship between vegetation density (*Hydrilla verticillata*, *Ceratophyllum demersum*, *Egeria densa*, *Vallisneria americana*, and *Najas guadalupensis*) and largemouth bass. Bailey (1978) examined fish communities in 31 Arkansas reservoirs before and after vegetation eradication with grass carp *Ctenopharyngedon idella*. These reservoirs ranges in size from 32-3603 ha, and the surface area coverage of aquatic vegetation (primarily *Ceratophyllum demersum*, *Cabomba caroliniana*, *Utricularia* sp., *Elodea densa*, and *Potamogeton* spp.) ranged from 0-95% (mean = 30%). He found no relationship between vegetation and the abundance of age-0 or harvestable largemouth bass. It appears that, in some instances, the abundance/production of largemouth bass may be positively related to vegetation density (or at least the presence of aquatic vegetation), and that this relationship applies to Flat Top Lake. However, this relationship does not appear to be species specific with respect to aquatic vegetation.

There were no apparent differences associated with the size distribution of largemouth bass ≥200 mm and density of aquatic vegetation in Flat Top Lake. However, Durocher et al. (1984) found numbers of largemouth bass ≥254 mm to respond positively to vegetation density, while no relationship could be determined for vegetation density and numbers of largemouth bass 152-254 mm in length. Wanjala et al. (1986) discovered differential habitat use by different sizes of adult largemouth bass in Alamo Lake, Arizona; largemouth bass 190-250 mm long and ≥380 mm long were closely associated with various types of littoral structure (vegetation, woody debris, man-made structures, etc.), whereas those 250-380 mm long were more abundant in open limnetic habitats, possibly due to their dependence on threadfin shad *Dorosoma petenense* for forage. Ware and Gasaway (1978) found no relationship between aquatic vegetation and the abundance of small (< 150 mm long) largemouth bass, but they did notice a decline in the numbers of intermediate and large fish following vegetation eradication in two Florida ponds. McClendon and Rabeni (1988) worked with smallmouth bass in the Jacks Fork River, Missouri, and found a positive relationship between proportional stock density and aquatic vegetation. These various investigations seem to indicate that a highly variable relationship exists between the size distribution of *Micropterus* spp. and aquatic vegetation. This could be dependent upon the species and amount of aquatic vegetation present, the availability of alternate cover types, the abundance/availability of suitable forage, the physical/chemical factors present, the morphometry of the water body, or differential survival rates of juvenile largemouth bass. Data from this study (Flat Top Lake) showed no relationship between largemouth bass size and aquatic vegetation density, although few very large fish were captured (Figure 9). This leads one to conclude that if a relationship exists, it may be controlled by multiple factors, including vegetation density, and that each system is likely to be unique.

Increasing the amount of vegetation/open water interface in Flat Top Lake had no effect on the abundance/size distribution of adult largemouth bass. However, Barnett and Schneider (1974), Cooper and Crowder (1979), Colle and Shireman (1980), Savitz et al. (1983), and Savino and Stein (1988) all suggested that the interface between complex structure (e.g. aquatic vegetation) and more open water provides "optimal" foraging locations for predators. This hypothesis is based on several studies that

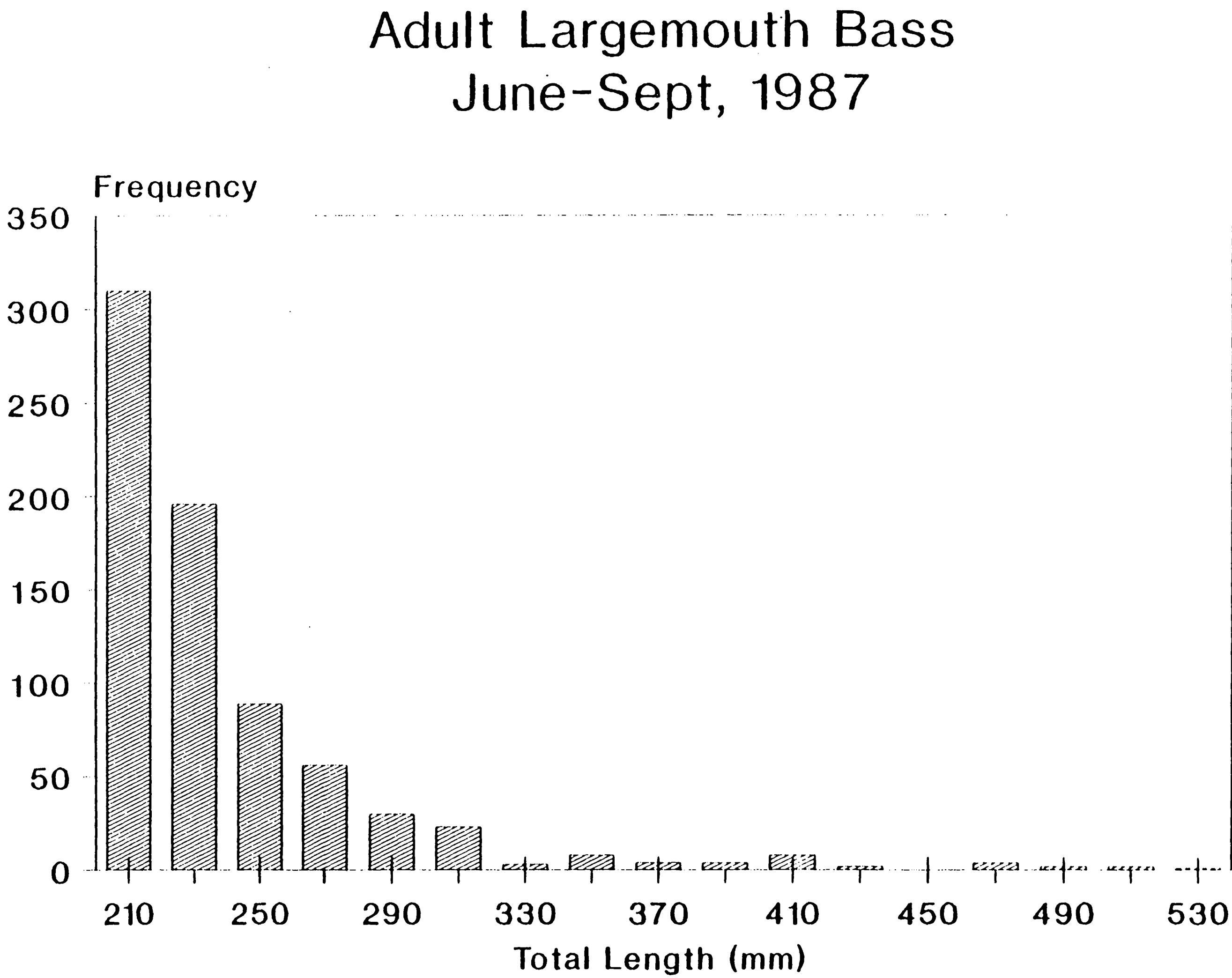


Figure 9. Length-frequency (mm) of adult largemouth bass captured in Flat Top Lake, June-September, 1987.

indicate the abundance of forage is positively related to aquatic vegetation (Cooper and Crowder 1979 - vegetation not specified; Orth et al. 1984 - *Zostera* spp., *Halodule* sp., *Thalassia* sp., *Syringodium* sp.; Wiley et al. 1984 - *Najas flexilis* and *Potamogeton crispus*; Gotceitas and Colgan 1987 - artificial vegetation; Killgore and Miller 1988 - *Hydrilla verticillata* and *Myriophyllum spicatum*). Conversely, the foraging efficiency (prey captured/attempt or prey ingested/prey density) of largemouth bass has been shown to decline with increasing structural complexity (Glass 1971; Savino and Stein 1982; Anderson 1984; Wiley et al. 1984). Therefore, whole prey may be more abundant in dense structure (e.g. aquatic vegetation), the ability of largemouth bass to capture prey may be greater in open water. Thus, the boundary between vegetation and open water may provide an ideal habitat for feeding largemouth bass.

