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The Effects of Macrophyte Structural Heterogeneity  
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Bass Foraging and Growth

presented by

Rahman David Valley

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Major professor

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**THE EFFECTS OF MACROPHYTE STRUCTURAL HETEROGENEITY AND FISH  
PREY AVAILABILITY ON AGE-0 LARGEMOUTH BASS FORAGING AND  
GROWTH**

**By**

**Rahman David Valley**

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## ABSTRACT

### THE EFFECTS OF MACROPHYTE STRUCTURAL HETEROGENEITY AND FISH PREY AVAILABILITY ON AGE-0 LARGEMOUTH BASS FORAGING AND GROWTH

By

Rahman David Valley

Age-0 largemouth bass (*Micropterus salmoides*; LMB), inhabiting vegetated lake areas, initially consume invertebrates until growing sufficiently large to consume more energetically-profitable fish (e.g., age-0 bluegill, *Lepomis macrochirus*; BG). Age-0 LMB success as piscivores may depend both on age-0 BG abundance and macrophyte assemblages, which can affect BG vulnerability to LMB. The widespread exotic macrophyte, Eurasian watermilfoil (*Myriophyllum spicatum*; EWM) typically increases macrophyte abundance and simplifies structure relative to native plant assemblages. Therefore, I hypothesized that: 1) age-0 LMB enjoy higher foraging success where plants are of moderate density (compared to dense), structurally heterogeneous (compared to EWM monocultures), and BG prey are abundant, and 2) age-0 LMB growth is higher in lakes dominated by native plants (compared to lakes dominated by EWM) and where age-0 BG prey are abundant. In an age-0 LMB foraging behavior experiment, dense plants and EWM monocultures significantly reduced LMB foraging success. In a multi-lake field study, EWM coverage did not significantly affect age-0 LMB growth. Macrophyte assemblages may have been sufficiently heterogeneous such that age-0 LMB could capture BG prey in all lakes. Age-0 BG prey abundance positively correlated with age-0 LMB growth. Overall, my data indicate that plant abundance and structure function in complex, scale-dependent ways to influence age-0 LMB foraging success.

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## INTRODUCTION

Largemouth bass (*Micropterus salmoides*; LMB) is a keystone species of north temperate lake food webs (Mittelbach et al. 1995, Power et al. 1996) and a popular sportfish. Therefore, understanding factors underlying LMB recruitment should promote effective management of both LMB populations and other features of lake ecosystems influenced by LMB. Mechanisms affecting recruitment of LMB are often size-dependent, such that rapid first year growth confers a survival advantage (see Garvey et al. 1998b for review). Specifically, larger age-0 LMB often enjoy higher overwinter survival than their smaller counterparts, due to greater energy reserves and reduced risk to predation (Garvey et al. 1998b).

First year growth of LMB and thus size entering winter is influenced by factors such as prey species composition and availability. Initially, age-0 LMB consume zooplankton and macroinvertebrates until they attain the size advantage needed to capture age-0 fish prey [typically age-0 bluegill (*Lepomis macrochirus*; henceforth BG) in north temperate lakes (Olson 1996) or age-0 shad (*Dorosoma* spp.) in reservoirs (Garvey and Stein 1998)]. Because fish prey are more energetically profitable than invertebrate prey, the shift to piscivory by age-0 LMB can be followed by rapid growth (Keast and Eadie 1985, Olson 1996, Garvey et al. 1998a). Together, the timing of the onset of piscivory, and the extent to which fish prey contribute to age-0 LMB diets once they are piscivorous, should determine in large part, age-0 LMB growth rates and recruitment.

Fish prey availability is often variable among systems and can affect the timing and degree of piscivory of age-0 LMB. Potential factors influencing fish prey availability include relative hatch dates of predator and prey (Miller and Stork 1984, Phillips et al.

1995), relative growth rates of predator and prey (Keast and Eadie 1985, Olson 1996), and total prey production (Miller and Stork 1984, Phillips et al. 1995, Garvey and Stein 1998).

In addition to prey fish size and abundance, physical habitat features, such as macrophyte structure, can affect LMB recruitment by mediating interactions between age-0 LMB and their fish prey. Theory predicts that an intermediate level of macrophyte abundance should produce maximum LMB growth (Crowder and Cooper 1979).

Numerous studies conducted on lakes and reservoirs (80-27,000 ha) have demonstrated that macrophyte coverage exceeding 10% of a system's total area promotes age-0 LMB abundance, presumably because macrophytes provide cover from predators of age-0 LMB (Durocher et al. 1984, Bettoli et al. 1992, Maceina 1996, Wrenn et al. 1996, Miranda and Pugh 1997). However, where total areal coverage of macrophytes exceeds 40-60%, low piscivory and/or poor growth by age-0 LMB commonly result (Colle and Shireman 1980, Bettoli et al. 1992, Maceina 1996, Wrenn et al. 1996, Miranda and Pugh 1997), presumably because visual and swimming barriers created by dense vegetation reduce the ability of LMB to forage successfully for fish prey (Glass 1971, Savino and Stein 1982, Anderson 1984). However, even within the 10-60% plant coverage range, the relationship between macrophyte coverage and LMB recruitment is highly variable within and among systems, such that a consistent optimal range of macrophyte coverage for LMB recruitment has not been identified. This relationship may vary, in part, because coarse measures of total vegetation abundance (such as percent areal coverage) do not represent the amount of critical edge (or patch) habitat that is consequential to LMB success (Annett et al. 1996, Dibble et al. 1996, Miranda and Pugh 1997).

Documenting the effects of macrophyte structural heterogeneity on LMB recruitment is important because invasive macrophyte species are now widespread throughout North America and fundamentally alter the nature of habitat structure. For instance, native macrophyte communities are structurally diverse; their patchy spatial distributions and mosaic of basal, medial, and canopy growth forms create numerous horizontal and vertical interstitial spaces (i.e., edge or habitat patches). Invasion by exotic macrophytes such as Hydrilla (*Hydrilla verticillata*) and Eurasian watermilfoil (*Myriophyllum spicatum*; henceforth EWM), reduce edge by forming extensive homogeneous monocultures (Madsen 1997). In particular, EWM grows rapidly, typically forming extensive homogeneous surface canopies that displace structurally-diverse native macrophytes (Madsen et al. 1991, Nichols et al. 1992). Plant biomass in EWM beds is partitioned towards the surface, thereby reducing sub-canopy light, oxygen, and pH (Titus and Adams 1979, Carpenter and Lodge 1986, Madsen 1997). As a result of the inhospitable foraging environment in the sub-canopy, trophic interactions may be restricted to the canopy where vegetation is extremely dense and interstitial spaces are few.

Despite the widespread occurrence of exotic macrophyte invasions, their effects on LMB recruitment are poorly understood. Furthermore, no studies have simultaneously evaluated the effects of macrophyte density, structure, and prey availability on age-0 LMB foraging and growth. Accordingly, I evaluated how macrophyte density, structure, and fish prey availability, affect age-0 LMB foraging success and growth at both small (aquaria) and large (multiple whole-lakes) scales. The small-scale experiment evaluated the relative effects of macrophyte density, structure,

and age-0 BG prey abundance on age-0 LMB foraging success. I hypothesized that age-0 LMB spend less time searching for prey and enjoy higher foraging success (i.e., higher attack and consumption rates) where plants are of moderate density (compared to high density), plants are structurally diverse (compared to EWM monocultures), and age-0 BG prey are abundant (compared to sparse). Furthermore, I expected high BG density to have a relatively small positive effect on LMB foraging success in high density plant treatments and EWM monoculture treatments, due to the inability of the LMB to detect and/or capture BG prey. In contrast, I expected BG density to have large effects on LMB foraging success in moderate density plant treatments and diverse structure treatments, due to the greater ability of the LMB to detect and/or capture prey. The multi-lake study assessed the generality of my experimental findings by evaluating age-0 LMB piscivory and growth along gradients of EWM coverage and age-0 BG prey abundance. I hypothesized that age-0 LMB piscivory and growth decline along a gradient of increasing EWM coverage. I also expected high age-0 BG prey abundance to have a relatively small positive effect on age-0 LMB piscivory and growth where EWM coverage was high. In contrast, I expected age-0 BG prey abundance to have large effects where EWM coverage was low.

## EXPERIMENTAL METHODS

*Treatments and Replication*—I used a 2x2x2 factorial design crossing EWM versus diverse plants, high versus moderate plant density, and high versus low BG density in 8 114-L rectangular glass aquaria in the laboratory. A preliminary power analysis indicated that at least 13 replicates would be needed to detect a large effect (i.e., 40%

difference between treatments,  $\beta = 0.20$ ) in any particular measured response. Therefore, every other day for 26 days, I conducted a complete set of replicates (i.e., 1 replicate per each of 8 treatments per trial day). Across trial days, each aquarium received at least 1 replicate of each treatment in random order. No more than 2 replicates of a given treatment were conducted in the same aquarium. Each aquarium contained one age-0 LMB foraging for age-0 BG (see “Fish” below).

*Experimental units*—Black construction paper was placed on three sides of each aquarium’s walls to confine the LMB’s field of view to within its experimental unit; the front wall remained open for observation (Figure 1). Small sponge-filters in each of the aquaria maintained both water quality and dissolved O<sub>2</sub> (approximately 7.5 mg/L). Although light intensity at the water’s surface ranged from 14.1 to 25.1  $\mu\text{ mol/s m}^2$  among aquaria, variability in light intensity did not bias results (see “Experimental Results”). Temperature remained constant at 22 °C.

*Plant characteristics*—I established plant treatments that differed according to structure and abundance by using plastic aquatic plants (manufactured by Second Nature Plantastics Plus, Oakland, NJ). Plastic foxtail plants that were 45.7 cm in length were modified to resemble EWM. Plants used in diverse native treatments resembled native plants commonly found in lakes, and differed in number and length (Table 1). I measured the volume of water displaced by each plant in order to hold plant volume constant in the EWM and diverse treatments (Table 1). To relate abundances of plants used in my experimental treatments to the field, I measured water volume displaced and dry weight of the real plants (dried at 105 °C for 48 h) that the plastic plants resembled. From these data, I estimated the “live biomass” equivalent of the plastic plants in each

treatment (Table 1). Estimated live biomasses represented by the plastic plants in experimental treatments were within the range of typical field values (Grace and Wetzel 1978). Eurasian watermilfoil plants were arranged uniformly on a 76 by 32 cm (5 mm mesh) metal grid. Plants in the diverse treatments were randomly assigned to uniform positions on a similar grid. The mosaic of vertical interstitial spaces present in native macrophyte beds in lakes was simulated in the aquaria by using plants of varying lengths. However, due to the small size of the aquaria, I could not simulate horizontal interstices (i.e., vegetation patches) that occur at spatial scales larger than those represented by my experimental aquaria.

