

## Lack of a unimodal relationship between fish growth and macrophyte cover in 45 north temperate lakes

K. Spence Cheruvellil<sup>1\*</sup>, N. A. Nate<sup>2,3</sup>, P. A. Soranno<sup>3</sup> and M. T. Bremigan<sup>3</sup>

Michigan State University, East Lansing, USA

With 5 figures and 3 tables

---

**Abstract:** Macrophytes have several important roles for fish populations in lakes. Theory and experimental evidence support the hypothesis of an optimal intermediate macrophyte cover for fish foraging and growth. However, few multi-lake studies of this relationship have been conducted at the whole-lake scale in north temperate lakes, and results to date have not been consistent. We examined the relationship between macrophyte cover and fish growth for two fish species that are tightly linked to macrophytes, largemouth bass (*Micropterus salmoides*) and bluegill (*Lepomis macrochirus*). We conducted our study on 45 thermally stratified north-temperate lakes using nine macrophyte cover metrics at both the whole-lake and littoral-zone scales. We found little evidence to support the hypothesis of an optimal intermediate range of any macrophyte cover metric for fish growth. However, growth for some ages of both species was negatively related to some of the macrophyte metrics at each spatial scale. These results should help direct more holistic management of lakes by informing the management of both macrophytes and fish, and serve as a caution to ecologists and managers attempting to extrapolate theoretical and experimental results to the whole-lake scale.

**Key words:** *Micropterus salmoides*, *Lepomis macrochirus*, optimal macrophyte cover, multi-lake study.

---

<sup>1</sup> **Author's addresses:** Center for Water Sciences, Departments of Zoology and Fisheries and Wildlife, 203 Natural Sciences Building, Michigan State University, East Lansing, MI 48824, USA.

<sup>2</sup> Wisconsin Department of Natural Resources, Bureau of Fisheries Management and Habitat Protection, P. O. Box 7921, Madison, WI 53707, USA.

<sup>3</sup> Department of Fisheries and Wildlife, Michigan State University, 13 Natural Resources Building, East Lansing, MI 48824, USA.

\* Corresponding author; E-mail: e-spencekl@msu.edu

## Introduction

Fish often constitute the top trophic level in lakes and play key roles in lake foodwebs. Fish size, and thus indirectly growth, often determines the extent of their influence. Early growth rates determine the age and size at maturity, which ultimately influence fecundity, recruitment, and mortality (DIANA 1995). Growth rates during early life stages also directly affect size-dependent mortality by influencing overwinter survival (ADAMS & DEANGELIS 1987, MADENJIAN & CARPENTER 1991) and by determining the timing and duration of vulnerability to predators (OSENBERG & MITTELBAACH 1989, OLSON 1996, VALLEY & BREMIGAN 2002 a). Although fish growth is strongly linked to water temperature and food availability (DIANA 1995), the physical habitat provided by macrophytes also influences growth (DIBBLE et al. 1996). In particular, growth rates of some fish species have been shown to be affected by the presence, cover, density, growth form, or species of lake macrophytes (e. g. MACEINA et al. 1991, BETTOLI et al. 1992).

Macrophytes are important for fish because they provide refuge from predators and a substrate for macroinvertebrate populations, which are a primary food source for many young fish (KEAST 1984). For fish growth, there exists a tradeoff between high and low levels of macrophyte density. At high levels of macrophyte density, macroinvertebrate density and biomass are often high due to increased substrate area (JEFFRIES 1993); however, in these dense macrophyte beds, bluegill (*Lepomis macrochirus*) and largemouth bass (*Micropterus salmoides*) prey capture rates generally decline due to increased search and pursuit time (DIBBLE et al. 1996). Therefore, it has been hypothesized that these contrasting forces can result in an optimal (intermediate) macrophyte density for centrarchid foraging and consequently growth.