Although no changes in largemouth bass abundance/size distribution were noted in Flat Top Lake following the vegetation manipulation, this could have been a reflection of the short-term nature (one month) of this experiment. It is also possible that the small home ranges/daily movements of largemouth bass (Mesing and Wicker 1986; Betsill et al. 1988) contributed to the lack of movement of fish into the experimentally manipulated locations.

Many factors, acting alone or in concert, could contribute to the largemouth bass habitat relationships found in Flat Top Lake and other studies. The species/growth patterns of aquatic vegetation should influence these interactions. The abundance/availability of prey could determine habitat use by largemouth bass. Various water quality parameters (pH, dissolved oxygen, temperature, etc.) could regulate habitat selection. Lake morphometry (depth, slope, substrate, etc.) could regulate habitat use. Aquatic vegetation could attract largemouth bass by providing cover and/or shade. Finally, increased utilization of vegetated habitat over open water habitat by adult largemouth bass may be an artifact of increased juvenile survival in vegetation.

Differences in aquatic vegetation (species, density, height, volume in water column, etc.) may have contributed to the inconsistency in largemouth bass abundance/aquatic vegetation relationships found between Flat Top Lake and other studies. Keast (1984) reported that the native *Potamogeton-Vallisneria* plant community had higher fish abundances than did areas of introduced *Myriophyllum spicatum* in Lake Opinicon, Ontario. However, in Flat Top Lake, largemouth bass utilized *Najas* and *Nitella* in proportion to their availability, while areas lacking in vegetation were underutilized (Table 6). While this was not conclusive, it suggested that both plant communities were acceptable habitat for largemouth bass, even though the growth patterns of *Najas* and *Nitella* were quite different. Thus, while differences in vegetation may have affected largemouth bass distributions in other systems, these differences appeared less important in Flat Top Lake.

The abundance/availability of prey was probably a factor regulating the distribution of adult largemouth bass in Flat Top Lake. Crowder and Cooper (1979a), Wiley et al. (1984), and Betsill et al. (1988) suggested that prey availability controlled the distribution of predators. As stated previously, prey abundance has been positively associated with aquatic vegetation (Cooper and Crowder 1979; Orth et al. 1984; Wiley et al. 1984; Killgore and Miller 1988). While complex habitats may reduce largemouth bass foraging efficiency (Glass 1971; Savino and Stein 1982; Anderson 1984; Wiley et al. 1984), it has been demonstrated that largemouth bass are able to capture prey (bluegill and fathead minnows *Pimephales promelas*) in densely structured habitats (artificial vegetation at 1000 stems/m^2) (Savino and Stein 1989). In Flat Top Lake, any loss in foraging efficiency of largemouth bass due to structural complexity of vegetated areas may have been compensated with increased prey abundance. Thus, if prey was more abundant in vegetated habitats than open water habitats, largemouth bass could have been attracted to areas of high vegetation due to foraging advantages. This will be discussed further in the next section.

Physical/chemical factors such as temperature, dissolved oxygen, and pH may have been important forces regulating largemouth bass distribution. Largemouth bass have upper and lower tolerance limits for these factors, and preferred ranges have been demonstrated for temperature (Coutant 1977). Holland and Huston (1984) found that the distributions of age-0 northern pike (*Esox lucius*) were at least partially influenced by interactions between aquatic vegetation density (*Ceratophyllum demersum*, *Potamogeton crispus*, *Sparaganium eurycarpum*, *Lemna* spp., *Elodea canadensis*, and *Sagittaria* spp.) and dissolved oxygen concentrations. However, there were never any measured physical/chemical parameters (temperature, dissolved oxygen, pH) that fell outside of an acceptable range for warmwater fish in water <4.5 meters deep in Flat Top Lake during the course of this investigation (June-September, 1987: surface temperature range = 17-26°C; minimum dissolved oxygen 4.74 mg/l; pH range = 6.6-7.4) (D. A. Coahran; unpublished data), although these were not measured at the specific locations where I sampled.

Largemouth bass are often associated with shoreline areas (Heidinger 1975; Mesing and Wicker 1986), and therefore, lake morphometry may have a significant influence on largemouth bass distribution. However, Wanjala et al. (1986) found that 250-380 mm largemouth bass utilized open limnetic habitat extensively, while Betsill et al. (1988) found that depth was not related to habitat use by largemouth bass. In Flat Top Lake, electrofishing was conducted in shallow water (0.3-3.0 m) at all locations. Also, lake morphometry between intermediate and low vegetation locations (sampled in 1986) was similar, although largemouth bass did not utilize both habitats equally. Thus, water depth/lake morphometry did not appear to directly affect largemouth bass distribution.

It is possible that largemouth bass utilized vegetated habitat simply for the cover or shading provided. Johnson et al. (1988) determined that adult largemouth bass selected a lower density of artificial cover than that preferred by their prey (bluegill). This may indicate habitat choice based on some mechanism other than prey availability. However, Helfman (1981) and Howick and O'Brien (1983) determined that the use of shade by largemouth bass increased predation efficiency at high light intensities. Therefore, cover may be an attractant in itself, or it may be selected for feeding advantages.

Finally, largemouth bass abundance in Flat Top Lake may be related to home range size and differential survival between vegetated and unvegetated habitats. Barnett and Schneider (1974) noted that areas of dense vegetation (*Hydrilla verticillata*, *Ceratophyllum demersum*, *Egeria densa*, *Vallisneria americana*, and *Najas guadalupensis*) had higher numbers of age-0 largemouth bass than areas of open water in Florida ponds. Colle et al. (1987) found that *Hydrilla verticillata* coverage was positively related to largemouth bass recruitment, also in Florida. In conjunction with this, largemouth bass have relatively small home range sizes (Hasler and Wisby 1958). Betsill et al. (1988) reported largemouth bass home range sizes of 0.37-1.11 ha in Texas impoundments, and Mesing and Wicker (1986) reported home range sizes of 0.01-5.16 ha in Florida lakes. Therefore, it is quite possible that increased abundance of adult largemouth bass in high vegetation is a result of increased survival of young largemouth bass in this habitat. This implies that adult largemouth bass are not selecting vegetated habitats, but rather that they establish a home range early in life that conveys survival advantages, and never leave it.

Many factors influenced the distribution of largemouth bass in Flat Top Lake. However, the differences in habitat use described in this study should accurately depict actual conditions in this reservoir with respect to vegetation density. Relative abundance estimates determined by night electrofishing have been shown to be accurate measures of largemouth bass density (Hall 1986). Daily movements of largemouth bass are generally minor (Mesing and Wicker 1986;Betsill et al. 1988), indicating that time of electrofishing should have little influence on perceived habitat use. Seasonal differences in the vulnerability of various sized largemouth bass to electrofishing may exist (Carline et al. 1984), but this should affect all samples within seasons equally.

Prey abundance/availability was probably the primary factor influencing the largemouth bass/aquatic vegetation relationship found in Flat Top Lake. While the other factors mentioned (vegetation type, water quality, cover, lake morphometry, and differential survival among habitat types) influenced largemouth bass distribution, prey abundance/availability was probably the dominant regulating mechanism. In fact, it is probable that vegetation, water quality, cover, lake morphometry, and predation all influenced the distribution of prey, which in turn influenced the distribution of predators.

The scope of this investigation was to assess the influence of submerged aquatic vegetation on the distribution of largemouth bass, and then to examine one potential regulating mechanism (trophic dynamics). Many questions remain that cannot be answered by the information collected here. First, few thorough evaluations of the effects of different species or configurations (density, patch size, patch shape, etc.) of aquatic vegetation on largemouth bass distribution have been conducted. Keast (1984) found that different species/growth patterns of vegetation affected fish and invertebrate communities in different ways. Thus, the results from Flat Top Lake can be applied to reservoirs containing dense stands of *Najas* sp. and *Nitella* sp., but the influence of other types of vegetation are unknown. In addition, the hypothesis that vegetation provides survival advantages for juvenile largemouth bass and that adult largemouth bass do not alter habitat use as they grow needs further investigation. This could be an important mechanism for controlling largemouth bass distributions in aquatic systems. Combinations of these factors with predator/prey interactions are very likely to have a great influence on largemouth bass abundance and size distribution.

