J. Aquat. Plant Manage. 40: 79-87

Effects of Selective Removal of Eurasian Watermilfoil on Age-0 Largemouth Bass Piscivory and Growth in Southern Michigan Lakes

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ABSTRACT

Controlling exotic aquatic weeds such as Eurasian watermilfoil (*Myriophyllum spicatum* L.) is a high priority for many aquatic plant management programs. Yet, the effects of Eurasian watermilfoil invasion and subsequent removal on sportfish production and food webs are insufficiently understood. Changes in aquatic plant abundance or architecture, caused by invasion and/or removal of exotic plants, may affect age-0 largemouth bass (*Micropterus salmoides* Lacepede) growth and recruitment. We hypothesized that age-0 largemouth bass piscivory and growth: 1) decreases along a gradient of increasing Eurasian watermilfoil coverage and 2) benefits from low-dose applications of fluridone herbicide intended to shift Eurasian watermilfoil dominated plant communities to native dominated plant communities. In a multiple lake evaluation of the effects of selective removal of Eurasian watermilfoil on age-0 largemouth bass, percent coverage of Eurasian watermilfoil ranged 8% to 50% in lakes treated with 5 to 7 ppb fluridone and 43% to 91% in reference lakes. Coverage of native plants ranged from 62% to 95%. Selective removal of Eurasian watermilfoil did not have a significant positive effect on age-0 largemouth bass growth. Rather, age-0 bluegill (*Lepomis macrochirus* Rafinesque) prey availability, which varied considerably among lakes, had a strong positive effect on age-0 largemouth bass piscivory and growth. Factors influencing age-0 bluegill availability to age-0 largemouth bass appear more related to size structure of largemouth bass and bluegill populations than to plant cover.

Key words: Sonar, fish, exotic, invasive plants, macrophyte, young-of-the-year.

INTRODUCTION

The harmful effects of invasive canopy-forming aquatic weeds, such as Eurasian watermilfoil and hydrilla (*Hydrilla verticillata* (L.F.) Royale), on native plant populations and lake aesthetics have been well demonstrated (Madsen 1997). However, the indirect effects of invasive aquatic plants, and their management, on sportfish populations and lake food webs are insufficiently understood. Early life stages of largemouth bass depend on aquatic plants for refuge from predators and for foraging for fish prey (Annet et al. 1996). Through alteration of plant abundance and architecture, invasion and subsequent removal of exotic plants alter largemouth bass habitat (Colle and Shireman 1980, Bettoli et al. 1992). Because largemouth bass are a popular sportfish and keystone species of north temperate lakes (Mittlebach et al. 1995), the indirect effects of invasive aquatic plants, and their management, on largemouth bass may also extend to food web dynamics and sportfish production.

Largemouth bass search aquatic plant beds for fish prey, particularly bluegill in north temperate lakes (Olson 1996a,b). Predator foraging success in aquatic plant beds is mediated by structural complexity, or the number, size, and partitioning of interstitial spaces between stems and leaves (Diehl 1988, Dionne and Folt 1991, Dibble and Harrel 1997, Valley and Bremigan 2002). Native plant communities can promote age-0 largemouth bass foraging success because their mosaic of architectural growth forms create numerous open spaces in which largemouth bass can maneuver and access prey (Valley and Bremigan 2002). In contrast, invasive aquatic plants typically form large, structurally-complex canopies (Colle and Shireman 1980, Lillie and Budd 1992, Engel 1995, Boylen et al. 1999) that create barriers to largemouth bass foraging (Valley and Bremigan 2002). As a result, age-0 largemouth bass may experience low foraging success and growth in lakes infested with invasive aquatic plants (Colle and Shireman 1980, Lillie and Budd 1992). Because slow first year growth of largemouth bass may reduce their likelihood of overwinter survival (Gutreuter and Anderson 1985, Miranda and Hubbard 1994, Garvey et al. 1998b, Ludsin and DeVries 1997), invasive aquatic plants potentially reduce largemouth bass recruitment. Therefore, management actions designed to remove invasive aquatic plants, while promoting diverse, native aquatic plant assemblages, should positively affect largemouth bass recruitment.

Fluridone herbicide appears to be a promising lake management tool in light of its non-toxicity to invertebrates and fish (McCowen et al. 1979, Hamelink et al. 1986) and its potential to specifically control Eurasian watermilfoil (Netherland et al. 1997, Getsinger et al. 2001). However, the effects of fluridone on Eurasian watermilfoil and native aquatic plants are highly dose dependant. Specifically, most aquatic plant species, including Eurasian watermilfoil, will not be affected if initial whole-lake concentrations of fluridone are less than 5 ppb (Getsinger et al. 2001). However, if whole-

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lake concentrations of fluridone exceed 10 ppb, fluridone can destroy native vegetation, and thus negatively affect food webs (Delong and Mundahl 1996, Pothoven et al. 1999). Both mesocosm and whole-lake studies have demonstrated that fluridone will specifically control Eurasian watermilfoil, and not harm native vegetation, at intermediate concentrations of 5 to 7 ppb (Netherland et al. 1997, Getsinger et al. 2001). Therefore, we sought to determine whether selective removal of Eurasian watermilfoil by whole-lake applications of fluridone at 5 to 7 ppb can benefit age-0 largemouth bass piscivory and growth.