*Fish*–Age-0 LMB and age-0 BG were collected from Big Crooked and Camp lakes (Kent Co., MI) and maintained in the laboratory. Largemouth bass were fed small shiners (*Notropis* spp.) until they were approximately 75-90 mm total length (TL). Once LMB reached the appropriate size, each was transferred to separate experimental aquaria. Each LMB remained in the same aquarium throughout the 26 d duration of the experiment. If a LMB became diseased or chronically inactive (two starved LMB never responded to the presence of BG prey), it was replaced by a LMB of similar size from the laboratory stock. For each trial, four BG were randomly assigned to each high BG density treatment and two BG were randomly assigned to each low BG density treatment. Bluegill densities were similar to prey densities used in other LMB foraging experiments (Savino and Stein 1982, Anderson 1984, Schramm and Zale 1985, McMahon and Holanov 1995). Because of the fragility of small age-0 BG, I obtained an estimate of BG size by measuring the TL of a subsample of BG ( $n = 10$  per trial day) chosen randomly throughout the experimental set up.

*Procedure*—Forty hours before a trial, the appropriate plant structure was placed into each aquarium. At the same time, a clear plexiglas divider was placed into the middle of the aquarium, confining the LMB to one side of the aquarium. On each trial morning, BG were selected from the stock and were either sacrificed and measured or placed into one of eight isolation chambers that were numbered according to the aquarium into which each chamber would be placed. Chambers were placed on the side of the aquarium without the LMB but directly adjacent to the divider such that both LMB and BG were visually aware of each other's presence. After 10 min, the BG in the first aquarium to be observed were released from the isolation chamber into the aquarium side opposite from the LMB. After 20 seconds, the divider was lifted and the trial began. Aquaria were observed sequentially; therefore, time in the isolation chambers ranged from 10 to 120 minutes. To account for differences in acclimation periods, I alternated the order in which aquaria were observed each trial day.

Observational methods were similar to those described by Anderson (1984). Briefly summarized, from behind a blind, I recorded LMB position in the aquarium and foraging behavior on a voice tape recorder, noting the time spent by the LMB searching for prey and the success or failure of each capture attempt. When possible, the positions of the BG were also noted. At the end of each trial day, the tape was replayed and a stopwatch was used to determine when attacks occurred and the success of each attack. The amount of time a LMB remained motionless (i.e., at the very beginning of the trial or when handling a prey; typically < 10 s) was subtracted from total search times. Each trial was terminated after 10 minutes, or earlier, if all BG were captured.

*Statistical Analyses*—Data were analyzed using SAS version 6.12 (SAS Institute Inc. 1990). I quantified LMB foraging success by evaluating the effects of plant density, plant structure, and BG density on the following LMB response variables: 1) time to first attack, 2) attack rate (number of attacks per min of search), 3) capture success (capture:attack ratio), 4) time to first consumption, and 5) total consumption (i.e., total number of BG consumed). A three-way ANOVA (type III sums of squares) was used to evaluate all response variables except attack rate. Due to the extreme skew and heterogeneous variances among treatments associated with attack rate (O'Brien test for unequal variances  $p = 0.05$ ), I evaluated the effect of each main factor (i.e., plant density, plant structure, and bluegill density) on attack rate with 3 one-way nonparametric Wilcoxin rank-sum tests. Although I could not statistically conclude the absence of significant interactions between factors on attack rate, ANOVA results from the other four response variables suggest interactions were not common in the experiment (see "Experimental Results"). Capture success values were arcsine square root ( $x$ ) transformed and times elapsed prior to the first attack and consumption were  $\log_e(x)$  transformed to normalize distributions and homogenize variances. If interaction terms were not at least marginally significant ( $p < 0.10$ ), they were dropped from each model.

## EXPERIMENTAL RESULTS

Because of the unanticipated loss of replicates (i.e., diseased or chronically inactive LMB), I completed 9-11 replicates per treatment. Largemouth bass grew approximately 1 mm per week, reaching 83-92 mm TL by experiment's end. Mean TL of BG (computed each trial day) ranged from 20 to 27 mm TL (coefficient of variation

ranged from 3 to 17). On average, BG lengths were 29% of LMB TL during the first trial and 27% during last trial (mean across all trials = 30%). No effects of date or aquarium/LMB/light intensity were detected for any of the measured variables (two-way ANOVA  $p > 0.10$ ); therefore, all trials were considered independent.

*Behavioral Observations*—Largemouth bass searched for prey by swimming in short quick movements, frequently changing direction and eye position. In the diverse plant treatments, LMB often used the entire depth of the aquarium to search for prey. In contrast, in the EWM treatments, LMB stayed below the canopy (i.e., lower half of the aquarium) to search for prey. Vegetation in the EWM treatments often obstructed the mobility of the LMB when it attempted to swim through the canopy and attack a BG. An attack was characterized by a LMB stopping its search abruptly, slowly stalking the detected prey, and finally making an accelerated movement towards the prey. Each accelerated movement was considered one attack. All BG that were detected by a LMB were attacked. Largemouth bass resumed aggressive search behavior shortly after ingesting a prey. Bluegill response to predation threat varied within treatments. Most BG observed (80%; evenly distributed among treatments) remained motionless in vegetation as the LMB searched. However, some (20%) BG did not attempt to hide from the LMB (i.e., “naive” BG) and swam into open water (i.e., open spaces in the diverse treatment or below the canopy in the EWM monoculture treatment). All BG that swam below the canopy in EWM treatments were quickly detected and attacked by the LMB. However, naive bluegill in diverse treatments were not detected as quickly as in EWM treatments, because vegetation patches in the diverse treatments often obstructed the LMB’s view of a BG in open water.

*Time to first attack*—Two replicates were omitted from this analysis because no BG were attacked. Both trials with no attacks were the EWM monoculture, high plant density, and low BG density treatment. Time elapsed prior to first attack varied significantly among treatments (ANOVA,  $p = 0.04$ ). As expected, time elapsed prior to first attack was greater in high plant density than moderate plant density treatments (ANOVA, main effect  $p = 0.02$ ; Figure 2A). Time elapsed prior to first attack was marginally higher in low BG than high BG density treatments (ANOVA, main effect  $p = 0.09$ ; Figure 2A). Contrary to my expectations, time elapsed prior to first attack did not vary significantly with plant structure (ANOVA,  $p = 0.49$ ; Figure 2A). Furthermore, ANOVA did not detect any significant interactions ( $p > 0.10$ ), thereby failing to support my hypothesis that BG density would have an effect on search times in moderate plant density treatments and diverse plant treatments but no effect in high plant density treatments and EWM monoculture treatments.

*Attack Rates*—Wilcoxin rank-sum tests indicated significant effects of plant structure ( $p = 0.005$ ) and plant density ( $p = 0.01$ ). As expected, LMB exhibited higher attack rates in treatments with moderate density plants and diverse plants (Figure 3). Surprisingly, BG density did not have a significant effect on attack rates by LMB ( $p = 0.25$ ; Figure 3).

*Capture Success*—Capture success (capture:attack ratio) averaged  $34.6 \pm 1.6\%$  and did not vary among treatments (ANOVA;  $p = 0.98$ ). In other words, each BG that was attacked had equal probability of capture, regardless of treatment.

*Time to first consumption*—Fifteen replicates were omitted from this analysis because no BG were consumed. Largemouth bass consumed zero BG in 11 of the 45 EWM monoculture replicates and only 4 of the 38 diverse plant replicates. The time to first consumption varied significantly among treatments (ANOVA,  $p = 0.006$ ). As expected, time elapsed prior to first consumption was greater in high plant density than in moderate plant density treatments (ANOVA, main effect  $p = 0.004$ ; Figure 2B) and greater (although only of marginal statistical significance) in low BG than high BG density treatments (ANOVA, main effect  $p = 0.06$ ; Figure 2B). Contrary to my expectations, time elapsed prior to first consumption did not vary significantly with plant structure (ANOVA,  $p = 0.36$ ; Figure 2B). Contrary to my expectations, no interactions occurred ( $p > 0.12$ ).

*Total Consumption*—The total number of BG eaten during the trials differed among treatments (ANOVA,  $p < 0.001$ ) and ranged from 0 to 4 (the maximum number of BG in the high BG density treatments). In the high BG density treatments, LMB consumed all four BG in 9 of the 42 replicates. In the low BG density treatments, LMB consumed both BG in 13 of the 41 replicates. Analysis of variance detected significant main effects of plant density ( $p = 0.02$ ) and BG density ( $p < 0.001$ ) and a nearly significant effect of plant structure ( $p = 0.06$ ). As expected, LMB consumed more BG in moderate plant density, diverse plant, and high BG density treatments (Figure 4). Again, contrary to expectations, no interactions were significant ( $p > 0.19$ ).

## FIELD METHODS

*Study lakes*—To assess the generality of my experimental results, I sought to evaluate the effects of plant density, plant structure, and age-0 BG prey availability on age-0 LMB diet and growth through a multi-lake field study. Age-0 LMB were sampled in multiple (five in 1998 and six in 1999) mesotrophic lakes in southern Michigan, each with a history of EWM infestation. Four lakes (Bass-1999, Big Crooked, Camp, Lobdell) were treated with herbicides (including 5-7 ppb fluridone) and three lakes (Bass-1998, Big Seven, and Heron) received no macrophyte management and remained infested with EWM, thereby establishing a gradient of EWM coverage among lakes (Table 2).

*Macrophyte surveys*—Percent cover of macrophytes during August 1998 and 1999 was determined using the point-intercept method (Madsen 1999). Briefly summarized, this entailed overlaying a grid of 150-250 uniformly spaced points (~ 50-100 m apart) onto each lake map. Using a global positioning system, points were located, depth was recorded, and species presence/absence was determined using visual inspection and/or a double-headed rake thrown from the boat. The outer edge of the littoral zone was defined as the greatest depth at which macrophytes typically occurred in each lake. Plant coverage *within* the littoral zone was used to evaluate LMB responses, even though many prior studies have used measures of *total* areal coverage of plants to evaluate LMB responses. Gradients of plant/EWM coverage within the littoral zone are likely to affect LMB and BG interactions and measures of total areal coverage may not reflect differences in littoral zone structure. For example, relatively deep lakes have relatively small littoral zones; therefore measures of total plant coverage will be inherently lower in

deep lakes compared to shallow lakes, even if plants are extremely dense within the littoral zone of deep lakes.