Predator/Prey Interactions as a Potential Mechanism for Influencing Habitat Utilization by Adult Largemouth Bass

Prey Abundance/Size Distribution and Aquatic Vegetation Density

Analyses of the potential prey base as it related to aquatic vegetation density focused on two prey types, crayfish and forage fish. Due to different gear types used for data collection, the abundance/size distribution of crayfish and forage fish were analyzed separately.

Crayfish

Catch/effort data from trap and SCUBA collections indicate that crayfish were more abundant at low vegetation than at high vegetation in Flat Top Lake. Ricketts (1975) found a similar negative relationship between density of aquatic vegetation (*Potamogeton* sp. and *Chara* sp.) and the catch/effort of crayfish using traps. Camougis and Hichar (1959) and Emery (1975) determined that crayfish abundance was positively associated with rocky substrata, although neither study indicated whether aquatic vegetation was present. Saiki and Tash (1979) captured more crayfish/trap in areas with dense aquatic vegetation (*Myriophyllum exalbescens*) than in habitats without vegetation. Saiki and Ziebell (1976) found abundance of adult crayfish to be positively associated with rocky areas, woody debris, and vegetation (*Myriophyllum exalbescens*). In Flat Top Lake, rocky substrate was present in much of the low vegetation habitat, but it was less common in high vegetation areas. Thus, it appears that crayfish distribution was influenced by the presence/absence of suitable cover in previous studies, and that rock substrate and some species of aquatic vegetation (*Myriophyllum*) were suitable. The relative value of *Najas* and *Nitella*, found in Flat Top Lake, as crayfish habitat were unknown.

The mean lengths of crayfish sampled by trapping or SCUBA were not influenced by the density of aquatic vegetation (*Najas*). Unfortunately, few small crayfish (< 30 mm carapace length) were sampled by either method. This was expected with traps, but Malley and Reynolds (1979), Distefano (1987), and Davies and Ramsey (1989) found that hand capture techniques adequately collected small crayfish. Small crayfish in Flat Top Lake managed to elude SCUBA divers, possibly by remaining hidden in vegetation and rocky habitats. Thus, the distribution of crayfish < 30 mm carapace length (cl), with respect to vegetation, was not adequately assessed in Flat Top Lake.

Differential habitat use by small (< 30 mm cl) and large crayfish of the genus *Orconectes* has been reported in trapping studies (Saiki and Ziebell 1976; Momot 1978) and aquarium studies (Stein and Magnuson 1976). Thus, it was possible that the distribution of small crayfish was different from the distribution of the larger crayfish sampled in Flat Top Lake, although the utilization of crayfish by largemouth bass was similar among all vegetation densities. Qualitative samples taken with a towed net in high density *Najas* habitats collected numerous small crayfish (Table 37). A similar sample could no be obtained at the low vegetation sites, as the towed net sampled the water column (and thus the vegetation), but not the reservoir bottom.

Table 37. Carapace lengths (mm) of crayfish captured in qualitative sampling (towed net) at high vegetation density, August 1987.

Length Class (mm)	Number Captured
1.0-4.0	0
4.1-8.0	0
8.1-12.0	9
12.1-16.0	10
16.1-20.0	2
20.1-24.0	0
24.1-28.0	0
28.1-32.0	1

Mean Length = 13.70

Standard Deviation = 3.90

Manipulation of the vegetation density appeared to have no influence on either crayfish abundance or size structure. However, catch rates of crayfish in September were very low, probably due to migration to deeper water associated with decreased temperatures. This type of movement has been noted in several other studies of orconectid crayfish (Momot 1967; Momot and Gowing 1972; Malley and Reynolds 1979).

Most of the crayfish consumed by adult largemouth bass in Flat Top Lake were < 30 mm cl (Figures 3-5). Small crayfish of this size were present at both high and low vegetation densities, although the differences in the relative abundance of these individuals between habitats was unknown.

Forage Fish

This study and others showed a strong positive relationship between forage fish and structure (particularly vegetation). Orth et al. (1984) stated that many species of marine fish were associated with stands of submerged vegetation (*Zostera* spp., *Halodule* sp., *Thalassia* sp., and *Syringodium* sp.). Increases in bluegill abundance/production have been related to increases in vegetation (*Hydrilla verticillata*) coverage (Colle et al. 1987) and artificial structure (Pardue 1973). When offered a choice of densities, bluegill chose the highest density of artificial vegetation available (Bickerstaff et al. 1984; Gotceitas and Colgan 1987). This affinity for structure appears to be increased for smaller fish. Many studies have shown juvenile centrarchids (bluegill and largemouth bass) to be more abundant in dense vegetation (*Hydrilla verticillata, Ceratophyllum demersum, Egeria densa, Vallisneria americana, Najas guadalupensis, Myriophyllum spicatum, Utricularia floridana, Eleocharis* *elongata, Panicum hemitomon*) than adults (Barnett and Schneider 1974; Summers 1980; Mittelbach 1986; Colle et al. 1987, Butler 1988, Killgore and Miller 1988). In Flat Top Lake, no difference in the abundance of forage fish was detected between reference and experimental areas. The association between forage fish and high vegetation density found in this study appears to be consistent with previous studies.

Forage fish may have been attracted to areas of high vegetation density for two primary, but not mutually exclusive, reasons: predator avoidance and foraging opportunities. Forage fish may have inhabited the dense stands of *Najas* in Flat Top Lake to reduce predation. Savino and Stein (1982), Wiley et al. (1984), and Rahel and Stein (1988) found that complex habitats (artificial vegetation, *Najas flexilis* and *Potamogeton crispus*, and tile shelters, respectively) all reduced the vulnerability of forage fish (bluegill, bluegill and largemouth bass, and johnny darters *Etheostoma nigrum*, respectively) to *Micropterus* spp. In addition, Werner et al. (1983a) and Johnson et al. (1988) showed that bluegill chose complex habitats (vegetation and artificial structures, respectively) over more open water to reduce predation, although foraging opportunities for bluegill were greater in the open water habitat.

The evidence is contradictory with regard to foraging opportunities for forage fish associated with complex structure. Prince et al. (1978) found primary productivity and nutrient concentrations to be greater on artificial structure (tire reefs) than in the littoral phytoplankton. Crowder and Cooper (1982), Anderson (1983), and Wiley et al. (1984) all noted increased abundances of invertebrates associated with increases in vegetation density. The type of vegetation is also a factor, as different species of vegetation have shown to have differential influences on invertebrate abundance (Gerrish and Bristow 1979; Keast 1984).

While invertebrate production may be increased by structure, the production of forage fish may not show a similar increase. Pardue and Nielsen (1979) determined that while artificial structure (pine board lattices) increased the abundance of invertebrates, no corresponding increase in forage fish production occurred. In addition, Werner et al. (1983a; 1983b) found that while macroinvertebrate (insects) densities were high in dense vegetation, foraging opportunities (and production) for bluegills were better in open water (feeding on zooplankton) and on a bare sand substrate (feeding on benthos). Conversely, Wiley et al. (1984) found a positive impact on forage fish production associated with increased macroinvertebrate production in dense aquatic vegetation (*Najas flexilis* and *Potamogeton crispus*). Therefore, it appeared that the relationship between vegetation density and the trophic dynamics of forage fish was unclear. The greater abundance of prey fish found in high vegetation as compared to low vegetation in Flat Top Lake may have been partially explained by differences in the abundance of food resources.

Other factors also affected the distribution of forage fish. Temperature, dissolved oxygen, and pH can control the utilization of certain habitats by fish. Light levels have been shown to influence bluegill distribution (Howick and O'Brien 1983) as has depth (Lynch and Johnson 1988). However, habitat selection by forage fish in Flat Top Lake was probably regulated by predation pressures and foraging opportunities.