In addition, because variability in the abundance of vulnerable-sized age-0 bluegill can drive patterns in age-0 largemouth bass growth (Olson 1996a, Garvey et al. 1998a), we simultaneously evaluated the effect of age-0 bluegill prey availability on age-0 largemouth growth and piscivory. Specifically, age-0 largemouth bass consume zooplankton and macroinvertebrates until they attain the size advantage needed to capture age-0 fish prey, with age-0 bluegill being their major fish prey in north temperate lakes (Olson 1996a). Because fish prey are more energetically profitable than invertebrate prey, the shift to piscivory by age-0 largemouth bass can be followed by rapid growth (Keast and Eadie 1985, Olson 1996a, Garvey et al. 1998a). Together, the timing of the onset of piscivory, and the extent to which fish prey contribute to age-0 largemouth bass diets once they are piscivorous, should determine in large part, age-0 largemouth bass growth rates and recruitment.

Fish prey availability is often variable among systems and can affect the timing and degree of piscivory of age-0 largemouth bass. 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 1996a,b), and total prey production (Miller and Stork 1984, Phillips et al. 1995, Garvey and Stein 1998). Less is known regarding the influence of vegetation cover on age-0 bluegill prey availability; however, conventional wisdom suggests that prey populations should accrue with increasing plant or Eurasian watermilfoil cover because the ability of predators such as largemouth bass to capture prey is reduced at high plant cover (Crowder and Cooper 1979, Savino and Stein 1982, Wiley et al. 1984).

Questions we addressed with this study were: 1) Does age-0 largemouth bass growth and piscivory decrease along a gradient of increasing Eurasian watermilfoil coverage? 2) Does management designed to selectively remove Eurasian watermilfoil while promoting native plants, benefit age-0 largemouth bass? 3) What are the relative effects of Eurasian watermilfoil cover and age-0 bluegill prey availability on age-0 largemouth bass piscivory and growth, and what factors influence bluegill prey availability?

MATERIALS AND METHODS

Study lakes. To determine whether selective removal of Eurasian watermilfoil benefits age-0 largemouth bass piscivory and growth, age-0 largemouth bass were sampled in multiple (five in 1998 and six in 1999) mesotrophic lakes in southern Michigan (Table 1), each with a history of Eurasian watermilfoil infestation. Two lakes that received little or no aquatic plant management and remained infested with Eurasian watermilfoil served as reference lakes (Table 1). Three treatment lakes (Big Crooked, Camp, and Lobdell) were treated with 5 to 7 ppb fluridone during May 1997 (Table 1). Bass Lake was a reference lake in 1998 but was treated with 6 ppb fluridone in May 1999, and thus served as a treatment lake during 1999. Big Seven Lake replaced Bass Lake as a reference lake in 1999. During 1998 and 1999, Big Crooked, Camp, and Lobdell lakes received numerous spot herbicide treatments and harvesting intended to remove any remaining Eurasian watermilfoil. Thus, differences in the aquatic plant communities and age-0 largemouth bass growth between treatment and unmanaged reference lakes cannot be attributed solely to fluridone. This

TABLE 1. LIMNOLOGICAL, AQUATIC PLANT ASSEMBLAGE, AND AGE-0 FISH CHARACTERISTICS OF REFERENCE AND TREATMENT LAKES IN MICHIGAN. COVER REFERS TO THE PERCENTAGE OF SAMPLED POINTS AT WHICH PLANTS WERE PRESENT. EURASIAN WATERMILFOIL AND NATIVE PLANT COVER CATEGORIES ARE NOT MUTUALLY EXCLUSIVE BECAUSE RAKE GRABS OFTEN CONTAINED BOTH EURASIAN WATERMILFOIL AND NATIVE PLANTS. THE EDGE OF THE LITTORAL ZONE WAS DEFINED AS THE MAXIMUM DEPTH THAT PLANTS OCCURRED IN EACH LAKE.

Lake[1]	Treatment or reference	Year	Size (ha)	Mean depth (m)	Total plant cover (%)	Littoral Eurasian watermilfoil cover (%)	Littoral native cover (%)	Mean CPE Age-0 LMB (No. m^{-2})	Mean LMB size late August (mm TL)	Mean CPE (no. m^{-2}) bluegill prey × 1000[3]
Bass[2]	REF	1998	74	2.4	74	46	66	0.018	58.8	1.6
Heron	REF	1998	53	3.4	72	43	79	0.037	55.2	4.9
Heron	REF	1999	—	—	70	44	80	0.028	51.3	20.8
Big Seven	REF	1999	64	3.2	84	91	87	0.007	67.2	16.8
Bass[2]	TRT	1999	—	—	55	15	62	0.016	57.8	0.91
Big Crooked	TRT	1998	64	4.5	50	8	95	0.037	72.7	62.4
Big Crooked	TRT	1999	—	—	45	21	85	0.025	65.7	72.8
Camp	TRT	1998	44	7.3	39	14	91	0.014	68.7	66.9
Camp	TRT	1999	—	—	37	19	93	0.022	75.8	519.7
Lobdell	TRT	1998	197	2.7	70	12	90	0.029	54.5	2.7
Lobdell	TRT	1999	—	—	73	50	86	0.013	57.0	3.6

[1]Getsinger et al. (2001) included these lakes in their analysis of the direct effects of fluridone on aquatic plant communities.
[2]Bass Lake, a reference lakes in 1998, was treated with 6 ppb fluridone in May 1999 and served as a treatment lake in 1999.
[3]Age-0 bluegill that were ≤40% of the mean age-0 largemouth bass TL for each lake and date combination were considered potential prey.

compromised our ability to evaluate the specific indirect effects of fluridone. Rather, we evaluate age-0 largemouth bass growth along a gradient of Eurasian watermilfoil coverage within the littoral zone, resulting in part from removal efforts such as fluridone applications.