*Largemouth bass and bluegill sampling*—During 1998, age-0 LMB and age-0 BG (age estimated from length distributions) were sampled in each of 5 lakes bi-weekly from late June (except for Lobdell L. in 1998 where LMB were not sampled until 21, July) through late August using both a 10 by 1.8-m (4-mm mesh) bag seine (3 sites per lake; 20 to 30 m length pulled parallel to shore; 0 to 1.5-m depth) and a 18.3 by 2.4-m (4-mm mesh) purse seine [3 sites per lake (same general area as bag seine sites); 1 to 2 m depth]. Each site was vegetated with submerged and/or floating leaf macrophytes and sites were evenly dispersed around each lake. Because the size of age-0 LMB collected by the 2 gears did not differ (sequential Bonferroni adjusted t-tests  $p > 0.05$ ; 12 of 15 comparisons), I used largemouth bass from both gears to evaluate growth. However, estimates of relative abundance were generated for LMB captured in bag seines only because catch per effort (CPE; No. per  $m^2$ ) of age-0 fish captured with the purse seine did not correlate with CPE of the bag seine ( $r = 0.30$ ) and because the purse seine caught relatively few age-0 LMB. In 1999, I sampled age-0 LMB and age-0 BG solely with the bag seine (6 sites per lake) on a monthly basis, from late June to late August. All age-0 LMB and age-0 BG captured each summer were preserved in 95% ethanol. Age-0 LMB were also sampled in late September 1999 using both the bag seine and electrofishing (120 volts pulsed-DC). However, size distributions generated from both gears indicated size-selectivity by both gears (Figure 5).

*Largemouth bass growth*—All LMB preserved (n = 1230) were later measured to the nearest millimeter TL and counted. A subset of LMB (n = 390; randomly pooled from all lakes) was measured, dried at 60°C for 72 hours, and weighed to the nearest milligram to develop a length-dry weight regression. To draw inferences regarding age-0 LMB growth across lakes and years, I computed an absolute growth rate using the mean dry mass of age-0 LMB captured in each lake during the first and last sampling period (typically late June through late August) in each year, divided by the number of growing degree days (gdd) that elapsed between these sampling dates in each year such that:

$$\text{absolute growth} = \frac{g(\text{final}) - g(\text{initial})}{\text{gdd}} \text{ where}$$

$$\text{gdd} = \text{cumulative gdd}(\text{final}) - \text{cumulative gdd}(\text{initial}) \text{ and}$$

$$\text{gdd} = \left( \frac{\text{maximum temperature} - \text{minimum temperature}}{2} \right) - 50$$

Growing degree day data were obtained from National Weather Service 1<sup>st</sup> order climate stations closest to the study lakes (Grand Rapids for Bass, Big Crooked, and Camp lakes and Detroit for Big Seven, Lobdell, and Heron lakes).

*Largemouth bass diets*—Gut contents from LMB were analyzed in a stratified manner such that all sizes of age-0 LMB captured in each particular lake on each sampling date were represented equally. A maximum of five LMB stomachs from each of three size classes (maximum TL – minimum TL / 3; calculated for each lake and each date) was analyzed per lake and date. Where possible, equal numbers of LMB were analyzed from each seine site within each lake. Stomach contents were identified, where possible, to family for macroinvertebrates and copepod zooplankton, and to genus for

cladoceran zooplankton, and measured using a microscope equipped with a drawing tube and digitizing tablet. Biomass of stomach contents was estimated by recording the appropriate body dimensions (e.g., head width or body length) and using length-dry mass regressions that corresponded to the body dimension measured (G.G. Mittelbach, Michigan State University, Kellogg Biological Station, unpublished data, R.D. Valley unpublished data). For the fish consumed that could be measured, I regressed the standard length (SL) of fish prey against LMB TL in order to estimate the SL and corresponding mass of prey fish ingested by other LMB that were too digested to be measured. Regressions were developed for both 1998 and 1999 even though 95% confidence intervals of both regression slopes overlapped (see “Field Results”). I characterized the degree of piscivory by first calculating the percent of LMB stomachs in each of the three size classes that contained at least one fish. Next, using these percentage values and the abundance of LMB in each size class, I calculated a weighted mean percent of LMB that had consumed at least one fish across the three size classes for each lake on each date. Finally, I averaged the daily mean value across sampling dates within each lake to characterize piscivory on a seasonal basis.

*Prey availability*—Because age-0 BG are the predominant fish prey of age-0 LMB in Michigan lakes (Olson 1996, this study; see “Field Results”), patterns of age-0 LMB diets were related to availability of vulnerable BG. All age-0 bluegill captured in the seines were preserved in 95% ethanol and later measured. Mean CPE (bag seine only) of vulnerable BG (defined as individuals  $\leq 40\%$  of the mean LMB TL; Lawrence 1958) was calculated for each lake on each date and averaged across sampling dates within each lake to characterize prey availability on a seasonal basis. Because age-0 BG were not

inshore by the first sampling period in 1999 in any of the lakes, this date was excluded from the analysis of relative density of BG prey.

*Statistical analyses*—Data were analyzed using SAS version 6.12 (SAS Institute Inc. 1990). Regression analysis was used to evaluate relationships between response variables and effect variables. Seasonal means for some response variables (e.g., percent piscivory and prey availability) for each lake were computed for 1998 and 1999 and values from lakes that were measured in both years were averaged across years. An exception was Bass L. where 1998 and 1999 were treated as independent in my analyses because this lake was not managed for EWM in 1998 but was treated with herbicides in 1999 (Table 2). In all, seven data points were used in the regression analyses: one point for each lake except Bass L., for which two were used. Variable distributions that were highly skewed were  $\log_e(x)$  transformed. Rejection criterion was set at  $\alpha = 0.05$ .

## FIELD RESULTS

*Macrophyte surveys*—Fluridone among other herbicides greatly reduced EWM cover in managed lakes while not reducing native plant cover or plant diversity (Madsen et al. *in press*). Total lake coverage of macrophytes (i.e., percent of sampled points with plants) varied from 37 to 84% but was similar between years (Table 2). Although not statistically significant, total plant coverage tended to decrease with increasing mean depth (regression,  $r^2 = 0.35$   $p = 0.16$ ; Table 2). Total littoral coverage of macrophytes was similar among lakes and years, ranging from 75 to 99% (mean = 88%; Table 2). Therefore, I did not evaluate whether plant coverage had an effect on LMB piscivory and growth. Despite the large range in EWM littoral coverage across lakes, native

macrophytes were common in all lakes (ranging from 62-99% littoral coverage; Table 2). Furthermore, extensive homogeneous beds of EWM did not typify any of the study lakes. Rather, EWM beds were often patchy with native plants interspersed between EWM patches (R.D. Valley personal observation).

*Effects of Eurasian watermilfoil and bluegill prey availability on age-0*

*largemouth bass growth*—Densities of age-0 LMB captured in bag seines ranged from 0.018-0.037 LMB per m<sup>2</sup> (mean = 0.027) in 1998 and 0.007-0.028 LMB per m<sup>2</sup> (mean = 0.019) in 1999 (Table 2). Because relative abundance of age-0 LMB did not differ greatly among my lakes (Table 2), I did not evaluate the relationship between age-0 LMB relative density and EWM coverage or prey density. Age-0 LMB size in late August was very similar between years [ranging in 1998 from 55 to 73 mm TL (mean = 62 mm TL); ranging in 1999 from 51 to 76 mm TL (mean 63 mm TL); Table 2]. Size of LMB collected with the bag seine in late September 1999 strongly correlated with LMB size in late August (regression,  $r^2 = 0.95$ ,  $p = 0.001$ ; mean size in late September 1999 = 66 mm TL). Size of LMB collected by electrofishing in late September 1999 also correlated with LMB size in late August but displayed a weaker relationship (regression,  $r^2 = 0.79$ ,  $p = 0.04$ ; mean size in late September 1999 = 74 mm TL; see Figure 5 for LMB distribution comparisons for both gears).

Surprisingly, EWM coverage could not explain variation in age-0 LMB absolute growth (regression,  $p = 0.62$ ; Figure 6). Both total age-0 BG density and the density of vulnerable age-0 BG varied considerably across lakes in 1998 and 1999 (Figure 7). Indeed, mean CPE of vulnerable BG explained a considerable amount of variation in LMB absolute growth rate (regression,  $r^2 = 0.61$ ,  $p = 0.04$ ; Figure 8). However, contrary

to my expectations, EWM coverage could not explain variation in the residuals from the above regression ( $p = 0.88$ ). In general, several size classes of age-0 BG were vulnerable in lakes where age-0 LMB grew relatively rapid. In contrast, age-0 LMB generally grew slowly where age-0 BG were too large or numerically few.

*Largemouth bass diets*—Of the 627 age-0 LMB diets analyzed, 113 of them contained fish prey. Of the 65 fish prey that could be identified, 38 (59%) were BG. Most of the other fish consumed were shiners. Largemouth bass initially consumed zooplankton and macroinvertebrates (mostly chironomids, and ephemeropteran and zygopteran nymphs), and then shifted to a diet of mostly fish at approximately 60-80 mm TL (Figure 9). Fish constituted the majority of prey biomass in LMB diets at sizes > 60 mm TL and occurrence of piscivory averaged 27% for LMB greater than this size. Fishless stomachs of LMB > 60 mm TL were typically empty, indicating that these LMB were specifically targeting fish as their prey. The size of fish consumed by age-0 LMB in 1998 and 1999 could be predicted by the following regression equations, respectively: fish prey SL =  $2.52 + 0.24 * \text{LMB TL}$  ( $r^2 = 0.52$ ;  $p < 0.001$ ); fish SL =  $-1.27 + 0.25 * \text{LMB TL}$  ( $r^2 = 0.47$   $p < 0.001$ ). Largemouth bass consumed fish prey that were on average 31% of their length.

As expected, piscivory was important for rapid growth of age-0 LMB. Mean percent occurrence of piscivory positively correlated with LMB absolute growth rate (regression,  $r^2 = 0.89$ ,  $p = 0.002$ ; Figure 10A). Largemouth bass exhibited relatively high growth in lakes where fish were relatively common in their diet. Furthermore, density of vulnerable BG prey positively correlated with mean percent occurrence of piscivory

(regression,  $r^2 = 0.70$ ,  $p = 0.02$ ; Figure 10B). Again, EWM coverage could not explain these residuals (regression,  $p = 0.46$ ).

## DISCUSSION

Integrating results from studies at multiple scales can lead to holistic understanding of ecosystem structure and function (Frost et al. 1988, Power et al. 1996, Stein et al. 1996). Accordingly, I combined both experimental and comparative approaches to evaluate the relative effects of macrophyte abundance, macrophyte structure, and fish prey availability on age-0 LMB foraging and growth. Despite the potential importance of these three factors, no studies have explored their relative effects on LMB recruitment. By mechanistically evaluating how habitat structure and prey availability affect age-0 LMB foraging success, my experiment provided a predictive framework for my field comparison. In turn, my field comparison explored the generality of my experimental results and identified patterns at the scale most relevant to managers. Below, I compare results both from the experiment and field study to evaluate the relative effects of macrophyte density, macrophyte structure, and fish prey availability on age-0 LMB foraging and growth.