Building upon these theoretical expectations, small-scale experiments have lent much insight into how macrophytes affect fish foraging and growth. These experiments have demonstrated that a unimodal relationship exists between bluegill growth and macrophyte stem density, with highest growth at an intermediate stem density (CROWDER & COOPER 1982). Experiments have also shown that macrophyte stem density affects both predator (largemouth bass) and prey (bluegill) behavior (SAVINO & STEIN 1982, ANDERSON 1984, GOTCEITAS & COLGAN 1987), and that largemouth bass predation success declines at high macrophyte stem density (SAVINO & STEIN 1982, VALLEY & BREMIGAN 2002 b). These results support the hypothesis of an optimal intermediate macrophyte density for centrarchid foraging and growth.

The results of these experiments have led to research examining whether this unimodal relationship between macrophytes and fish growth exists at the whole-lake scale. To date, studies from southern U. S. lakes and reservoirs constitute the majority of whole-lake studies examining the relationship be-

tween macrophyte cover and fish growth, and a review of these studies demonstrates the intractable nature of this problem. These studies have found both linear and non-linear relationships between macrophyte cover and fish growth, depending upon the fish species, age and size and range of macrophyte cover studied (e. g. COLLE & SHIREMAN 1980, DUROCHER et al. 1984, MACEINA 1996). In addition, the range of macrophyte cover identified as best for fish growth varies by study: at the low end, macrophyte cover between 10 and 30 % was positively correlated with young largemouth bass abundance, while at the high end, macrophyte cover between 40 and 72 % resulted in low piscivory or poor growth by young largemouth bass (COLLE & SHIREMAN 1980, DUROCHER et al. 1984, BETTOLI et al. 1992, MACEINA 1996, WRENN et al. 1996, MIRANDA & PUGH 1997, BROWN & MACEINA 2002). In addition, few studies have examined the relationship between macrophytes and fish in multiple north temperate lakes. In one exception, a study of 25 Ontario lakes found that bluegill abundance (growth was not measured) was correlated with near-shore macrophyte cover (HINCH & COLLINS 1993). The paucity of data on north temperate lakes and the variable results obtained by southern U. S. studies have made it difficult to identify a consistent optimal lake macrophyte cover range for fish growth in these lakes, even for individual fish species, and have demonstrated the need for examining the relationship between macrophyte cover and fish growth in a wider range of north temperate lakes.

Based on current knowledge, most managers of north temperate lakes have extrapolated experimental results to the whole-lake scale, managing macrophytes based on the assumption that there is an optimal intermediate macrophyte cover for fish growth in lakes. Toward this end, lakes with high levels of macrophyte cover or nuisance macrophyte species are managed to reduce these levels through physical (harvesting) or chemical (herbicide) means (MADSEN 1997), and systems with low levels of macrophytes are often managed to increase structural habitat by adding wooden shelters (BROWN 1986, TUGEND et al. 2002). However, ecologists remain uncertain about the relationship between whole-lake macrophyte cover and fish growth and the degree to which experimental results translate to the whole-lake scale. Additionally, lake managers are confronted with making decisions about macrophyte manipulations without clear guidelines describing the optimal range of macrophyte cover for fish growth.

Ecologists and managers alike recognize the difficulties inherent in extrapolating small-scale experimental results to the whole lake scale (e. g., CARPENTER 1989). In this case, there are likely many additional macrophyte metrics and lake characteristics that may explain variability in fish growth at the whole-lake scale. For example, based on theoretical and model predictions (TREBITZ & NIBBELINK 1996), experiments (SMITH 1993), and recent field studies (OLSON et al. 1998, UNMUTH et al. 1999), we would expect centrarchid

fish growth to be higher in lakes with high amounts of macrophyte edge habitat. Macrophyte growth form and species may also be important at the whole-lake scale because, although macrophytes in experiments are for practical purposes often homogeneous or artificial (e. g. rope, a single plastic macrophyte species), a lake contains many different macrophyte growth forms and species, each with different implications for fish growth. Particularly for U. S. lakes, there is much concern that the spread of the canopy-forming, non-native macrophyte Eurasian watermilfoil (*Myriophyllum spicatum*; hereafter milfoil) may adversely affect fish growth (e. g., KEAST 1984, ENGEL 1995, VALLEY & BREMIGAN 2002 b). We also know that lake characteristics such as morphology, water chemistry and clarity, and productivity may help account for variability in fish growth. For example, lake productivity is related to increased fish biomass and recruitment (e. g. GRANT & TONN 2002, HAKANSON & BOULION 2001). Therefore, it is likely essential for studies to include additional lake and macrophyte measures in order to better understand the relationship between macrophytes and fish growth at the whole-lake scale.