Aquatic plant surveys. Surveys for plant cover were conducted during August 1998 and 1999 using the point-intercept method (Madsen 1999). Briefly summarized, this method entailed overlaying a grid of 150 to 250 uniformly spaced points approximately 50 to 100 m apart onto each lake map. Using a global positioning system, points were located, depth was recorded, and presence of plant species were noted visually or with a double-headed rake thrown from the boat. The outer edge of the littoral zone was defined as the maximum depth at which plants occurred in each lake. Detailed results from these plant surveys and the direct effects of fluridone on plant communities are summarized in Getsinger et al. (2001).

Largemouth bass population sampling. During 1998, age-0 largemouth bass were collected in each lake bi-weekly from late June through late August (n = five sampling periods) using both a 10 by 1.8-m (4-mm mesh) bag seine (three sites per lake; 20 to 30 m in length pulled parallel to shore; 0 to 1.5-m depth) and an 18.3 by 2.4-m (4-mm mesh) purse seine (three sites per lake; 1 to 2 m depth). Because capturing age-0 largemouth bass in vegetation can be difficult (Dibble et al. 1996, Miranda and Pugh 1997), both gears were used to determine the most efficient method for capturing age-0 largemouth bass and bluegill in our lakes. Although we did not rigorously evaluate the relative efficiency of the purse and bag seines, the purse seine caught relatively few age-0 largemouth bass compared to the bag seine. Therefore, in 1999, we collected age-0 largemouth bass and bluegill solely with the bag seine (six sites per lake) on a monthly basis, from late June to late August (n = three sampling periods). Our choice of seine sites were based on location and sampling feasibility. Attempts were made to widely disperse sites around each lake; however, the presence of dense vegetation or woody debris precluded consideration of some sites. Shoreline seining has been identified as an effective method for sampling mid-water juvenile fishes in moderately dense vegetation (Pierce et al. 1991). All age-0 largemouth bass and age-0 bluegill captured were preserved in 95% ethanol. Age-0 largemouth bass were also collected 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 (Valley 2000). Therefore, we did not use age-0 largemouth bass size data collected in late September. Rather, seasonal growth rates were based on changes in average largemouth bass size between late June and late August.

Largemouth bass growth. A total of 1,230 largemouth bass were preserved and later measured to the nearest millimeter total length (TL). A subset of 390 largemouth bass, randomly pooled from all lakes, was measured and dried at 60C for 72 hours, and weighed to the nearest mg to develop a length-dry weight regression (Busacker et al. 1990). To draw inferences regarding age-0 largemouth bass growth across lakes and years, we computed an absolute growth rate (Busacker et al. 1990):

$$Growth = \frac{mg_{final} - mg_{initial}}{gdd}$$

where [$mg_{initial}$ = the mean dry mass of age-0 largemouth bass captured in late June of each year] and [mg_{final} = the mean dry mass of age-0 largemouth bass captured in late August of each year]; *gdd* = the number of cumulative growing degree days that elapsed between June and August sampling dates. Growing degree day data are routinely collected by the National Weather Service (NWS) and are expressed as the average between the daily maximum and minimum temperatures F minus 50, i.e., the minimum temperature F required for growth of terrestrial plants. Growing degree day data were obtained from NWS first order climate stations closest to Grand Rapids for Bass, Big Crooked, and Camp lakes and Detroit for Big Seven, Lobdell, and Heron lakes). We use degree days rather than calendar days because: 1) seasonal differences in temperature would otherwise confound growth comparisons between years, 2) study lakes in the Detroit area were warmer than lakes in the Grand Rapids area (168 dd difference by late Aug. 1998 and 201 dd difference by late Aug. 1999) and 3) the relationship between degree days and largemouth bass growth in MI lakes should always be positive, because MI lake temperatures generally do not exceed physiologically optimal levels for largemouth bass.

Largemouth bass diets and prey availability. Gut contents from largemouth bass were analyzed in a stratified manner such that all sizes of age-0 largemouth bass captured in each particular lake on each sampling date were represented equally (diet is greatly dependent on size; Olson 1996a, Valley 2000). A maximum of five largemouth bass stomachs from each of three size classes (maximum TL – minimum TL ÷ 3; calculated for each lake and date combination) was analyzed per lake and date. We characterized the degree of piscivory by first calculating the percent of largemouth bass stomachs in each of the three size classes that contained at least one fish. Next, using these percentage values and the abundance of largemouth bass in each size class, we calculated a weighted mean percent of largemouth bass that had consumed at least one fish for each lake, on each date. Finally, we averaged the daily mean value across sampling dates within each lake to characterize piscivory on a seasonal basis.

Because age-0 bluegill are the predominant fish prey of age-0 largemouth bass in Michigan lakes (Olson 1996a) age-0 largemouth bass growth also was related to availability of vulnerable age-0 bluegill prey, defined as those bluegill ≤40% of the mean TL of age-0 largemouth bass (Lawrence 1958). Mean catch per unit effort (CPE) of vulnerable bluegill in bag seines (sites pooled within lakes and averaged across dates) was used as a relative measure of prey availability.

Statistical analyses. Data were analyzed using SAS version 6.12 (SAS Institute, Inc. 1989). Regression analysis was used to evaluate relationships between response variables and effect variables. Seasonal means in each lake for percent piscivory and prey availability were computed by averaging values across dates within 1998 and 1999. Variable distributions that were highly skewed were $\log_e$ (x) transformed. Rejection criterion was set at $\alpha = 0.05$.