*Effect of macrophyte density on age-0 LMB foraging and growth*—Dense macrophytes can reduce the ability of LMB to forage successfully for fish. Similar to previous experimental studies with juvenile and adult LMB (Glass 1971, Savino and Stein 1982, Anderson 1984, Gotceitas and Colgan 1987, Hayse and Wissing 1996), in my experiment, dense macrophytes lengthened LMB search times, and reduced their attack and consumption rates. Dense vegetation in my experiment reduced interstitial spaces

and created numerous visual and swimming barriers to the LMB. As a result, prey were not often encountered, and thus not often attacked or consumed in the high plant density treatment. Furthermore, similar to other studies (Glass 1971, Savino and Stein 1982, Anderson 1984), I did not detect effects of plant density on prey capture success by LMB (but see Gotceitas and Colgan 1987). Rather, foraging success by age-0 LMB depended primarily on the ability of LMB to locate prey. In my field study, I could not adequately determine whether age-0 LMB piscivory and growth were negatively related to dense cover of littoral macrophytes, because littoral macrophyte coverage was consistently high among my lakes (ranging 74-99% cover). In addition, no prior field studies have evaluated the effect of littoral plant coverage on LMB recruitment. However, previous field studies have demonstrated lower piscivory and/or growth by age-0 LMB where macrophytes (mostly exotics; e.g., EWM and Hydrilla) are relatively dense (i.e., > 40-60% total areal coverage; Colle and Shireman 1980, Bettoli et al. 1992, Miranda and Pugh 1997, Maceina 1996). Nevertheless, measures of total areal coverage by previous investigators may or may not have reflected differences in littoral macrophyte coverage within/among their system(s). Therefore, large-scale effects of plant density on LMB recruitment remain unclear.

*Effect of macrophyte structure on age-0 LMB foraging and growth*—In addition to high macrophyte density, homogeneous macrophyte structure also may reduce LMB foraging success and growth. However, the effects of macrophyte structure on LMB have been less well studied (Dibble et al. 1996). In my experiment, both attack and consumption rates were lower in EWM monoculture treatments compared to diverse, native plant treatments. Age-0 LMB could more easily access BG prey in diverse, native

plant treatments compared to EWM monoculture treatments, due to relatively numerous interstitial spaces in the native plant treatment. Although search times did not significantly differ between EWM and native treatments in my experiment, my experimental set-up did not mimic the harsh environment (i.e., low light, O<sub>2</sub>, and pH) of EWM sub-canopies that has been documented in infested lakes (Titus and Adams 1979, Carpenter and Lodge 1986, Madsen 1997). I hypothesize that in EWM-infested lakes, age-0 LMB are often forced to forage within EWM canopies (rather than below, as LMB did in my experiment) where interstitial spaces are few, and thus experience higher prey search costs than in diverse plant assemblages.

In the field study, given the large gradient of EWM cover among the lakes (8-92%), I expected LMB to eat fish less frequently and grow more slowly in lakes with high EWM coverage. However, age-0 LMB piscivory and growth did not significantly correlate with EWM coverage. The lack of a negative effect of high EWM coverage on age-0 LMB piscivory and growth may be related to the patchy distribution of EWM in reference lakes as opposed to the homogeneous monocultures that my experiment simulated. As a result of patchy EWM growth and the high frequency of native plants in the reference lakes, moderate degrees of structural heterogeneity (and thus favorable foraging environments for age-0 LMB) were likely present among all study lakes. Eurasian watermilfoil has been present in many lower MI lakes since the early 1960's (Coffey and McNabb 1974). Apparently, EWM's aggressive behavior declines through time, on the order of 10 to 15 years (Carpenter 1980, Smith and Barko 1990, Engel 1995). Perhaps this explains why I did not see extensive homogeneous monocultures of EWM, and a corresponding negative effect on age-0 LMB.

Other studies support my experimental results by demonstrating high foraging success by multiple age classes of LMB in habitats with numerous interstitial spaces (Engel 1987, Smith 1993, Hayse and Wissing 1996). Patchy, heterogeneous macrophytes may maintain a balance between LMB and BG populations by providing refuge for fewer small BG than is provided by large homogeneous areas of vegetation. When refuge patches become overly crowded, juvenile (including age-0) BG are forced to search for new refuge areas, and thus become vulnerable to predation by LMB (Hayse and Wissing 1996). As a result, both LMB and BG may experience high growth rates in patchy, heterogeneous macrophyte assemblages. In contrast, poor LMB and BG size structure is common in lakes dominated by monocultures of invasive macrophyte species such as EWM (Engel 1995, Olson et al. 1998, Unmuth et al. 1999).

Despite the potential importance of macrophyte heterogeneity for LMB production, both conceptual and quantitative models that predict LMB production as a function of macrophyte structure do not exist and require further exploration at both whole-system and experimental scales. Coarse measures of total macrophyte coverage that are commonly used may not accurately measure structural heterogeneity and may inadequately characterize habitat perceived by LMB (Annett et al. 1996, Dibble et al. 1996, Miranda and Pugh 1997). Alternatively, explicit measures of structure (i.e., number, size, surface area, or spatial arrangement of vegetation patches, or macrophyte species composition and distribution) may provide greater insight into the relationship between habitat structure and LMB recruitment (Dibble et al. 1996, Weaver et al. 1997).

*Effect of fish prey availability on age-0 LMB foraging and growth*—In addition to macrophyte effects on LMB population dynamics, factors that influence prey fish size and abundance may affect age-0 LMB foraging and growth. However, surprisingly, BG density did not have a large effect on LMB foraging success in my experiment. The small size of the aquaria may have limited my ability to create contrasts in BG prey availability that may be present in lakes. Indeed, CPE of vulnerable age-0 BG was highly variable in the study lakes and, as expected, BG prey availability and piscivory by age-0 LMB had a positive effect on LMB growth in the field study. Age-0 LMB grew relatively slowly if fish were not present in their diets. Olson (1996) also found a high correlation between age-0 LMB piscivory and growth in Michigan lakes. However, compared to my lakes, frequency of piscivory by age-0 LMB was generally higher in Olson's lakes and LMB switched to piscivory at a smaller size (50 mm TL compared to 60 mm TL in my lakes in 1998 and 70 mm TL in 1999), suggesting length at diet shift to fish by age-0 LMB varies among lakes and over time.

Catch per effort of vulnerable BG was highly variable among the study lakes. Factors that could contribute to high variability in CPE of vulnerable BG include those that influence age-0 BG size: 1) early spawning of LMB (relative to BG), 2) slow growth of age-0 BG, 3) fast growth of age-0 LMB, and those that also influence age-0 BG abundance: 4) long spawning duration of BG (affects both abundance and size), and 5) high total reproductive output by adult BG. Although I could not rigorously evaluate the relative contribution of these factors to the observed variability in the CPE of vulnerable BG, factors 3, 4, and 5 appear especially important.

**Age-0 LMB growth:** Although cause and effect are unclear, my data suggest age-0 LMB growth positively influenced BG vulnerability. Similar to results reported by Olson (1996), as fish became increasingly common in their diet, age-0 LMB grew more rapidly and additional size classes of BG became vulnerable (e.g., Big Crooked and Camp lakes). In contrast, piscivory and growth by age-0 LMB was relatively low in Heron L. despite a relatively high CPE of small (although not vulnerable) age-0 bluegill (i.e., 25-30 mm TL) during both 1998 and 1999. Competition for macroinvertebrate prey with the relatively abundant juvenile BG (40-120 mm TL) that were present in Heron L. (R.D. Valley and M.T. Bremigan unpublished data) may explain why age-0 LMB were unable to gain the necessary size advantage to consume age-0 BG and thus grow rapidly Heron L. (Olson et al. 1995).

**Bluegill spawning duration:** Variability in BG spawning duration among my study lakes may also explain variability in the production of vulnerable BG. The appearance of small age-0 bluegill late in the season (late August) in some lakes (e.g., Big Crooked, Camp, and Heron lakes in 1998 and 1999) was indicative of a protracted spawn. Small age-0 BG were not present in seine hauls during late summer 1998 and 1999 in Bass L., where age-0 LMB growth was poor in both years, indicating BG spawned over a relatively short time period in this lake.

**Reproductive output by adult BG:** My data also suggest that differences in total reproductive output by adult bluegill among lakes may explain variability in age-0 BG prey availability. This variability in age-0 BG CPE did not appear driven by predation intensity by juvenile and adult LMB because predator density was highest in lakes where age-0 BG abundance was highest (e.g., Big Crooked, Camp, and Heron lakes; S.M.

Hanson and M.T. Bremigan unpublished data). Rather, adult BG size-structure may play a large role in determining both BG spawning duration and total reproductive output. Generally speaking, parental male BG provide care for eggs deposited by one or more size-selective females (Gross 1980, 1982). Brood size and nest success positively relate to the amount of fanning and guarding care parental males provide (Bain and Helfrich 1983, Coleman et al. 1985, Claussen 1991). In populations dominated by relatively small BG (e.g., BG < 150 mm TL), relatively few BG fry may be produced over a short period of time because energetic constraints restrict the amount and duration of parental care put forth by small males (Gross 1980, Coleman and Fischer 1991, Wiegman and Baylis 1995). Furthermore, small female BG may produce fewer eggs over a relatively short period of time compared to their larger counterparts (Gross 1980, Coleman et al. 1985). Small clutches of eggs deposited in male-occupied nests increase the probability that males will abandon their nests (Claussen 1991, Coleman and Fischer 1991). In fact, Gross (1980) demonstrated the importance of adult body size for reproduction by observing a 50% reduction in BG fry production as a result of only a 6% reduction in adult body size. Therefore, BG populations dominated by relatively small individuals may produce relatively few BG fry due to their short spawning seasons. In contrast, the protracted spawning seasons and high BG fry production that appear characteristic of BG populations with larger individuals may positively influence age-0 BG prey availability to age-0 LMB.

I explored (post hoc) whether adult BG size could indeed explain variation in the abundance of late-hatched (i.e., vulnerable) BG in the study lakes. Data from spring electrofishing surveys conducted in the study lakes during spring 1998 and 1999 were

used to explore this hypothesis. Adult BG body size was characterized as the 90th percentile total length. All BG < 25 mm TL in late August were assumed to belong to a late-hatched cohort because length of the first hatched cohort of BG in late August is typically 30-40 mm in north temperate lakes (Breck 1993, Cargnelli and Gross 1996). Indeed, adult BG body size positively correlated with the CPE of late hatched BG ( $r^2 = 0.61$   $p = 0.04$ ; Figure 11), supporting the hypothesis that adult BG size structure affects age-0 BG prey production.