Several important aspects of prey (crayfish, fish, and insects) abundance and size distribution were not addressed by this study. The distribution of juvenile crayfish needs to be investigated further, and an accurate method for sampling these organisms needs to be developed. A possible procedure for this type of sampling might involve an area sampler in which the substrate and all vegetation above it are thoroughly examined, and all organisms present captured, similar to the throw-trap described by Kushlan (1981), or the pop-net described by Serafy et al. (1988). Larval fish and insects were not sampled in Flat Top Lake, although these consumed by adult largemouth bass. Future studies should attempt to establish the relationship between their abundance and vegetation density. Crayfish are an important component in many aquatic systems, and factors affecting their distribution should be further investigated, with an emphasis on juveniles. Finally, while there is good evidence to show that forage fish inhabit areas of dense vegetation to avoid predation, the trophic advantages/disadvantages of such habitat selection are not as well established. Further study is needed in these areas.

Predator/Prey Dynamics and Vegetation - The Predator Perspective

In general, samples from 1986 and 1987 indicated that vegetation density had very little influence on the foraging patterns of largemouth bass in Flat Top Lake. It appeared that prey acquisition by largemouth bass was not affected by vegetation density, at least at the vegetation density/prey availability combinations found in Flat Top Lake.

By examining the stomach contents of fish, a sample of food intake from prior time periods is collected. The rate of food evacuation varies with water temperature and prey type. Gannon (1976) and Strauss (1979) both stated that results from food habits studies can be misleading if corrections are not made for differential evacuation rates of different prey items. Largemouth bass in Flat Top Lake consumed crayfish, fish, and insects; crayfish were the dominant item by weight. Reported evacuation rates for largemouth bass feeding on fish (Molnar and Tolg 1962; Beamish 1972; Lewis et al. 1974; Adams et al. 1982a), smallmouth bass feeding on crayfish (Emery 1975), and bluegill feeding on insects (Seaburg and Moyle 1964) are all similar. Probst et al. (1984) assumed that the evacuation rates of crayfish and fish consumed by smallmouth bass were not different. This assumption was made for fish, crayfish, and insects consumed by largemouth bass in Flat Top Lake.

It was assumed that largemouth bass were foraging in the locations where they were captured. Both the home ranges and daily movements of largemouth bass have been demonstrated to be relatively small (Mesing and Wicker 1986; Betsill et al. 1988). Thus, it appears reasonable that foraging and capture locations would be in the same habitat type (e.g. vegetation density).

Few differences in the numbers, size, or biomass of prey items consumed by largemouth bass in Flat Top Lake were associated with vegetation density. Many authors have observed that complex habitats (e.g. aquatic vegetation) reduces the foraging efficiency of predators, particularly piscivores (Glass 1971; Crowder and Cooper 1979b; Heck and Thoman 1981; Savino and Stein 1982; Anderson 1984; Bickerstaff et al. 1984; Wiley et al. 1984; Gotceitas and Colgan 1987). In conjunction with this, vegetation has been associated with increased densities of prey. This produces a model in which high vegetation densities have abundant but relatively unavailable prey, while low vegetation densities have sparse but readily available prey resources. Therefore, one would expect largemouth bass at intermediate levels of vegetation to forage more efficiently than those at either high or low vegetation (Glass 1971; Crowder and Cooper 1979b; Savino and Stein 1982; Anderson 1984; Wiley et al. 1984). Also, foraging conditions for largemouth bass at high and low vegetation should be similar, although for different reasons.

In Flat Top Lake, consumption of prey was not different among high, intermediate, or low vegetation densities as sampled in 1986. Thus, the hypothesis that intermediate vegetation provided better foraging conditions than did high or low vegetation was not supported by the data from Flat Top Lake. Samples collected in 1987 revealed no difference in the biomass of prey consumed by largemouth bass at high and low vegetation densities. Thus, either biomass consumed is a poor estimator of foraging efficiency (because all predators may consume similar amounts of prey, although the foraging time necessary to acquire this prey may differ), the previously described model is incorrect, or factors other than vegetation density were the controlling mechanisms for largemouth bass foraging patterns.

Aquatic vegetation density did not appear to affect the energy intake of largemouth bass in Flat Top Lake. Based on the mean biomass of prey ingested/predator, a conservative estimate of largemouth bass daily consumption in Flat Top Lake would have been in the range of 1.5-2.3% of their body weight at 18-25°C. This was at the lower end of the range of daily consumption predicted with a bioenergetics model for age-1 largemouth bass of 2.0-6.0% of the fish's body weight at similar temperatures in an Ohio impoundment (Carline 1987). Several studies have shown that, although predators may spend more time foraging in complex habitats, they appear to acquire equal amounts of prey when compared with more open habitats in both laboratory and field studies (Savino and Stein 1982; Anderson 1984; Holland and Huston 1984; Gotceitas and Colgan 1987). Savino and Stein (1988) and Annett (1989) found that largemouth bass were more likely to forage in complex habitats (artificial vegetation and natural vegetation, respectively) than open water. However, Glass (1971) reported a decrease in the amount of prey consumed by largemouth bass at high structural densities (1000 stems/m^2 of wooden dowel-rods) over more open habitats. Largemouth bass in Flat Top Lake were able to acquire the same biomass of prey/predator in *Najas* and *Nitella* as they were in areas devoid of aquatic vegetation. Therefore, if aquatic vegetation reduced largemouth bass foraging efficiencies, then this was compensated with increased abundance/availability of prey in vegetated habitats.

Different sizes of prey have different values to predators. Adams et al. (1982a) suggested that consuming smaller prey imposed growth/survival penalties on largemouth bass. However, Werner et al. (1983b) indicated that there was no disadvantage in feeding on small prey items, provided that enough prey was ingested. In addition, several studies have shown small fish (Savitz and Janssen 1982; Winemiller and Taylor 1987) and small crayfish (Stein and Murphy 1976; Crowl 1984) to be more efficient forage for predators than large fish or crayfish. Thus, if foraging conditions were better at one vegetation density than another, the sizes of prey ingested by predators might differ, due to optimal foraging by predators (Werner 1974; Stein 1977; Anderson 1984). However, no differences were found in the sizes of crayfish or fish consumed by largemouth bass among the different levels of vegetation density found in Flat Top Lake.

Based on the findings of several studies (Barnett and Schneider 1974; Colle and Shireman 1980; Savitz et al. 1983; Orth et al. 1984), the biomass of prey consumed per predator was expected to be greater at the experimentally manipulated vegetation stations than at the reference stations. These previous studies stressed the importance of the vegetation/open water ecotone to predators. However, the data from Flat Top Lake dispute this hypothesis in that no differences in foraging patterns of largemouth bass were associated with an increase in the amount of this ecotone, although the experiment in Flat Top Lake only lasted one month.

On the whole, vegetation density did not influence the foraging success of individual largemouth bass in Flat Top Lake. The amounts, sizes, and types of prey ingested by largemouth bass were similar among all habitat types. Other investigations have suggested that these parameters might differ among habitats if there were differences in the trophic value of different densities of vegetation to largemouth bass. It is possible that vegetation (at the densities present in this study) had no influence on the foraging dynamics of adult largemouth bass. Vegetation densities in Flat Top Lake were not directly comparable with most of the other work mentioned previously, as the measurements from other studies were generally in stem density or g dry wt/m^3 and vegetation in Flat Top Lake was measured in g dry wt/m^2. However, based on personal observations, the *Najas* habitat in Flat Top Lake was comparable to many other types of aquatic vegetation habitat. Most of the previous studies involved largemouth bass and forage fish. Few studies have evaluated predator/prey interactions between largemouth bass and crayfish, and the influence of vegetation on these interactions. Also, a reduction in foraging efficiency at higher vegetation densities may have had no effect on the biomass consumed by largemouth bass, as they may simply alter their foraging strategies to fit their environment. Finally, any reduction in foraging efficiency associated with dense vegetation may be counteracted by increased prey density, resulting in no net impacts to the trophic dynamics of largemouth bass.