RESULTS AND DISCUSSION

Aquatic plant surveys. Prior to application with fluridone in 1997, both treatment and reference lakes contained modest coverages of native plants in addition to Eurasian watermilfoil (Getsinger et al. 2001). Fluridone reduced Eurasian watermilfoil in treatment lakes without greatly impacting total plant cover or native plant diversity (Getsinger et al. 2001). Getsinger et al. (2001) do not include the effects of fluridone in Bass Lake. In Bass Lake, total plant cover declined by 20% during the year of treatment (1999) but returned to pre-treatment levels by 1-yr post-treatment (2000). This pattern likely reflects removal of Eurasian watermilfoil from sites solely containing Eurasian watermilfoil in 1999 and subsequent spread of natives in 2000.

During the years of fish sampling (1998 and 1999), total plant coverage (i.e., percent of all sampled points with plants), ranged from 37% to 84% among lakes, and was similar between years (Table 1). In 1998, 1-yr post treatment with fluridone, littoral coverage of Eurasian watermilfoil in treatment lakes ranged from 8% to 14% (Table 1). Eurasian watermilfoil coverage in treatment lakes increased in 1999, 2-yrs post treatment with fluridone, and ranged from 19% to 50%. Littoral coverage of Eurasian watermilfoil in Bass Lake decreased from 46% in 1998 to 15% in 1999 after treatment with fluridone. Eurasian watermilfoil coverage in reference lakes remained similar between years, ranging from 43% to 91%.

Despite a gradient in Eurasian watermilfoil coverage among treatment and reference lakes, native aquatic plant coverage ranged from 62% to 95% among all lakes (Table 1). Furthermore, extensive monospecific beds of Eurasian watermilfoil did not typify any of the study lakes. Rather, we observed Eurasian watermilfoil beds to be patchy, with native plants interspersed between Eurasian watermilfoil patches. The long period of time Eurasian watermilfoil has been present in Michigan lakes may explain why extensive homogeneous monocultures of Eurasian watermilfoil did not occur in these lakes. Eurasian watermilfoil has been present in many lower Michigan lakes since the early 1960s (Coffey and McNabb 1974) and some studies (Carpenter 1980, Smith and Barko 1990, Engel 1995) report that Eurasian watermilfoil's aggressive behavior often declines through time, on the order of 10 to 15 years.

Age-0 largemouth bass abundance, size, and diet. Mean densities of age-0 largemouth bass captured in bag seines ranged from 0.014 to 0.037 largemouth bass per m^2 in 1998 and 0.007 to 0.028 largemouth bass per m^2 in 1999 (Table 1). Mean age-0 largemouth bass size in late August was similar between years (ranging from 55 to 73 mm TL among lakes in 1998 and from 51 to 76 mm TL in 1999; Table 1). Of the 627 age-0 largemouth bass diets analyzed, 18% of them contained fish prey. Of the 65 fish prey that could be identified, 59% were bluegill. Most of the other fish consumed were shiners (*Notropis* spp.). 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 to 80 mm TL (Valley 2000). Fish constituted the majority of prey biomass in largemouth bass diets at sizes >60 mm TL and occurrence of piscivory averaged 27% for largemouth bass greater than this size. Largemouth bass consumed fish prey that were on average 31% of their length (Valley 2000).

Effects of Eurasian watermilfoil and bluegill prey availability on age-0 largemouth bass growth. Eurasian watermilfoil coverage could not explain variation in age-0 largemouth bass absolute growth ($p = 0.37$; Figure 1). Big Crooked and Camp lakes, the two lakes with the highest age-0 largemouth bass growth rates, had relatively low Eurasian watermilfoil coverage. However, Lobdell Lake, produced the lowest value of age-0 largemouth bass growth in 1998, despite low Eurasian watermilfoil coverage. Lakes with relatively high Eurasian watermilfoil coverage (i.e., Bass 1998, Big Seven, Heron, Lobdell 1999) produced low to moderate age-0 largemouth bass growth rates (Figure 1). Although selective mortality of small individuals could have biased our estimates of growth, estimates would be conservative because growth would be positively biased in lakes with low overall growth.

Both total age-0 bluegill density and the density of vulnerable age-0 bluegill varied considerably among lakes in 1998 and 1999 (Table 1, Figure 2). Interestingly, mean CPE of vulnerable bluegill did not increase with Eurasian watermilfoil coverage ($p = 0.40$), and actually displayed a negative trend (Table 1). Mean CPE of vulnerable bluegill explained a considerable amount of variation in largemouth bass absolute growth rate ($p = 0.001$; Figure 3). In general, largemouth bass grew more rapidly in lakes where vulnerable bluegill were abundant. Eurasian watermilfoil coverage could not explain variation in the residuals from the above regression ($p = 0.45$), and thus we did not find neither a significant negative effect of Eurasian watermilfoil coverage, or a significant positive effect of Eurasian watermilfoil removal efforts on age-0 largemouth bass growth.