The relative effects of age-0 LMB growth, protracted BG spawning seasons, and BG reproductive output on CPE of vulnerable BG may vary among lakes. For example, each factor appeared important for BG prey availability in Big Crooked and Camp lakes. Rapid LMB growth, protracted BG spawning seasons, and high total reproductive output by BG appeared to contribute to high availability of vulnerable BG in Big Crooked and Camp lakes. In Heron L., slow age-0 LMB growth seemed to negatively affect vulnerable BG availability. In Bass L., the absence of a protracted spawn by BG may have negatively affected vulnerable BG availability. Finally, in Big Seven and Lobdell lakes, BG apparently did not spawn successfully, and thus vulnerable BG availability was low.

## SUMMARY

Together, my experiment and field study demonstrated that macrophyte density, macrophyte structure, and BG prey availability can all affect age-0 LMB success and can potentially influence recruitment. My experiment demonstrated that dense and/or homogeneous macrophytes can reduce age-0 LMB foraging success. Macrophyte

structure in all study lakes appeared heterogeneous, perhaps explaining why I did not observe effects of macrophyte density and structure on LMB piscivory and growth in the field study. Future studies should quantify the degree of structural heterogeneity at the whole-system scale and evaluate whether LMB recruitment is higher in systems with heterogeneous structure (i.e., patchy macrophyte beds with a diversity of growth forms) compared to systems with homogeneous structure (i.e., extensive monocultures of invasive macrophytes).

My field study demonstrated that age-0 BG prey availability is highly variable among systems. Two previously unidentified factors appear especially important for explaining variation in age-0 BG prey abundance: 1) spawning duration by adult BG and 2) total reproductive output by adult BG. High BG prey abundance was typical in lakes where adult BG produced many BG fry over an extended time. I found adult BG size-structure to positively correlate with age-0 BG prey abundance. Mechanisms underlying variability in BG fry production need further exploration.

From a lake management perspective, evaluation of the indirect effects of specific activities, such as herbicide application, on LMB recruitment is difficult given the complexity of lake ecosystems. However, these analyses are critical to establishing effective and responsible management policies.

## APPENDIX

Tables and figures

Table 1. Characteristics of plant assemblages (species composition and relative abundance) simulated in each experimental treatment, total water volume displaced by the plants, estimated total live plant biomass, and plastic plant components. EWM is Eurasian watermilfoil.

| Treatment Assemblage | Treatment Density | Volume Displaced (ml) | Estimated Biomass (g dry/m <sup>2</sup> ) | Components (qty*)            | Length (cm) |
|----------------------|-------------------|-----------------------|---|------------------------------|-------------|
| EWM monoculture      | Moderate          | 287                   | 93.01                                     | Modified foxtail plants (14) | 45.7        |
| EWM monoculture      | High              | 553.5                 | 179.38                                    | Modified foxtail plants (27) | 45.7        |
| Diverse Native       | Moderate          | 290                   | 76.97                                     | <i>Anarchis = Elodea</i>     | 30.5        |
| -                    | -                 | -                     | -   | <i>Anarchis</i>              | 38.1        |
| -                    | -                 | -                     | -   | <i>Cabomba</i>               | 38.1        |
| -                    | -                 | -                     | -   | <i>Cabomba</i>               | 45.7        |
| -                    | -                 | -                     | -   | <i>Hygrophila</i>            | 38.1        |
| -                    | -                 | -                     | -   | large-leaf <sup>†</sup>      | 38.1        |
| -                    | -                 | -                     | -   | <i>Valisneria</i>            | 45.7        |
| Diverse Native       | High              | 549                   | 161.72                                    | <i>Anarchis</i> (2)          | 30.5        |
| -                    | -                 | -                     | -   | <i>Anarchis</i>              | 38.1        |
| -                    | -                 | -                     | -   | <i>Cabomba</i>               | 30.5        |
| -                    | -                 | -                     | -   | <i>Cabomba</i>               | 38.1        |
| -                    | -                 | -                     | -   | <i>Cabomba</i>               | 45.7        |
| -                    | -                 | -                     | -   | <i>Hygrophila</i>            | 30.5        |
| -                    | -                 | -                     | -   | <i>Hygrophila</i>            | 38.1        |
| -                    | -                 | -                     | -   | <i>Hygrophila</i>            | 45.7        |
| -                    | -                 | -                     | -   | large-leaf <sup>†</sup>      | 30.5        |
| -                    | -                 | -                     | -   | large-leaf <sup>†</sup>      | 38.1        |
| -                    | -                 | -                     | -   | large-leaf <sup>†</sup>      | 45.7        |
| -                    | -                 | -                     | -   | <i>Valisneria</i> (2)        | 30.5        |
| -                    | -                 | -                     | -   | <i>Valisneria</i>            | 38.1        |
| -                    | -                 | -                     | -   | <i>Valisneria</i>            | 45.7        |
| -                    | -                 | -                     | -   | <i>Anarchis</i>              | 30.5        |
| -                    | -                 | -                     | -   | <i>Hygrophila</i>            | 38.1        |

\* Quantity = 1 if not noted.

† Leaves from Amazon Sword plants were attached to polypropylene rope to resemble a broad-leaf pondweed (e.g., *Potamogeton amplifolius*)

Table 2. Limnological and macrophyte assemblage characteristics of the six study lakes in Michigan. Cover refers to the percentage of sampled points at which plants were present. Total plant cover indicates the percent occurrence of plants sampled over the entire lake, whereas littoral plant cover indicates the percent occurrence of plants sampled only in the littoral zone. Littoral zone is defined as the area from shore to the depth at which plants consistently occurred.

| Lake        | County  | Year | Size (ha) | Mean Depth (m) | Total Phosphorus ( $\mu\text{g/l}$ ) † | Total Plant Cover (%) | Littoral Plant Cover (%) | Littoral EWM Cover (%) | Littoral Native Cover (%) | Mean CPE Age-0 LMB ‡ (# / m <sup>2</sup> ) | Mean LMB Size Late August ‡§ (mm TL) |
|-------------|---------|------|-----------|----------------|--|-----------------------|--------------------------|------------------------|---------------------------|--|--------------------------------------|
| Bass*       | Kent    | 1998 | 74        | 0.6            | 13.6                                   | 74                    | 75                       | 44                     | 62                        | 0.018                                      | 58.8                                 |
| Heron       | Oakland | 1998 | 53        | 3.3            | 12.0                                   | 74                    | 79                       | 42                     | 77                        | 0.037                                      | 55.2                                 |
| Heron       |         | 1999 |           |                | 14.4                                   | 73                    | 87                       | 49                     | 84                        | 0.028                                      | 51.3                                 |
| Big Seven   | Oakland | 1999 | 64        | 3.2            | 24.6                                   | 84                    | 92                       | 92                     | 83                        | 0.007                                      | 67.2                                 |
| Bass*       |         | 1999 |           |                | 14.2                                   | 56                    | 85                       | 18                     | 80                        | 0.016                                      | 57.8                                 |
| Big Crooked | Kent    | 1998 | 64        | 4.5            | 16.4                                   | 50                    | 98                       | 8                      | 95                        | 0.037                                      | 72.7                                 |
| Big Crooked |         | 1999 |           |                | 22.2                                   | 45                    | 87                       | 21                     | 86                        | 0.025                                      | 65.7                                 |
| Camp        | Kent    | 1998 | 44        | 7.3            | 17.5                                   | 39                    | 99                       | 14                     | 99                        | 0.014                                      | 68.7                                 |
| Camp        |         | 1999 |           |                | 24.3                                   | 37                    | 98                       | 19                     | 96                        | 0.022                                      | 75.8                                 |
| Lobdell     | Genesee | 1998 | 197       | 2.7            | 16.4                                   | 71                    | 92                       | 12                     | 91                        | 0.029                                      | 54.5                                 |
| Lobdell     |         | 1999 |           |                | 12.7                                   | 72                    | 74                       | 48                     | 70                        | 0.013                                      | 57.0                                 |

\* Bass Lake, infested with EWM in 1998, was treated with fluridone (6 ppb) in May 1999.

† All forms of phosphorus were converted to phosphate using persulfate oxidation (Menzel and Corwin 1965), and then measured using ascorbic-molybdate colorimetry (Murphy and Riley 1962).

‡ CPE values were calculated for LMB captured in bag seines only. Mean LMB size was calculated for LMB captured both in bag and purse seines in 1998 and in bag seines only in 1999 (see "Field Methods").

§ Mean LMB August sizes reported were computed from LMB collected during the last week in August 1998 and 1999.

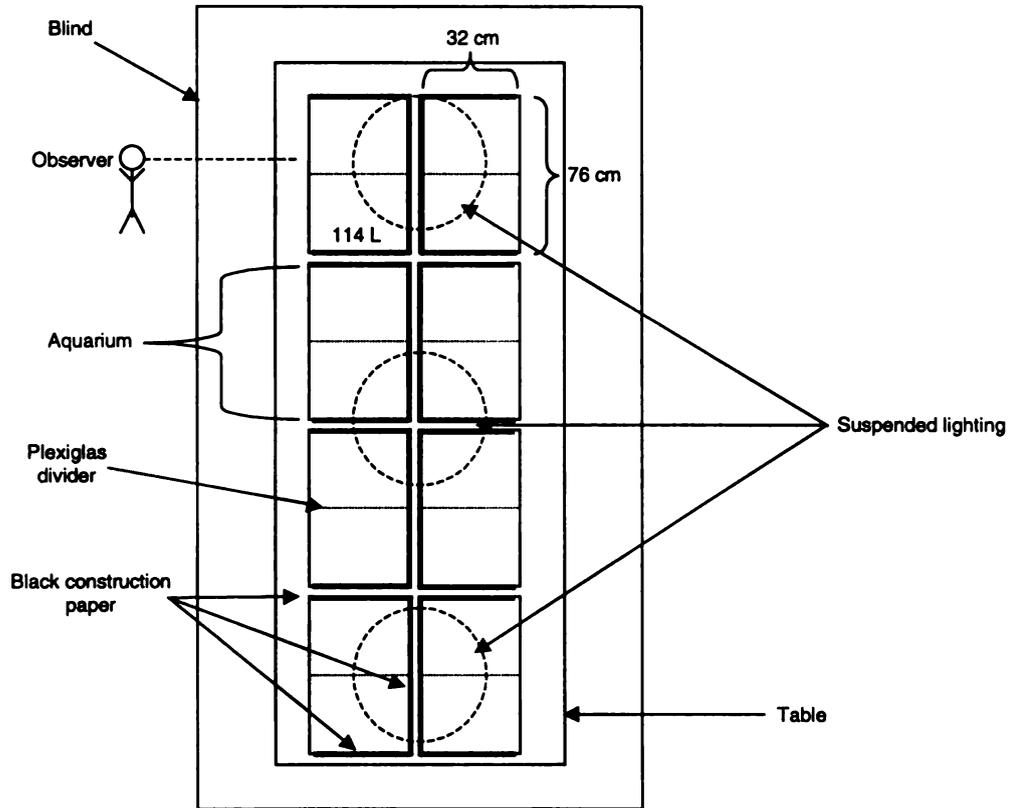


Figure 1. Top-down view of the laboratory set-up for the age-0 largemouth bass foraging behavior experiment.