Predator/Prey Dynamics and Vegetation - The Community Perspective

Results from Flat Top Lake showed that while the abundance of adult largemouth bass was approximately twice as great at high vegetation as it was at low vegetation, the ratios of prey available/predator and prey consumed/predator were similar between high and low vegetation. This was true for all adult largemouth bass (Table 8) as well as for largemouth bass 213-250 mm in length (a group defined by the upper and lower quartiles of the lengths of all adult largemouth bass sampled in 1987) (Table 38). Thus, high vegetation areas were able to support a greater number of predators than low vegetation areas.

The increase in vegetation/open water interface (experimental manipulation) had no significant effects on the abundance of potentially available prey, or in the consumption of prey/predator (numbers and biomass). Thus, the enhanced ecotone area created did not affect 213-250 mm largemouth bass from a trophic standpoint during the duration of this experiment.

Vegetation density did not influence size selection of crayfish by largemouth bass in Flat Top Lake. Sizes of available and ingested crayfish were similar between high and low vegetation (Figures 3 and 4). The mean lengths of crayfish sampled by traps and SCUBA were not significantly different between high and low vegetation densities (Table 15 and 16). Also, vegetation density had no relationship with the mean lengths of crayfish consumed by largemouth bass (Table 30). Thus, the sizes of crayfish potentially available to and consumed by adult largemouth bass in Flat Top Lake were not related to aquatic vegetation density.

Table 38. Relative abundance (catch/effort)* of 213-250 mm largemouth bass in Flat Top Lake, June and August, 1987. Means, with standard deviation in parentheses (n=3 for all samples).

	Mean Catch/Effort of 213-250 mm Largemouth Bass	
Month	High Vegetation	Low Vegetation
June	9.1111	5.1111
	(2.0092)	(3.4048)
August	11.1111	4.6667
	(1.0184)	(0.8819)
	ANOVA P-Values	Vegetation P=0.0046 Month P=0.6409 Interaction P=0.4615

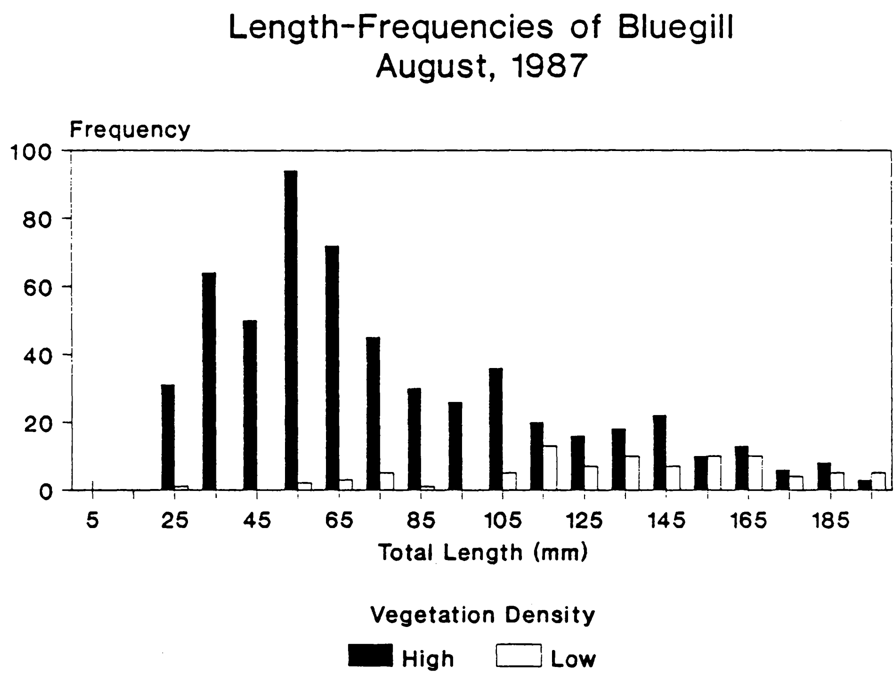
* catch effort = number fish captured/1000 seconds of electorfishing

Aquatic vegetation did appear to influence the sizes of forage fish potentially available to largemouth bass, and the sizes of forage fish consumed by largemouth bass. Visual evaluation of these data indicated that the sizes of available forage fish were similar between high and low vegetation in June (Figure 6), but smaller forage fish were more available at high vegetation in August (Figure 7). Mean length comparisons of these samples supported these conclusions (Table 19). Length-frequencies of bluegill and largemouth bass in August indicated that young bluegill were more abundant in high vegetation than low vegetation until reaching a length of approximately 110 mm, and largemouth bass were more abundant in high vegetation than low vegetation until reaching a length of approximately 100 mm (Figure 10). Analyses of the relative size of all prey fish consumed by largemouth bass revealed no differences between high and low vegetation (Table 31). However, length-frequency plots of available and consumed forage fish (Figures 6-7) revealed differences in the sizes of smaller forage fish (< 80 mm) consumed by largemouth bass at high and low vegetation. To verify this, I compared the mean lengths of ingested forage fish < 80 mm long between high and low vegetation (June and August 1987). The mean length of 1-79 mm forage fish ingested by largemouth bass was significantly greater at high vegetation than at low vegetation (Table 39). The very small sizes of forage fish consumed at low vegetation (5-25 mm) was possibly an indication of decreased forage fish availability at low vegetation compared to high vegetation. This may have led to inferior foraging opportunities for largemouth bass feeding on fish at low vegetation than at high vegetation. Adams et al. (1982a) found largemouth bass growth rates were positively associated with prey size (gizzard shad). Also, optimal foraging models (Werner 1974; Werner and Hall 1974) suggested that foraging on smaller prey is less efficient than consuming intermediate sized prey, and that as foraging conditions deteriorate smaller prey will be added to the diet.

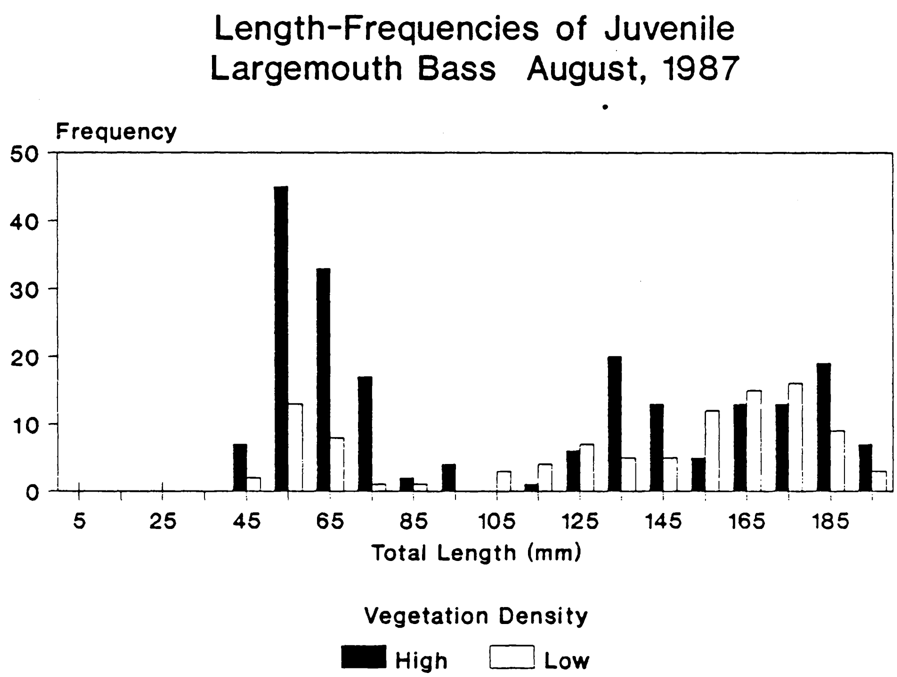
Thus, larger sizes of forage fish were more abundant at high vegetation than at low vegetation. This may have been caused by the extirpation of intermediate sized forage fish from low vegetation habitats that lacked suitable refugia from predators (Wiley et al. 1984).