Piscivory was of primary importance for rapid growth of age-0 largemouth bass in our lakes. Mean percent occurrence of piscivory was positively correlated with largemouth bass absolute growth rate ($p < 0.001$; Figure 4A). Largemouth bass exhibited relatively high growth in lakes where fish were relatively common in their diet. Furthermore, density of vulnera-

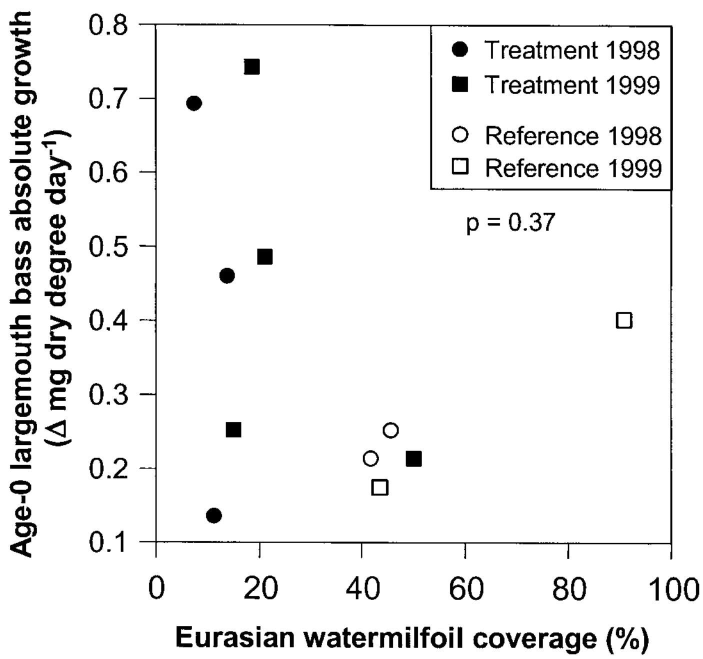

Figure 1. Relationship between littoral coverage of Eurasian watermilfoil and absolute growth of age-0 largemouth bass.

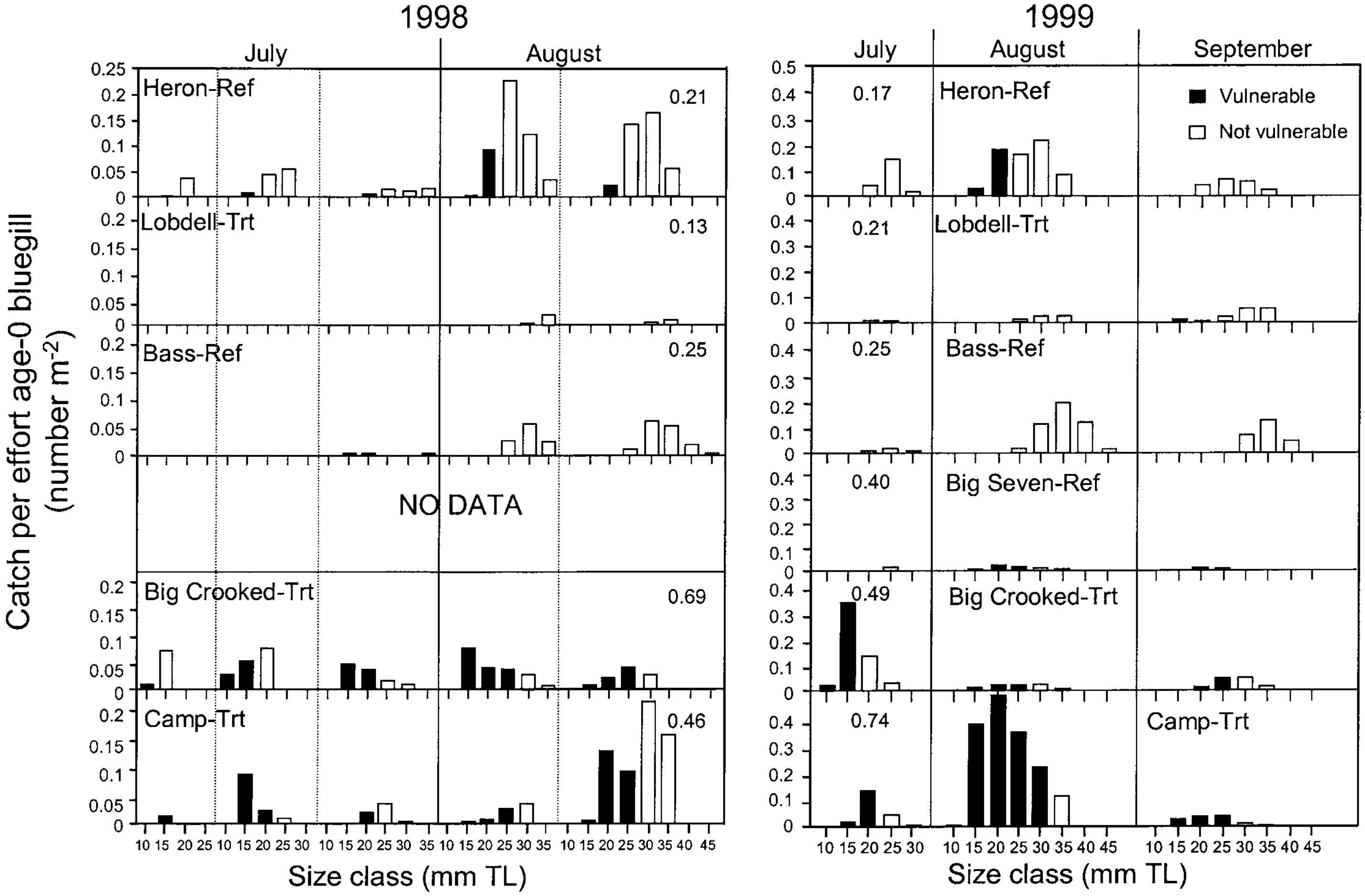

Figure 2. Catch per effort of age-0 bluegill captured in seine hauls during summer 1998 and 1999. Dashed vertical lines separate each sampling date and solid vertical lines separate months. Values in the upper right of each lake's distribution in 1998 and upper left in 1999 indicate the absolute growth (Δ mg dry degree day^{-1}) 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.

ble bluegill prey was positively correlated with mean percent occurrence of piscivory ($p < 0.001$; Figure 4B). Eurasian watermilfoil coverage explained a marginal amount of the 11% residual variation from the preceding regression ($p = 0.06$), and age-0 largemouth bass experienced lower than predicted piscivory as Eurasian watermilfoil coverage increased.