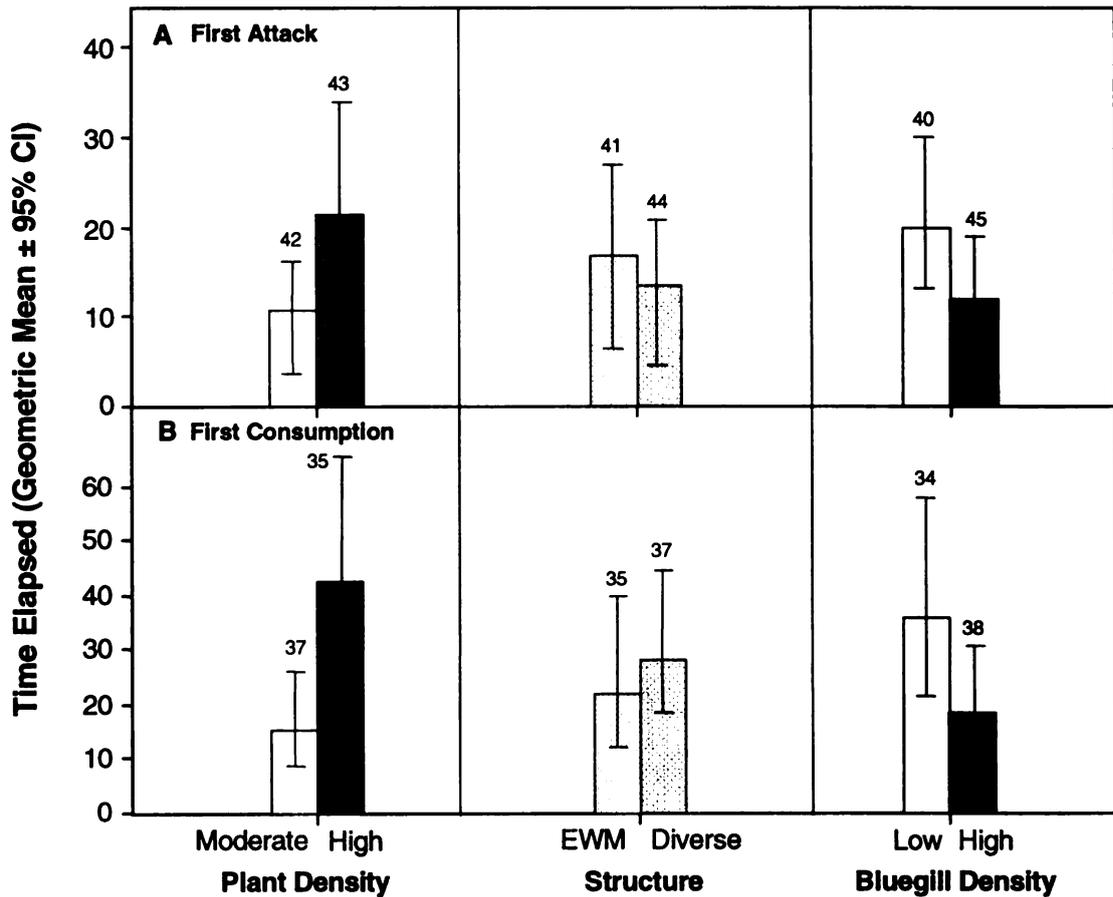


Figure 2. Geometric mean number of seconds ( $\pm$  95% CI) elapsed before a largemouth bass attacked (A), and consumed (B) its first bluegill prey in moderate and high plant density treatments, Eurasian watermilfoil (EWM) monocultures and diverse plant treatments, and low and high bluegill density treatments. Main effect p-values from a three-way ANOVA are reported. No interactions were significant. Numbers above bars denote the number of replicates.

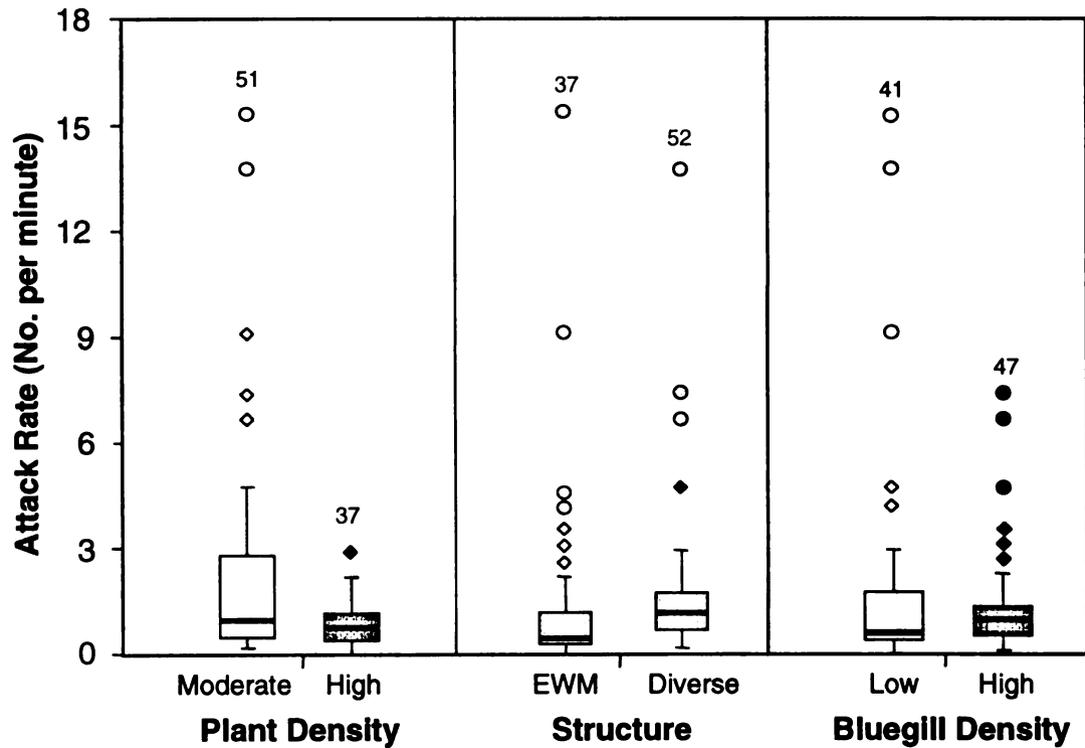


Figure 3. Box plots of attack rate (attacks per minute of search) by largemouth bass on bluegill in each treatment of the largemouth bass foraging experiment. Comparisons shown are attack rates in moderate and high plant density treatments, Eurasian watermilfoil (EWM) monoculture and diverse plant treatments, and low and high bluegill density treatments. P-values from Wilcoxin rank-sums tests are reported. Boxes represent the range in which 50% of the data points fall (i.e., interquartile range or IQR). Whiskers represent the range of data that fall within 1.5 times the IQR. Diamonds represent data points that are within 3 times the IQR. Circles represent outliers. Numbers above plots denote the Wilcoxin mean rank score.

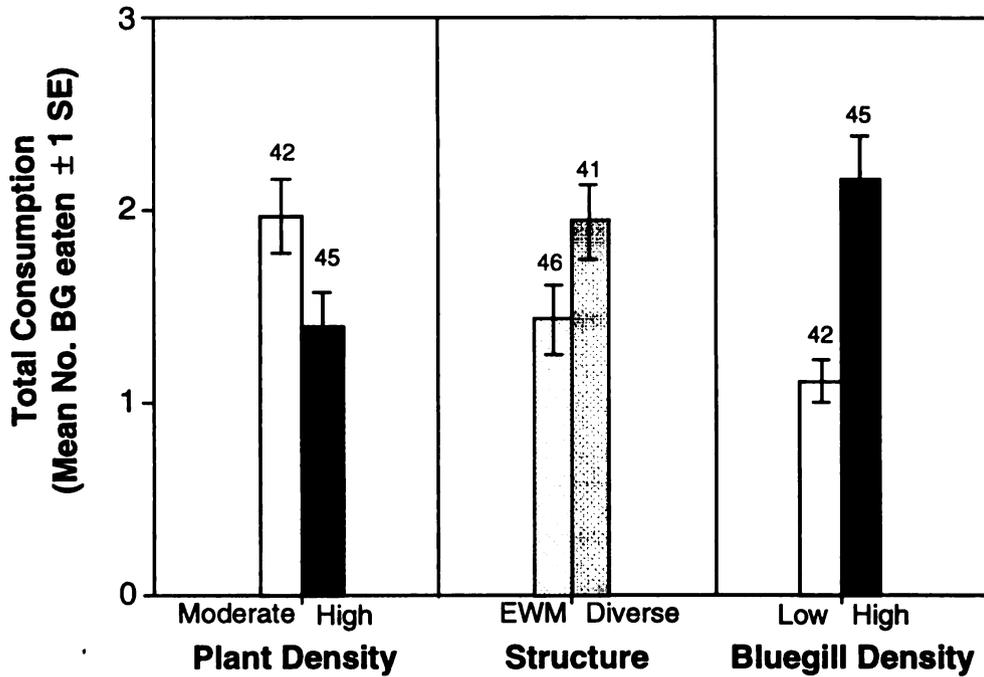


Figure 4. Mean number ( $\pm 1$  SE) of bluegill (BG) consumed by age-0 largemouth bass in the largemouth bass foraging experiment. Comparisons shown are total consumption in moderate and high plant density treatments, Eurasian watermilfoil (EWM) monocultures and diverse plant treatments, and low and high bluegill density treatments. Main effect p-values from a three-way ANOVA are reported. No interactions were significant. Numbers above bars denote the number of replicates.