Several authors have found a positive or parabolic relationship between the amount of aquatic vegetation present and the production of largemouth bass (Ware and Gasaway 1978; Durocher et al. 1984; Wiley et al. 1984). Conversely, it is also well documented that predator efficiency decreases with increasing structural complexity in laboratory studies (Glass 1971; Savino and Stein 1982; Anderson 1984) and pond studies (Crowder and Cooper 1979b). Therefore, vegetation must provide some attraction/benefit to largemouth bass other than trophic resources, and/or the decrease in predation efficiency has no significant effect on largemouth bass.

The latter hypothesis is more plausible, for two reasons. First, potentially available prey was generally more abundant in areas of dense vegetation, as noted in this and other studies (Saiki and Ziebell 1976; Saiki and Tash 1979; Heck and Thoman 1981; Orth et al. 1984; Wiley et al. 1984; Bettoli 1987). This increase in potentially available prey may have offset any penalties associated with decreased predation efficiency in dense vegetation, as has been suggested by Anderson (1983). Second, most of the studies examining structure/predation efficiency relationships are based on metabolic costs associated with increased search time and swimming speed demonstrated by predators in structurally complex habitats. Largemouth bass can and do minimize the metabolic costs of foraging by altering predation strategies to fit their environment (e.g. in dense vegetation they adopt an ambush feeding mode) (Glass 1971; Adams et al. 1982b; Savino and Stein 1982; Howick and O'Brien 1983: Savino



Captured by electrofishing



Captured by electrofishing

Figure 10. Length-frequencies of bluegill and largemouth bass in Flat Top Lake, August, 1987.

Table 39. Mean lengths (mm) of small and intermediate sized forage fish (1-79 mm long) consumed by largemouth bass at high and low vegetation in Flat Top Lake, 1987. Means, with standard deviation in parentheses; n = 3 for all samples except low vegetation-June, where n = 2.

	Mean Lengths of Forage Fish < 80 mm	
Month	High Vegetation	Low Vegetation
June	26.00	11.84
	(8.58)	(1.45)
August	38.55	20.01
	(6.41)	(7.71)
	ANOVA P-Values	Vegetation P=0.0106 Month P=0.0899 Interaction P=0.2554

and Stein 1988). In conjunction with this, the actual metabolic cost of swimming is relatively low (Carline 1987).

Therefore, while the time required to capture prey may be greater in high vegetation density than in low vegetation density (under conditions of equivalent prey densities between high and low vegetation), the energetic cost to individual predators may be similar. If prey is significantly more abundant in high vegetation than in low vegetation, foraging efficiencies of largemouth bass may actually be greater in high vegetation densities.

In general, the abundance of largemouth bass and the abundance of ingestible forage fish were positively associated with aquatic vegetation in Flat Top Lake and other systems. The relationship between potentially available crayfish and aquatic vegetation in Flat Top Lake was not determined, although crayfish were heavily utilized by adult largemouth bass at both high and low vegetation densities. Therefore, high vegetation sites in Flat Top Lake could provide more foraging opportunities for adult largemouth bass than did areas of low vegetation density. This could explain the positive relationship between aquatic vegetation and adult largemouth bass abundance in Flat Top Lake.

As with most research, this study generated more questions than it answered. Unfortunately, no reliable estimates of crayfish ($<$ 30 mm cl) abundance at high and low vegetation were obtained. However, crayfish may have been equally abundant in all habitats in Flat Top Lake. This hypothesis is supported by the actual consumption of crayfish by predators in this study. The role of crayfish in this type of community needs to be further investigated, as they were a major contributor to largemouth bass production in Flat Top Lake.

Clupeids were not present in Flat Top Lake, but they seem to be an important prey item of largemouth bass in systems where they occur simultaneously (Adams et al. 1982a; Carline et al. 1984; Storck 1986). Clupeids are planktivores, and may be negatively associated with aquatic vegetation (Bettoli 1987). Consequently, in a system dominated by clupeids, a different relationship between largemouth bass and aquatic vegetation may be expected.

The species composition and growth patterns of aquatic vegetation are likely to influence predator/prey interactions.The species composition/growth patterns of vegetation distribution should be investigated with regard to largemouth bass habitat use and trophic ecology. Evidence from this study indicates that a decrease in vegetation abundance in Flat Top Lake could have deleterious effects on the production of largemouth bass. However, the effects of an increase in vegetation, particularly a large increase, are unknown. Based on the overall productivity and morphometry of Flat Top Lake, a major increase in aquatic vegetation, given current conditions, is unlikely.

As a final suggestion, the influence of aquatic vegetation on different sizes of largemouth bass and the fidelity of the vegetation association with largemouth bass growth should be reviewed. This study did not examine the trophic dynamics of largemouth bass < 200 mm in length. Also, 90% of the adult largemouth bass captured in this study were less than 300 mm in length (Figure 9). Therefore, the importance of aquatic vegetation to largemouth bass may change with different sizes of largemouth bass.

Management Implications

Results of this study, integrated with information from other research, indicate that aquatic vegetation should be used as a tool for managing warmwater fisheries. The ideal range of total vegetation coverage is unknown. Approximately 13% of the surface area of Flat Top Lake was covered by high densities of submerged vegetation. Durocher et al. 1984 suggested that 20% surface area coverage was a minimum amount of aquatic vegetation for optimal largemouth bass production in reservoirs. Colle and Shireman (1980) stated that largemouth bass condition factors were greater in lakes with $<30\%$ surface area coverage of *Hydrilla verticillata*. Wiley et al. (1984) found that 36% surface area coverage of *Najas flexilis* and *Potamogeton crispus* was the optimal level of submerged vegetation for largemouth bass production in ponds. Based on these findings, it appears that largemouth bass production in Flat Top Lake could benefit from increased amounts of submerged vegetation over the present level, possibly as much as a twofold increase. However, given current conditions in Flat Top Lake (nutrient inputs, morphometry, and temperature) an increase of this magnitude is unlikely. The distribution of vegetation should be manipulated so that interferences with other uses (e.g. swimming, sailing, withdrawal for other uses, etc.) are minimized. I believe that a complete, or even partial, reduction of vegetation in Flat Top Lake would be detrimental to the largemouth bass population, unless this was accompanied by an increase in available prey in open littoral areas (e.g. clupeid introduction) and a significant decrease in fishing mortality in order to offset the loss of production accompanying a decrease in vegetation. Vegetation in Flat Top Lake, and similar systems, should be managed to maintain/improve the sport fishery. This study detected no benefits to largemouth bass associated with increasing the amount of vegetation/open water interface, although the duration of the experiment was only one month. However, no detrimental effects on largemouth bass were discovered either. Hurley and Harrell (1989) found that mechanical harvesting of *Hydrilla verticillata* had no effects on fish populations in the Potomac River, Maryland. Vegetation control can be undertaken using mechanical, chemical, or biological methods. Of the three, mechanical techniques are the most easily controlled. Data from this and other studies suggest that eradication of aquatic vegetation is undesirable, and that mechanical harvesting does not negatively influence fish populations. Thus, mechanical harvesting may be a better option for controlling aquatic vegetation. Creating necessary openings in vegetation beds may provide a means for manipulating vegetation to benefit multiple use of a reservoir without negatively impacting largemouth bass populations.

Conclusions

1.) Largemouth bass were more abundant in high and intermediate vegetation densities than in low vegetation.

2.) There were no differences in the size distributions of adult largemouth bass among high, intermediate, and low vegetation densities.

3.) Increasing the vegetation/open water ecotone appeared to have no effect on the abundance/size distribution of adult largemouth bass over a one month time period.