Contrary to expectations, the selective removal of Eurasian watermilfoil did not significantly increase age-0 largemouth bass growth in our lakes. Because aquatic plant communities were diverse both in treatment and reference lakes, structural complexity likely did not vary greatly, and age-0 largemouth bass could successfully capture prey among all lakes. Structural complexity, or the number, size and arrangement of interstitial spaces between stems and leaves affects the ability of littoral predators to forage successfully for prey (Savino and Stein 1982, Diehl 1988, Dionne and Folt 1991, Dibble and Harrel 1997, Valley and Bremigan 2002). Specifically, experiments have demonstrated that visual and swimming barriers created by dense stems and leaves reduce the ability of juvenile and adult largemouth bass to locate, attack, and consume fish prey (Savino and Stein 1982, Anderson 1984, Dibble and Harrel 1997, Valley and Bremigan 2002).

The relationship between structural complexity and largemouth bass in lakes has been difficult to quantify, and thus is less clear (Dibble et al. 1996). In lakes, scale-dependent, spatially-explicit characteristics of the littoral landscape likely affect largemouth bass success. For example, in lakes, largemouth bass foraging success may depend both on micro-scale factors such structural complexity within beds, and macro-scale, or lake-wide factors such as the size, number, and spatial arrangement of aquatic plant beds (Forman and Godron 1986, Annet et al. 1996, Dibble et al. 1996). Traditional coarse measures of vegetation abundance, such as total areal coverage of vegetation, cannot detect differences in the structure of the littoral landscape and thus may inadequately characterize habitat as perceived by largemouth bass (Annet et al. 1996, Dibble et al. 1996, Miranda and Pugh 1997).

Factors influencing age-0 bluegill prey availability. Because age-0 bluegill prey availability had such strong effects on age-0 largemouth bass growth and piscivory, and may vary independently of aquatic plant cover, we explore factors that may explain variability in the CPE of vulnerable age-0 bluegill. Previous studies have identified several factors influencing bluegill prey availability to age-0 largemouth bass and in-

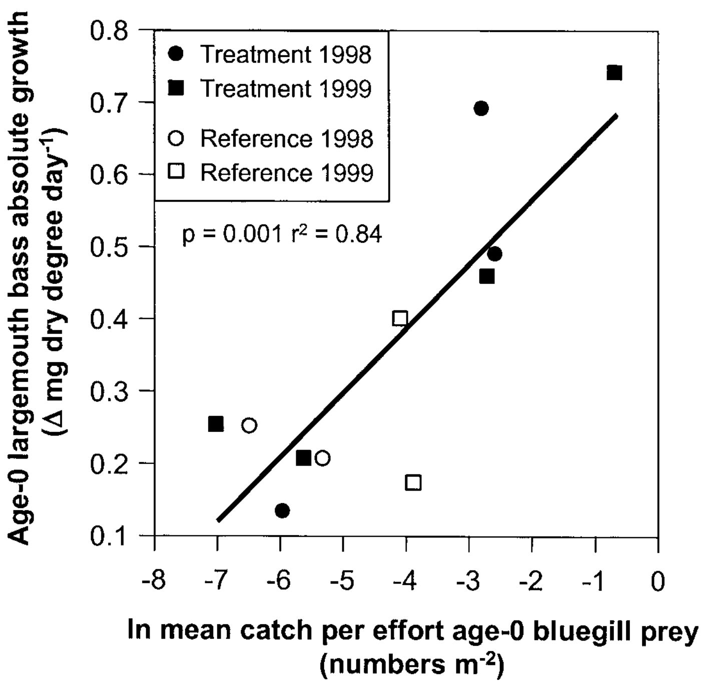

Figure 3. Relationship between mean catch per effort of vulnerable age-0 bluegill and absolute growth of age-0 largemouth bass.