To address such issues, we performed a field study of largemouth bass and bluegill growth and a variety of macrophyte cover metrics in 45 north-temperate lakes. We asked whether or not a unimodal relationship existed between fish growth (ages 1–5 y) and macrophyte cover in north temperate lakes. Macrophytes were examined at two spatial scales: the whole lake and the littoral zone (the region from zero depth to the deepest depth of consistent macrophyte growth). Recognizing that additional macrophyte metrics and lake characteristics may account for the variability in fish growth at the whole-lake scale, we also examined whether dense macrophyte cover, the amount of macrophyte-open water edge habitat, macrophyte growth form (e. g. emergent, floating), macrophyte species, and lake characteristics (e. g. lake morphology, water chemistry) help explain patterns in fish growth across lakes.

## Methods

### Study lakes

We chose study lakes from a subset of 697 Michigan public inland lakes >20 ha that the Michigan Department of Environmental Quality sampled for water chemistry and morphometric characteristics during 1972–1988 [U. S. Environmental Protection Agency's data storage and retrieval system (STORET)]. We reduced our sample population of lakes to 350 lakes using the following criteria: lakes that were located in the lower peninsula of Michigan, U. S. A., lakes that were likely to have a pelagic zone that would stratify (mean depth >2 m), lakes that could be sampled in one day (lake area <140 ha), and lakes that had a bathymetric map. For lakes that were sampled more than once in a summer, we randomly chose one sample date, and for lakes that were sampled more than once during the 17 years we chose the most recent year. We then

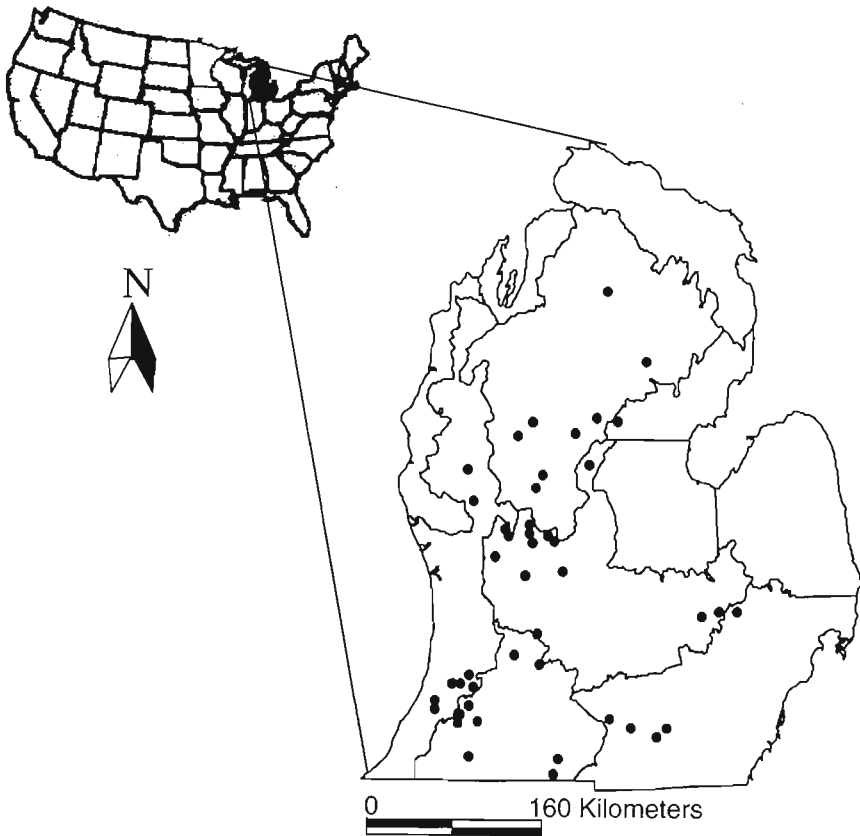


Fig. 1. Forty-five study lakes in lower-peninsula Michigan with ecoregion sub-sections outlined (ALBERT 1995).