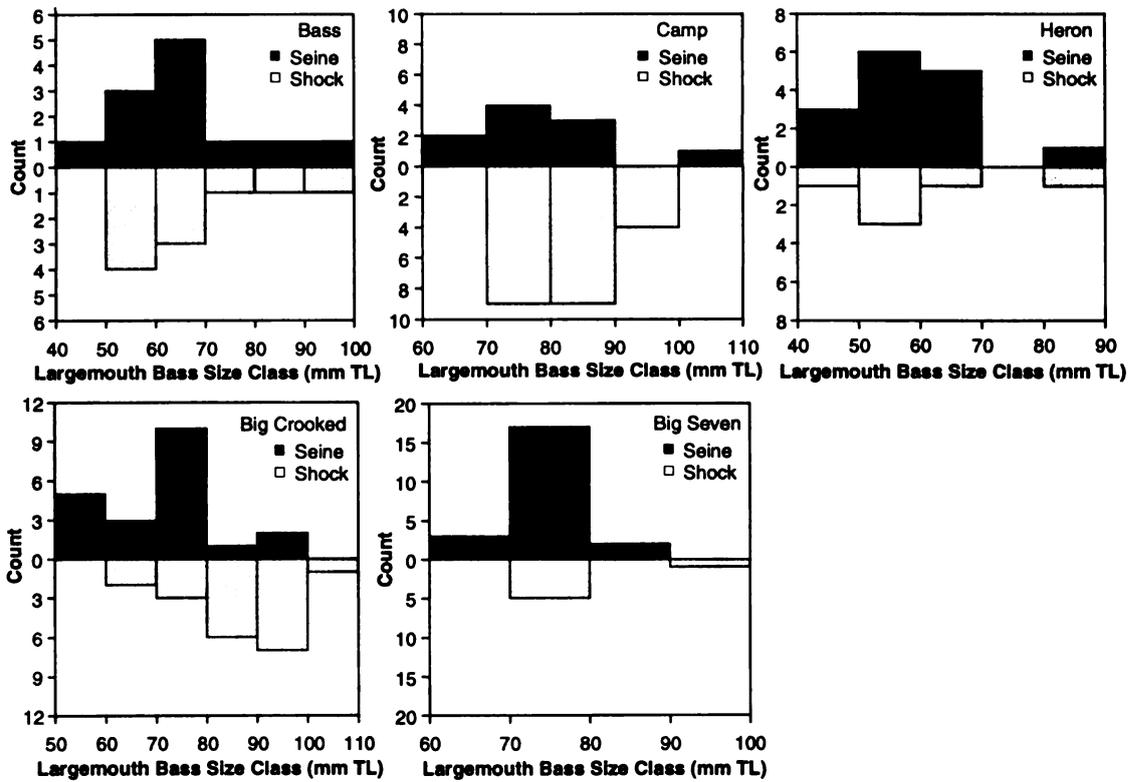


Figure 5. Size distributions of age-0 largemouth bass collected in late September 1999 both from electrofishing (120 volts pulsed-DC) and shoreline seining.

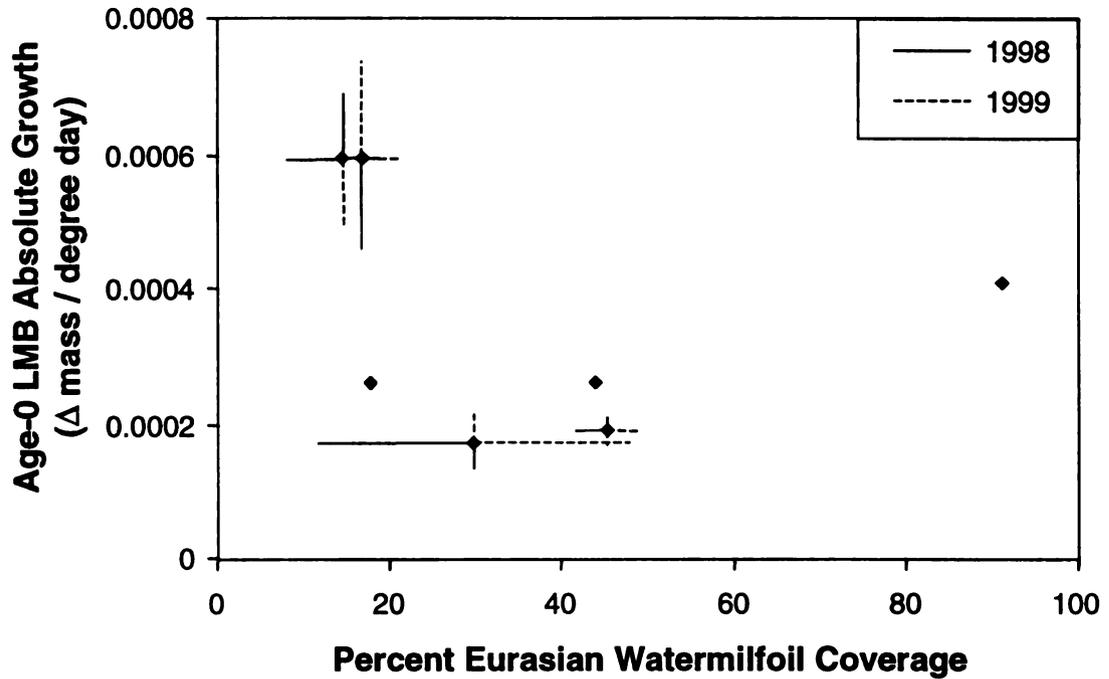


Figure 6. Relationship between Eurasian watermilfoil coverage and absolute growth (standardized to growing degree days) of age-0 largemouth bass (LMB). Vertical and horizontal bars are used for lakes were measured in both years and represent the range of means in 1998 (solid line) and 1999 (dashed line); points in the middle represent the mean effect and response for each lake measured in both years.

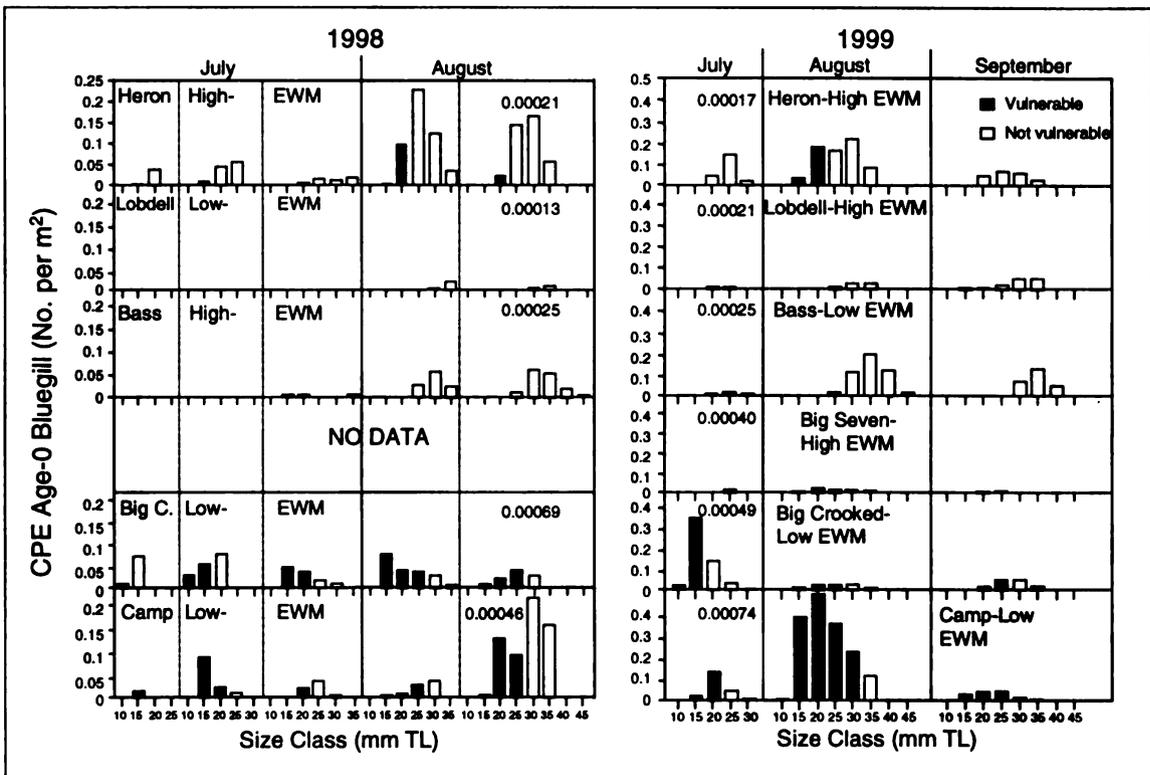


Figure 7. Catch per effort (CPE; No./ m<sup>2</sup>) of age-0 bluegill (determined by length distributions) captured in seine hauls during summer 1998 and 1999. Black bars represent vulnerable bluegill (individuals  $\leq 40\%$  of the mean largemouth bass TL). Open bars are bluegill that were too large for age-0 largemouth bass to consume. Dashed vertical lines separate each sampling date and solid vertical lines separate months. Values in the upper right of each lake's distribution in 1998 and upper left in 1999 indicate the absolute growth of age-0 largemouth bass. Lakes are ordered by ascending age-0 largemouth bass absolute growth rates in 1999. Note y-axis scales differ between 1998 and 1999. All lakes with  $< 42\%$  littoral coverage of EWM were designated as "low" EWM lakes.

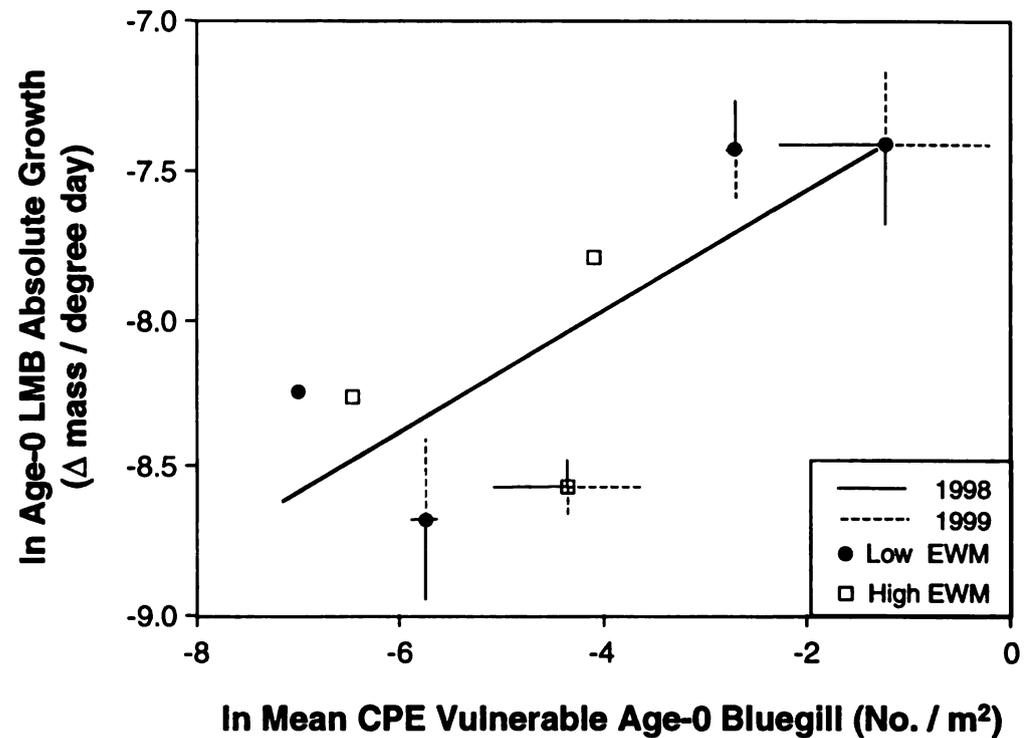


Figure 8. Relationship between mean CPE of vulnerable age-0 bluegill [individuals  $\leq$  40% of the mean length of age-0 largemouth bass (LMB) captured during the same period] and absolute growth (standardized to growing degree days) of age-0 LMB. Vertical and horizontal bars are used for lakes measured in both years and represent the range of means in 1998 (solid line) and 1999 (dashed line); points in the middle represent the mean effect and response for each lake measured in both years. All lakes with  $<$  42% littoral coverage of EWM were designated as “low” EWM lakes.