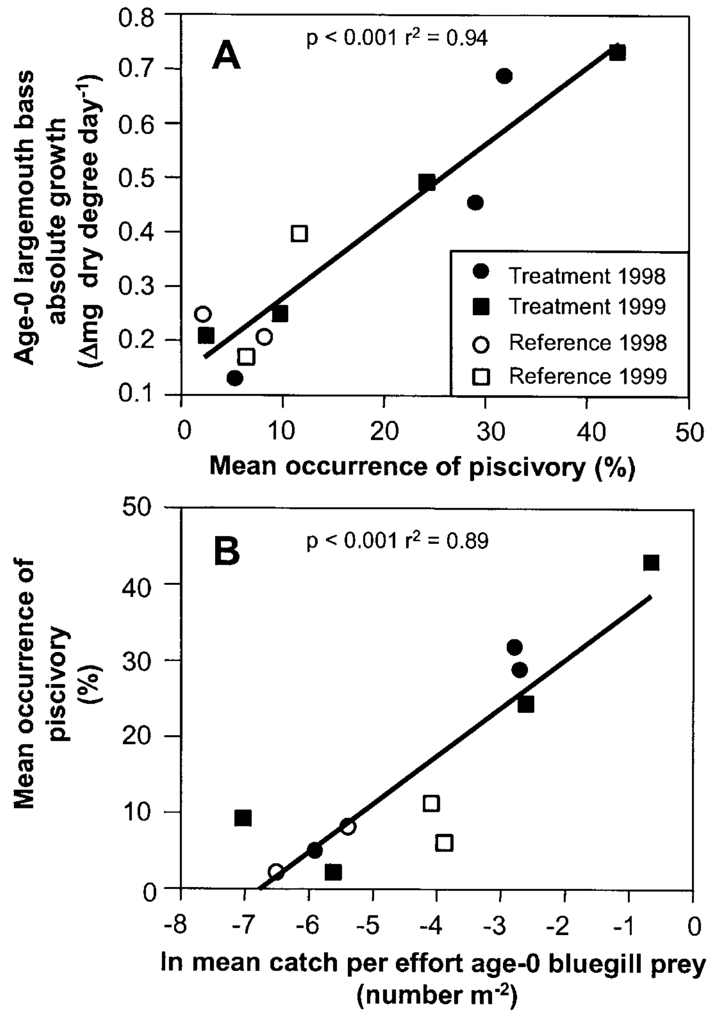

Figure 4. Absolute growth of age-0 largemouth bass as a function of mean percent occurrence of piscivory (A) and mean percent occurrence of piscivory as a function of catch per effort of vulnerable age-0 bluegill (B). Frequency of piscivory was estimated from diet analysis as the proportion of largemouth bass stomachs that contained fish and reflects seasonal means.

clude those that influence size of age-0 largemouth bass relative to age-0 bluegill, such as: 1) timing of spawning of largemouth bass relative to bluegill (Miller and Storck 1984, Phillips et al. 1995), 2) growth of age-0 bluegill (Olson 1996a,b), and 3) growth of age-0 largemouth bass (Olson 1996a,b), and those factors that influence age-0 bluegill abundance, such as: 4) spawning duration of adults (affects both abundance and size; Gross 1980, Claussen 1991), and 5) total reproductive output by adult bluegill (Gross 1980, Claussen 1991). Although we could not rigorously evaluate the relative contribution of these factors to the observed variability in the CPE of vulnerable bluegill, factors 3, 4, and 5 appear especially important.

First, although cause and effect are unclear, our data suggest age-0 largemouth bass growth positively influenced bluegill prey availability by affecting the proportion of the age-0 bluegill cohort that was vulnerable to predation. For example, at similar times of year, similar-sized age-0 bluegill were vulnerable to predation by age-0 largemouth bass in some lakes (e.g., Big Crooked and Camp) and not in others (e.g., Bass and Heron; Figure 2), even though largemouth bass appeared to hatch at similar times. Rapid growth early in the summer by age-0 largemouth bass in Big Crooked and Camp lakes was presumably the result of high availability of macroinvertebrate prey (Cheruvelil 2000) or the presence of small (15 to 20 mm TL), vulnerable age-0 bluegill prey in mid to late July (when age-0 largemouth bass in lower Michigan typically switch to piscivory; Olson 1996a). In contrast, low macroinvertebrate availability or the absence of small age-0 bluegill prey in mid to late July may explain the low proportion of vulnerable age-0 bluegill in Bass and Heron lakes.

Second, variability in bluegill spawning duration among our study lakes also may explain variability in total bluegill prey availability. The appearance of small age-0 bluegill (15 to 25 mm TL) 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. In contrast, in Bass Lake, where age-0 largemouth bass growth was poor in both years, small age-0 bluegill were not present in seine hauls in late August, indicating bluegill spawned over a relatively short time period in this lake.

Finally, our data also suggest that differences in total reproductive output by adult bluegill among lakes may explain variability in age-0 bluegill prey availability. Variability in age-0 bluegill CPE did not appear driven by predation intensity by juvenile and adult largemouth bass because predator density was highest in lakes where age-0 bluegill abundance was highest (e.g., Big Crooked, Camp, and Heron lakes; Hanson 2001). Rather, adult bluegill size-structure may have played a role in determining both bluegill spawning duration and total reproductive output. In general, large bluegill, >150 mm TL, are more fecund compared to their smaller counterparts

(Gross 1980, Coleman et al. 1985), more fit to successfully guard nests against predators (Bain and Helfrich 1983, Coleman et al. 1985), and are able to provide parental care for eggs and fry for longer periods of time (Gross 1980, Coleman and Fischer 1991). Therefore, the protracted spawning seasons and high bluegill fry production that appear characteristic of bluegill populations with larger individuals may positively influence age-0 bluegill prey availability to age-0 largemouth bass. In contrast, bluegill populations dominated by relatively small individuals may produce relatively few bluegill fry due to their short spawning seasons.

We explored (post hoc) whether adult bluegill size could indeed explain variation in the abundance of late-hatched bluegill in the study lakes. Data from fall and spring electrofishing surveys conducted in the study lakes during 1998 and 1999 were used to explore this hypothesis. Adult bluegill body size was characterized as the mean 90th percentile total length of bluegill, computed across fall 1998 and spring 1999 surveys and across fall 1999 and spring 2000 surveys. All bluegill <25 mm TL in late August were assumed to belong to a late-hatched cohort because length of the first-hatched cohort of bluegill by late August is typically 30 to 40 mm in north temperate lakes (Breck 1993, Cargnelli and Gross 1996). Indeed, adult bluegill body size positively correlated with the CPE of late-hatched bluegill ($p = 0.001$; Figure 5), supporting the hypothesis that adult bluegill size structure affects age-0 bluegill prey production.