chose 54 lakes to sample using a stratified random design from the above 350 lakes using three replicates of a factorial design of water clarity (Secchi disk depth; 2.1–3.4, 3.5–5.5 and 5.6–9.8 m), mean lake depth (0.6–2.6, 2.7–3.5 and 3.6–8.2 m), and lake area (20–49 and 50–140 ha). To increase our statistical power, we also included seven additional lakes for which we had data (not chosen with the above stratified random method), bringing the total to 61 lakes. However, because fish growth data was not available for all lakes (see below), our final sample size was 45 lakes. These geographically diverse lakes are located in six ecoregion subsections across lower-peninsula Michigan, U. S. A. (ALBERT 1995, Fig. 1). No study lakes were stocked with bluegill and one lake was stocked with largemouth bass during our study period of 1990–2002 [Maple Lake, Van Buren Co; Michigan Department of Natural Resources (MI-DNR) Statewide Fisheries Database]. Thirty-three lakes were granted at least one herbicide permit from 1990–2002 [Michigan Department of Environmental Quality (MI-DEQ) Water Division, Surface Water Quality Assessment Section, Aquabase]. Four lakes support the non-native zebra mussel (*Dreissena polymorpha*; Michigan Sea Grant 2003).

**Table 1.** Forty-five study lake locations, morphometry, and years of macrophyte and fish surveys. Bolded entries are the lakes sampled by Michigan State University May 2000 (growth year 1999); the MI-DNR 1990–2002 sampled the remaining lakes. Lakes are in increasing order of macrophyte % cover (lake). BG = bluegill, LMB = largemouth bass, and N/A = data not available.

Lake, County	Area (ha)	Mean depth (m)	BG survey	LMB survey	Macrophyte survey
Brandywine, Van Buren	27.2	3.0	1998	1998	2001
Duck, Allegan	48.0	4.6	1996	1996	2002
Fish, Barry	65.0	9.1	1993	1993	2001
Donnel, Cass	96.9	7.6	1992	1992	2001
Robinson, Newaygo	53.9	5.5	1992	1992	2001
Van Auken, Van Buren	96.1	6.4	1991	1991	2002
Deep, Lenawee	25.6	7.3	1998	1998	2001
Clear (1), Ogemaw	69.2	3.7	1990	1990	2002
Baptist, Newaygo	33.5	6.7	2000	2000	2001
Round (1), Jackson	61.0	2.4	1994	1994	2001
Cowden, Montcalm	51.8	5.2	1997	1997	2002
Cary, Branch	32.0	6.4	1998	1998	2002
Swains, Jackson	27.2	5.5	1995	1995	2001
Todd, Osceola	29.5	6.4	1994	1994	2002
Eagle, Van Buren	78.0	7.3	1995	1995	2001
<b>Camp, Kent</b>	<b>62.3</b>	<b>7.3</b>	<b>N/A</b>	<b>1999</b>	<b>1999</b>
Nevins, Montcalm	20.9	7.0	1993	N/A	2001
Sunrise, Osceola	31.5	7.9	1996	1996	2001
Lake of the Woods, Van Buren	113.8	4.6	1997	1997	2001
Round (2), Jackson	26.4	5.5	1999	1999	2001
Stevenson, Isabella	55.8	4.0	2001	2001	2002
Winfield, Montcalm	47.6	5.2	2001	2001	2001
Nichols, Newaygo	63.0	4.9	1995	1995	2001
<b>Big Crooked, Kent</b>	<b>63.9</b>	<b>4.5</b>	<b>N/A</b>	<b>1999</b>	<b>1999</b>
Gilead, Branch	52.6	5.8	1991	1991	2002
Englewright, Newaygo	21.3	5.8	1994	N/A	2002
Clifford, Montcalm	78.7	4.6	1999	1999	2001
Pratt, Gladwin	72.8	3.0	1991	1992	2002
Huzzy, Van Buren	31.5	4.6	1993	1993	2002
Rush, Van Buren	46.5	4.9	1996	1996	2002
Section One, Crawford	22.7	2.4	2002	2002	2002
Pretty, Mecosta	47.6	3.4	2000	2000	2001
<b>Bass, Kent</b>	<b>74.5</b>	<b>2.4</b>	<b>N/A</b>	<b>1999</b>	<b>1999</b>
Woodard, Ionia	28.7	2.7	1998	1998	2001
Maple, Van Buren	69.6	2.1	1995	1995	2002
Saddle, Van Buren	117.3	2.4	1999	1999	2001
<b>Lobdell, Genessee</b>	<b>220.6</b>	<b>2.1</b>	<b>N/A</b>	<b>1999</b>	<b>1999</b>
Lake 14, Van Buren	27.2	2.1	1992	N/A	2001
<b>Heron, Oakland</b>	<b>53.4</b>	<b>3.4</b>	<b>N/A</b>	<b>1999</b>	<b>1999</b>
Mecosta, Mecosta	116.9	3.4	2001	2001	2001
Carter, Barry	28.3	2.7	1993	1993	2002
George, Clare	52.8	2.7	1992	1992	2002
Cranberry, Clare	41.7	2.4	1994	1994	2002
<b>Big Seven, Oakland</b>	<b>68.8</b>	<b>3.2</b>	<b>N/A</b>	<b>1999</b>	<b>1999</b>
Clear (2), Barry	74.5	2.1	N/A	1999	1999