4.) Large adult crayfish may have been more abundant in low vegetation habitats than in high vegetation, although the abundance of juvenile crayfish, which were ineffectively sampled, was unknown with respect to vegetation density.

5.) Forage fish were more abundant in high vegetation habitats than in low vegetation, particularly after age-0 fish were large enough to be sampled.

6.) Increases in the ecotone between vegetation and open water had no apparent effects on crayfish or forage fish.

7.) Despite differences in prey availability, no differences were noted in the biomass of prey consumed by individual largemouth bass among the vegetation levels tested.

8.) Crayfish and forage fish (mostly bluegill) were the principal prey base for adult largemouth bass in Flat Top Lake.

9.) The abundance of adult largemouth bass was greater in high vegetation habitats than in low vegetation, and this appeared to be directly related to increased forage abundance at high vegetation.

10.) Increases in the vegetation/open water interface had no influence on the trophic dynamics of largemouth bass over a one month period.

11.) The ecotone between vegetation and more open water did not appear to influence predator/prey interactions in Flat Top Lake. This ecotone may be more important to fish species other than largemouth bass and bluegill.

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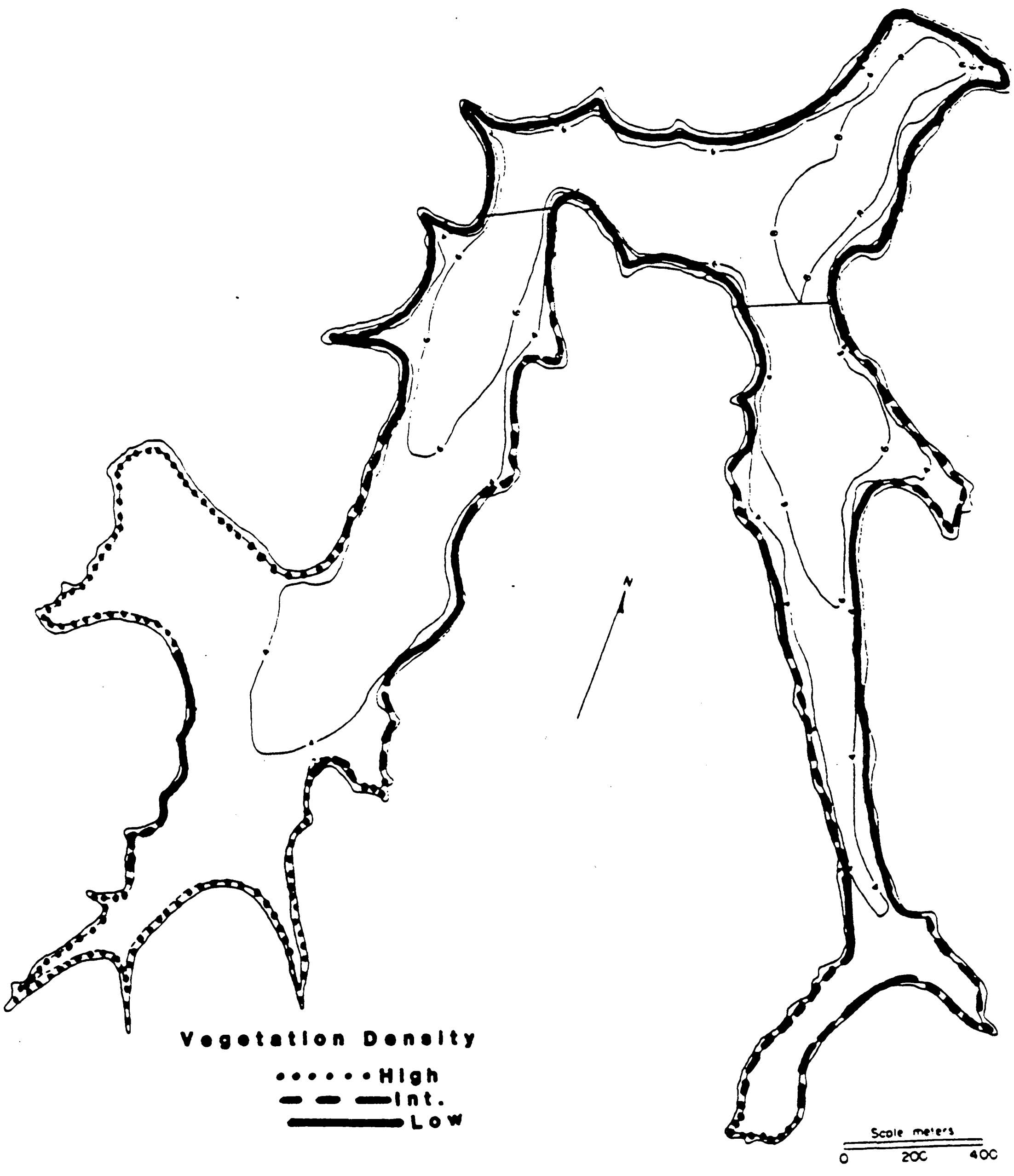
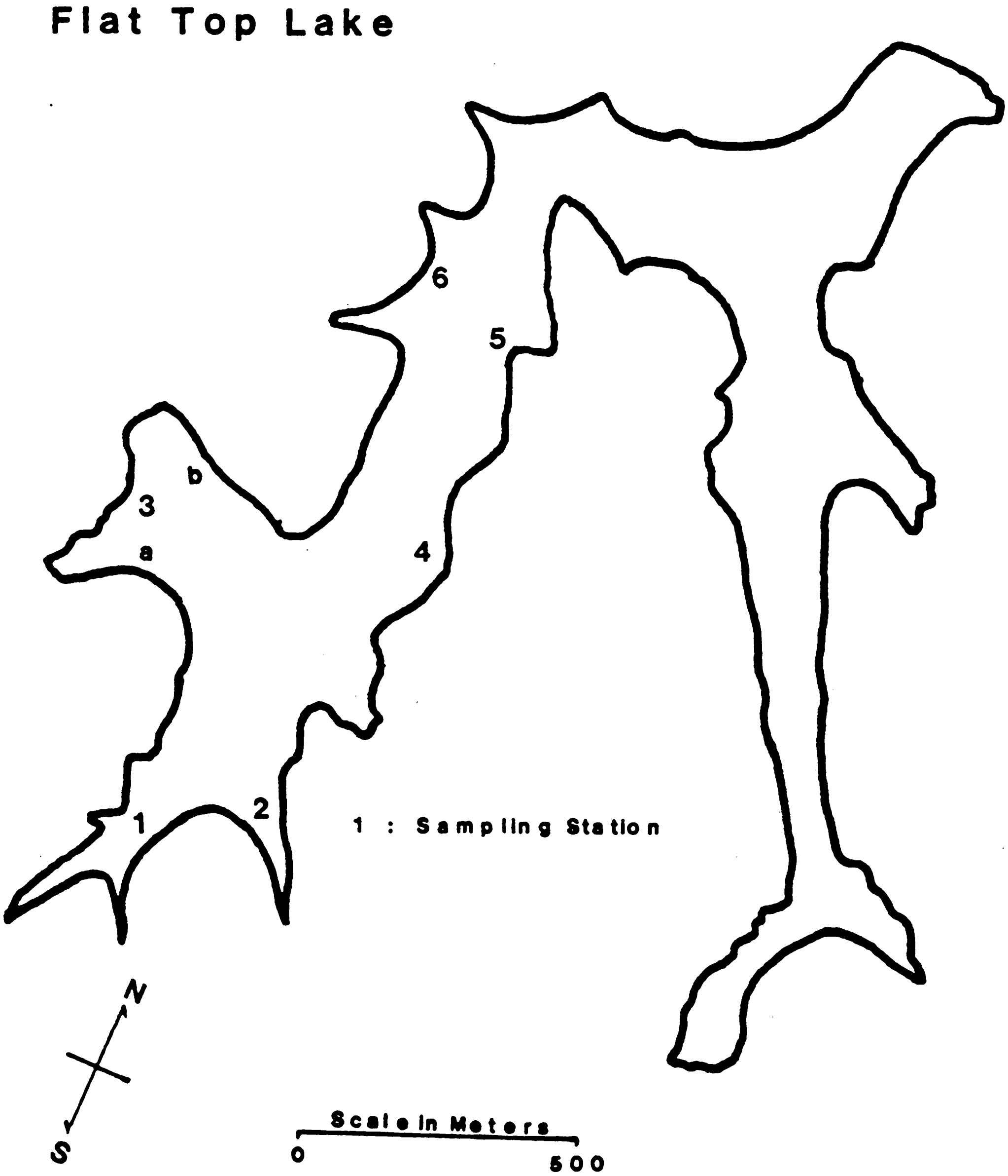
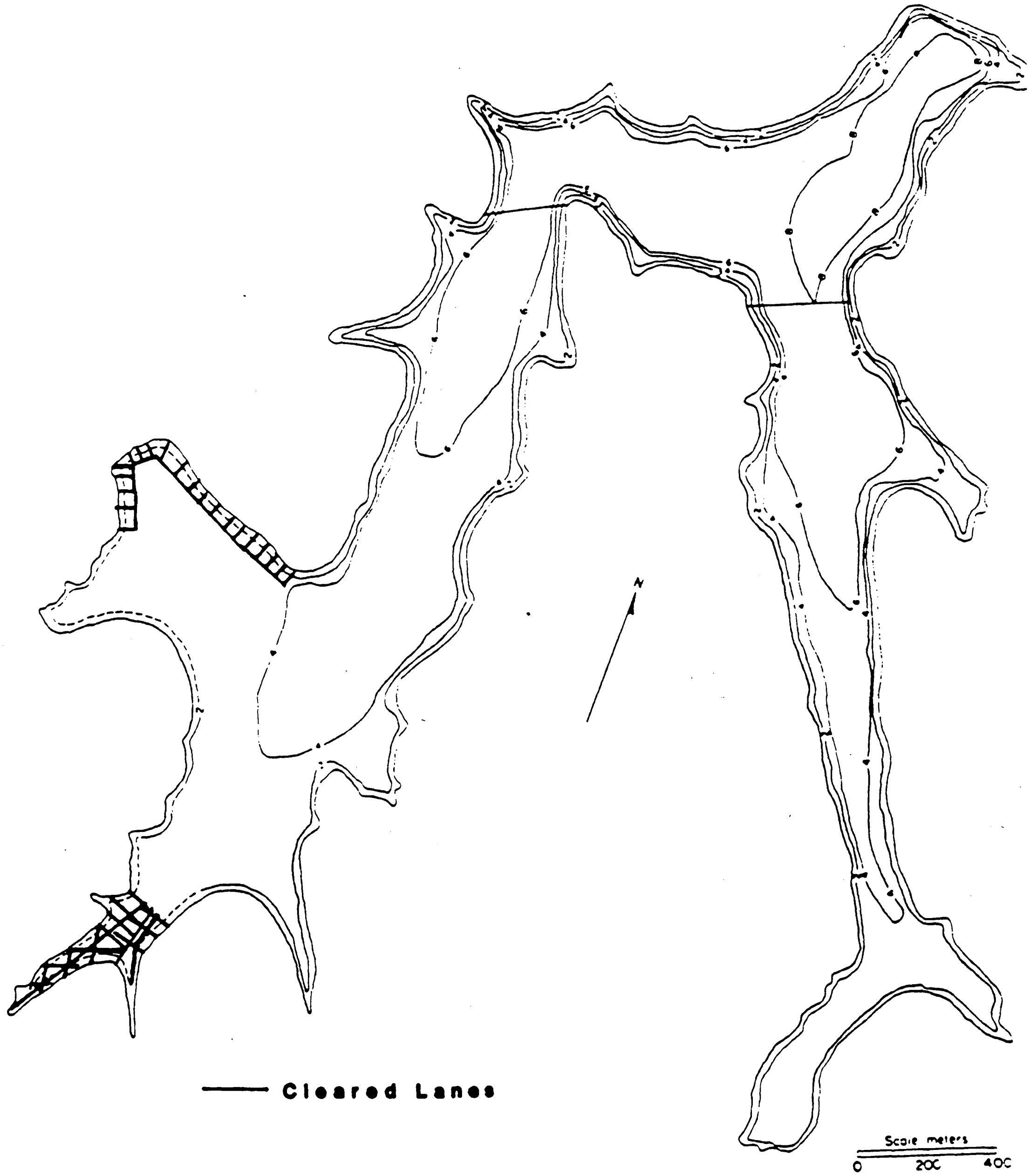
APPENDICES