The relative effects of age-0 largemouth bass growth, protracted bluegill spawning seasons, and bluegill reproductive output on CPE of vulnerable bluegill may vary among lakes. For example, each factor appeared to contribute to high availability of vulnerable bluegill in Big Crooked and Camp lakes. In Heron and Bass lakes slow age-0 largemouth bass growth seemed to correspond with low vulnerable bluegill

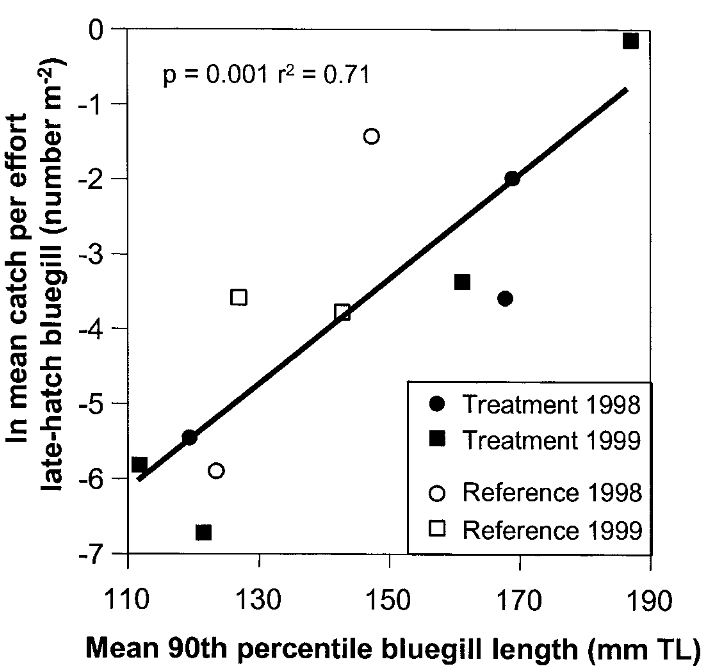

Figure 5. The relationship between adult bluegill size and the catch per effort of bluegill <25 mm TL during late August.

availability. In Bass Lake, the absence of a protracted spawn by bluegill also may have negatively affected vulnerable bluegill availability. Finally, in Big Seven and Lobdell lakes, age-0 bluegill were scarce throughout the entire summer, suggesting that bluegill did not spawn successfully.

In conclusion, we did not document a significant positive effect of selective removal of Eurasian watermilfoil on age-0 largemouth bass piscivory and growth. Nevertheless, growth was highest in two of the four fluridone-treated lakes, Big Crooked and Camp, with high bluegill prey availability and low in the other two treatment lakes, Bass 1999 and Lobdell, with low bluegill prey availability. Fluridone removed Eurasian watermilfoil while not impacting native plants, and remained low in treatment lakes throughout the duration of the study (Getsinger et al. 2001). Still, we could not separate effects of fluridone from the cumulative effects of other management activities, such as spot herbicide treatments and harvesting, that occurred in these lakes during the study. Because diverse vegetation was present in all lakes before and after fluridone applications, it is likely that fluridone and other plant management actions did not create large contrasts in structural complexity among our lakes.

Even though we did not find a positive effect of Eurasian watermilfoil removal on age-0 largemouth bass, the finding of no negative effects has important implications for risk assessment of fluridone use (or other actions designed to selectively remove Eurasian watermilfoil). In other words, this study demonstrates that the risk of indirectly harming largemouth bass populations with low-dose fluridone applications should be relatively low when applied to lakes with modest initial cover of native vegetation. Other, parallel studies conducted on the same lakes as this study also demonstrate no negative effects on zooplankton (K. L. Rogers and P. A. Soranno, unpublished data), macroinvertebrates (Cheruvelil et al. 2001), and adult largemouth bass (Hanson 2001). Still, these results should not be applied to situations where Eurasian watermilfoil dominates a waterbody and native species are few. In these situations, fluridone may have a negative effect on invertebrates and fish by removing an excessively large amount of plant cover from the waterbody (Delong and Mundahl 1996, Pothoven et al. 1999). In addition, factors such as prey availability may strongly affect age-0 largemouth bass, but may not vary predictably with plant assemblages or their management. Rather, size structure of age-0 largemouth bass and age-0 bluegill cohorts and reproductive dynamics of adult bluegill may play a larger role in age-0 bluegill prey availability. The complexity underlying habitat and prey dynamics makes it difficult to detect the effects of aquatic plant management on sportfish such as largemouth bass and demonstrates that the effects of a given plant management technique will not be the same in all lakes.

ACKNOWLEDGMENTS

We would like to thank the Army Corps Research and Development Center, especially J. Madsen, C. Owens, and R. Stewart for their training, sampling equipment, and help conducting the aquatic plant surveys. T. Brunger, K. Cheruvelil, C. Downing, S. Hanson, A. Mahan, V. Moore, K. Rogers, M. Sanborn, T. Schuh, R. Serbin, P. Soranno, and A. Wilson provided invaluable field and laboratory assistance. J. Garvey,

W. Haller, G. Mittelbach, and P. Soranno, and three anonymous reviewers provided helpful comments on earlier drafts of this manuscript. Funding for this research was provided by a fellowship from the Aquatic Ecosystem Restoration Foundation and the Aquatic Plant Management Society and by support from Michigan State University Extension, Michigan State University Agricultural Experiment Station, and Michigan State University Department of Fisheries and Wildlife.

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