## Macrophytes

We sampled seven lakes in 1999, 21 lakes in 2001, and 17 lakes in 2002 (Table 1). Macrophytes were sampled in all lakes from mid-July to early September because this is a representative time to sample many lake characteristics (STEMBERGER & LAZORCHAK 1994), and because during this time period lakes were thermally stratified and macrophytes were at or near maximum growth. We sampled macrophytes using the point intercept method (Madsen 1999). For each lake, we placed a grid of sample points, each associated with a latitude and longitude, over the lake using a geographic information system (GIS). The sample points were 40, 50, or 100 m apart, depending on lake surface area (40 m for lakes with a surface area of <49 ha, 50 m for lakes with a surface area of 50–139 ha, and 100 m for the lake with a surface area of 221 ha), resulting in 130–400 sample points per lake. In the field, we located each sample point using a global positioning system, we recorded water depth, and we assessed macrophyte presence either by visual inspection (shallow sites) of approximately  $2 \times 2$  m area at the sample point location or by multiple 2-sided rake throws (deep sites; MADSEN 1999). This estimate was then extrapolated to the entire cell that the sample point represented, thus assuming that our point assessment was representative of that sample grid. In 2001 and 2002, we assigned macrophyte presence at each site to four macrophyte growth form/ species categories (emergent macrophytes, floating leaf macrophytes, all submersed macrophytes, and milfoil) and we assigned each category to an areal cover estimate: 0–20 %, 20–40 %, 40–80 %, and 80–100 % cover. For the seven lakes sampled in 1999, we recorded macrophyte presence for each macrophyte species and then later assigned them to the above four macrophyte categories; no areal cover estimates were taken.

From these field data, we calculated nine macrophyte metrics for each lake. First, to calculate whole-lake macrophyte % cover, we assigned each sample site a binary macrophyte code (macrophyte presence or absence), irrespective of areal cover estimates, and divided the number of sites with macrophytes present by the total number of sites in each lake. To calculate the 'littoral' % cover metrics (littoral % cover, % emergent, % floating, % submersed, % milfoil), we divided the number of sites with macrophytes present (total or by macrophyte category) by the number of sites in the littoral zone (area from zero depth to that of consistent macrophyte growth (98 % of vegetated points) = 5.3 m) rather than the entire lake. We calculated percent dense cover (lake) and percent dense cover (littoral) similarly, however, we only included sample sites with  $\geq 40$  % cover. Finally, we calculated the amount of open water-macrophyte edge habitat by extrapolating sample site macrophyte presence to the entire 40–100 m<sup>2</sup> sampled grid by creating 20–50 m buffers around each sample site with macrophytes. We then digitized macrophyte 'beds', areas of contiguous macrophyte presence, in Arc View (ESRI version 3.2), and calculated the ratio of the total perimeter of macrophyte beds to the total area of macrophyte beds (m<sup>-1</sup>).