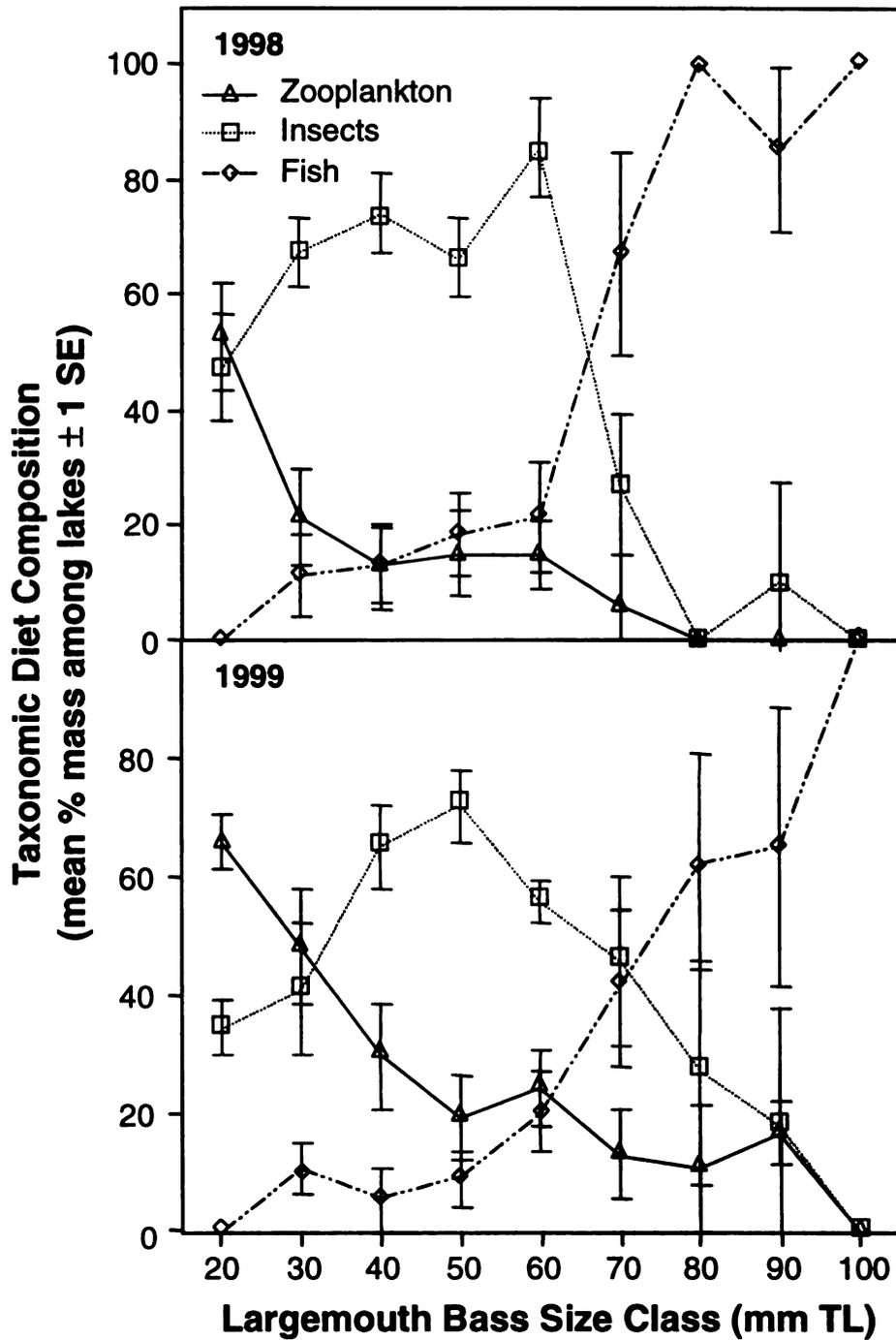


Figure 9. Taxonomic diet composition of age-0 largemouth bass in 1998 and 1999. Values reported in 1998 and 1999 are means (weighted by sample size for each size class in each lake) of 5 and 6 lakes respectively ( $\pm 1$  SE).

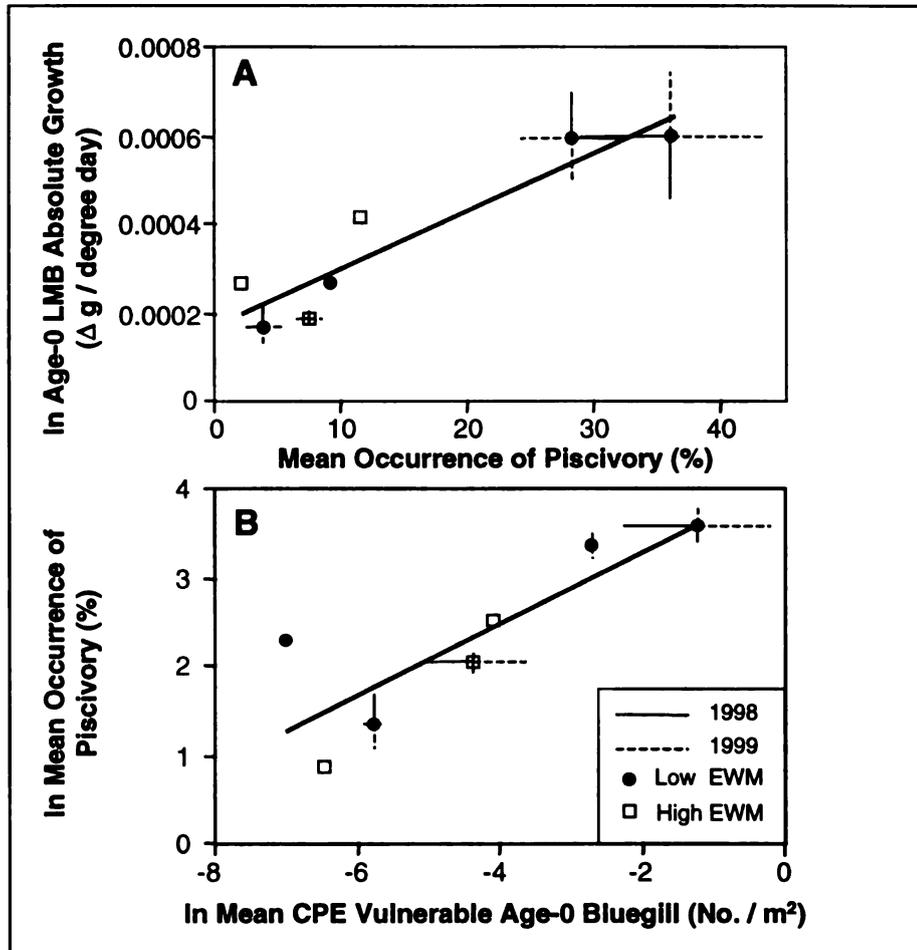


Figure 10. Absolute growth (standardized to growing degree days) of age-0 largemouth bass (LMB) as a function of mean percent occurrence of piscivory (A) and mean percent occurrence of piscivory as a function of bluegill prey availability (CPE of bluegill  $\leq$  40% of the mean length of age-0 LMB captured during the same period; B). Frequency of piscivory was estimated from diet analysis as the proportion of LMB stomachs that contained fish and reflects seasonal means. Vertical and horizontal bars are used for lakes measured in both years and represent the range of means in 1998 (solid line) and 1999 (dashed line); points in the middle represent the mean effect and response for each lake measured in both years. All lakes with  $<$  42% littoral coverage of EWM were designated as “low” EWM lakes.

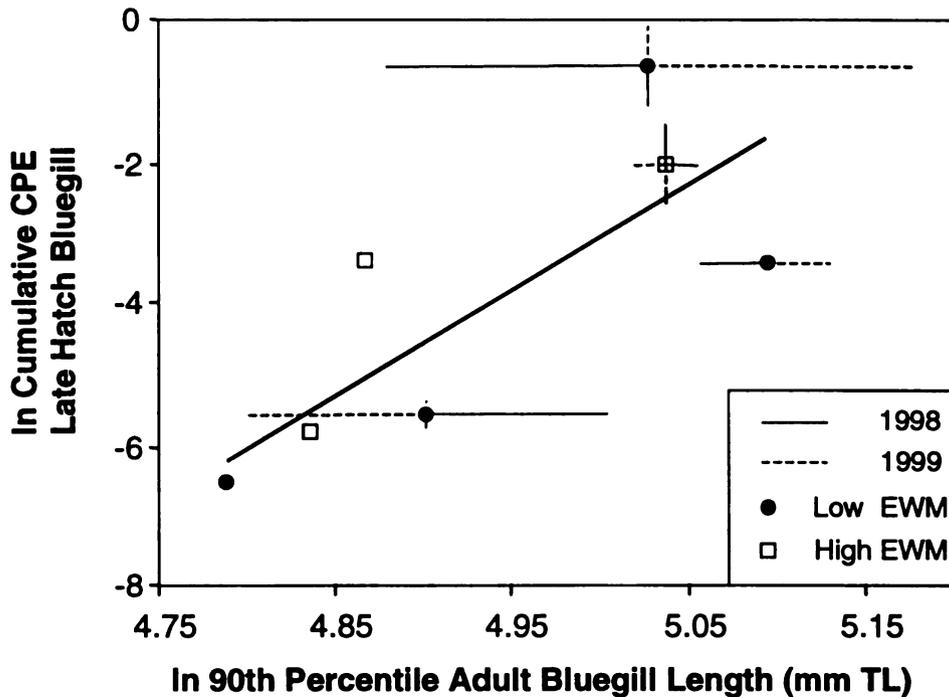


Figure 11. The relationship between adult bluegill size and the catch per effort (CPE) of bluegill < 25 mm TL during late August. Adult bluegill were captured during spring 1998 and 1999 electrofishing surveys. Vertical and horizontal bars are used for lakes measured in both years and represent the range of means in 1998 (solid line) and 1999 (dashed line); points in the middle represent the mean effect and response for each lake measured in both years. All lakes with < 42% littoral coverage of EWM were designated as “low” EWM lakes.

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