Appendix Figure 1. Distribution of aquatic vegetation in Flat Top Lake, September-October, 1986.



Appendix Figure 2. Distribution of sampling stations in Flat Top Lake, June-September, 1987.



Appendix Figure 3. Patterns of experimental vegetation manipulation in Flat Top Lake, September, 1987.

Appendix Table 1. Age and growth of sport fishes in Flat Top Lake, for fish collected in Fall, 1986. Back-calculated mean lengths (mm) at age, with sample sizes in parentheses.

	Back-Calculated Mean Lengths (mm) at Age			
Age (yrs)	Largemouth Bass	Bluegill	Yellow Perch	Black Crappie
1	78 (67)	36 (82)	75 (46)	74 (21)
2	126 (55)	65 (66)	122 (44)	137 (19)
3	237 (13)	112 (38)	181 (14)	189 (8)
4	295 (13)	151 (12)	227 (14)	223 (6)
5	331 (12)	181 (5)	253 (11)	250 (4)
6	349 (7)	200 (4)	266 (5)	278 (3)
7	416 (2)	- -	296 (1)	- -

Appendix Table 2. Length-weight regression equations used to back-calculate live weights of ingested prey items (length in mm, weight in g). Carapace length for crayfish, total length for fish.

Length-Weight Regression Equations.

Crayfish

Carapace Length/Weight

$\text{Log}_{10}\ \text{Weight} = 2.910\ (\text{Log}_{10}\ \text{Carapace Length}) - 3.418$
$r^2 = 0.8172 \quad n = 924$

Carapace Length/Chelae Length

$\text{Log}_{10}\ \text{Carapace Length} = 0.7967\ (\text{Log}_{10}\ \text{Chelae Length}) + 0.4556$
$r^2 = 0.9045 \quad n = 279$

Bluegill

$\text{Log}_{10}\ \text{Weight} = 3.090\ (\text{Log}_{10}\ \text{Length}) - 4.903$
$r^2 = 0.9868 \quad n = 2841$

Black Crappie

$\text{Log}_{10}\ \text{Weight} = 3.119\ (\text{Log}_{10}\ \text{Length}) - 5.157$
$r^2 = 0.9969 \quad n = 76$

Bullhead

$\text{Log}_{10}\ \text{Weight} = 3.216\ (\text{Log}_{10}\ \text{Length}) - 5.265$
$r^2 = 0.9484 \quad n = 13$

Green Sunfish

$\text{Log}_{10}\ \text{Weight} = 3.075\ (\text{Log}_{10}\ \text{Length}) -4.829$
$r^2 = 0.9922 \quad n = 79$

Largemouth Bass

$\text{Log}_{10}\ \text{Weight} = 3.014\ (\text{Log}_{10}\ \text{Length}) - 4.927$
$r^2 = 0.9961 \quad n = 1250$

Yellow Perch

$\text{Log}_{10}\ \text{Weight} = 3.109\ (\text{Log}_{10}\ \text{Length}) - 5.157$
$r^2 = 0.9809 \quad n = 148$

Appendix Table 3. Shoreline lengths of sampling stations in Flat Top Lake, 1987.

Vegetation Density	Sampling Station	Shoreline Distance (m)
High (Experimental)	1	998
High (Reference)	2	854
High	3	1176
Reference	3A	608
Experimental	3B	568
Low	4	960
Low	5	632
Low	6	822

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