## Water chemistry and clarity

We sampled water chemistry and clarity of the 45 study lakes on the same date that we sampled macrophytes. At the deepest spot of each lake, we took two Secchi disk depth

measurements over the shady side of the boat, we took an integrated epilimnetic water sample with a tube sampler for phosphorus, chlorophyll-a and total alkalinity, and we determined total alkalinity ( $\text{CaCO}_3$ ) on-site with a titration test kit (LaMotte). For chlorophyll-a analysis, we filtered water on site through a glass fiber filter (Whatman GF-C) and stored it on ice in the dark until it was returned to the lab and frozen. Chlorophyll-a concentrations were determined fluorometrically with phaeopigment correction following 24-hour extraction in ethanol (NUSCH 1980). Total phosphorus was determined using a persulfate digestion (MENZEL & CORWIN 1965) followed by standard colorimetry (MURPHY & RILEY 1962).

### **Fish growth**

For 38 of the 45 lakes, we obtained bluegill and largemouth bass mean length at age summaries from the MI-DNR Statewide Fisheries Database and related archives. These data were from surveys conducted by the MI-DNR personnel between 1990 and 2002 (Table 1) using single or multiple gear types, primarily electrofishing and trap, fyke or gill netting. Individual lengths at age were determined from fish scales collected from a length-stratified sub-sample of fish for each species, lake, and year. Mean lengths at age were then calculated for each species, lake, and year for all gear types combined. For the remaining seven lakes (Table 1, bolded entries), we collected scales from largemouth bass in May 2000 (to estimate growth during 1999) by electrofishing and calculated mean lengths at ages. The use of scales for bluegill age determination has been validated (REGIER 1962), and precision is similar for largemouth bass age determination using scales, otoliths and sectioned otoliths (LONG & FISHER 2001). We examined statistical outliers (outside the 1.5 interquartile range) and removed 16 fish samples with mean length at age values that did not fall within the range of plausible values for these lakes (lengths greater than the Michigan state record for that age). We then used mean size at age data to calculate annual fish growth increments (an estimate of the magnitude of annual growth) for each species, age, and lake. We calculated growth increments as the difference between mean lengths for adjacent ages (e.g. [mean length at age 5 y] – [mean length at age 4 y] for bluegill in each lake and year). Because the accuracy of age estimation tends to decrease with increasing fish age (CASSELMAN 1983), we limited the ages included in our analyses to those most accurately aged and for which we had sufficient sample size (ages 1–5 y). The number of lakes for each fish species and age increment ranged from 13–35 with the majority of species-age combinations including > 21 lakes.

### **Statistical analyses**

We performed transformations for variables to meet normality assumptions when necessary (natural log, square, or square root arcsine). We explored relationships between mean incremental fish growth and whole-lake and littoral-zone macrophyte metrics using nonlinear and linear regression and considered relationships significant for  $\alpha < 0.1$ . Because we were examining general trends, using  $\alpha 0.1$  increased our ability to detect real trends (i.e., reduce the chance of Type II error) by accepting a slightly higher chance of finding a trend that was spurious (i.e., Type I error). For nonlinear



analyses, we fit quadratic curves to the data based on our expectation of unimodal relationships between fish growth and macrophyte cover with highest growth at an intermediate macrophyte cover.

We next examined whether macrophyte metrics (whole-lake and littoral) and lake characteristics used in combination were important for explaining variability in fish growth. However, we first tested for collinearity in the predictor variables by calculating a correlation matrix for the nine macrophyte metrics, two morphometry variables and four water chemistry and clarity variables using both uncorrected and Bonferroni-corrected probabilities. We then examined relationships between fish growth and more than one predictor variable with two approaches based on the results of the correlation matrix: 1) for metrics that were not highly correlated, we used multiple regressions that included more than one predictor variable, and 2) for metrics that were highly correlated, we regressed residuals from significant univariate whole-lake regressions versus additional macrophyte metrics (whole-lake and littoral) and lake characteristics (GRAHAM 2003).

Because both fish growth and macrophyte cover can vary within a lake among years as well as among lakes, we also explored how temporal variability may have influenced our ability to detect patterns between fish growth and macrophyte metrics. We examined temporal variation two ways: 1) we quantified variability over time in seven of our study lakes for which we had multiple years of both macrophyte cover and largemouth bass growth data using repeated measures analyses and analysis of variance analyses, and 2) we regressed the residuals of the significant relationships between macrophyte cover and fish growth versus the difference in years between the macrophyte survey year and the fish growth year (Table 1).

## Results

The 45 study lakes had large ranges of lake morphometry (Table 1), water chemistry (total alkalinity = 44–224 mg L<sup>-1</sup> CaCO<sub>3</sub>), lake productivity (total phosphorus = 5.7–65.9 µg L<sup>-1</sup>), and water clarity (Secchi disk depth = 0.9–6.6 m). Lake area and mean depth were not correlated with each other ( $p = 0.15$ ), nor were they correlated with any water chemistry, productivity or clarity variables (total alkalinity, chlorophyll-a concentration, total phosphorus concentration, Secchi disk depth;  $p > 0.1$ ). However, Secchi disk depth was correlated with chlorophyll-a concentration ( $r = -0.44$ ,  $p = 0.09$ ) and chlorophyll-a concentration was correlated with total phosphorus concentration ( $r = 0.46$ ,  $p = 0.05$ ). Therefore, we included just total phosphorus in our multiple regression models to examine whether lake productivity can help explain variation in fish growth.

At the whole-lake scale, macrophyte cover in the 45 lakes ranged from 18–99 %, macrophyte dense cover ranged from 7–76 %, and macrophyte edge ranged from 14.8–57.2 m<sup>-1</sup>. At the littoral-zone scale, macrophyte cover ranged from 30–99 %, macrophyte dense cover ranged from 9–95 %, emergent cover ranged from 0–45 %, floating cover ranged from 0–72 %, sub-

**Table 2.** Correlation matrix for the nine macrophyte metrics and mean depth. Numbers are  $\pm r$ , Bonferroni-corrected probability.  $N = 45$  lakes for all metrics except dense macrophyte % cover (lake and littoral), for which  $N = 38$  lakes. Bold entries are significantly correlated using Bonferroni-corrected probabilities at  $\alpha < 0.05$ . Litt = littoral, emerg = emergent, float = floating-leaf, sub = submersed, and edge units are perimeter: area,  $m^{-1}$ .

	Mean depth (m) <sub>a</sub>	% cover (lake)	% cover (litt) <sub>b</sub>	% emerg (litt) <sub>b</sub>	% float (litt) <sub>b</sub>	% sub (litt) <sub>b</sub>	% milfoil (litt) <sub>b</sub>	% dense (lake)	% dense (litt)
% cover (lake)	<b>-0.75,</b> <b>0.00</b>								
% cover (litt)	+0.14, 1.00	+0.43, 0.06							
% emerg (litt)	+0.32, 0.90	-0.23, 1.00	+0.33, 0.56						
% float (litt)	0.00, 1.00	+0.10, 1.00	+0.29, 1.000	<b>+0.49,</b> <b>0.01</b>					
% sub y(litt)	+0.11, 1.00	<b>+0.50,</b> <b>0.01</b>	<b>+0.92,</b> <b>0.00</b>	+0.14, 1.00	+0.08, 1.00				
% milfoil (litt)	-0.08, 1.00	+0.34, 0.45	+0.35, 0.43	+0.03, 1.00	+0.27, 1.00	+0.38, 0.22			
% dense (lake)	-0.49, 0.09	<b>+0.86,</b> <b>0.00</b>	<b>+0.57,</b> <b>0.01</b>	-0.18, 1.00	+0.30, 1.00	<b>+0.55,</b> <b>0.01</b>	+0.25, 1.00		
% dense (litt)	+0.30, 1.00	+0.20, 1.00	<b>+0.87,</b> <b>0.00</b>	+0.40, 0.50	+0.42, 0.32	<b>+0.74,</b> <b>0.00</b>	+0.34, 1.00	<b>+0.59,</b> <b>0.00</b>	
Edge (lake)	<b>+0.61,</b> <b>0.00</b>	<b>-0.87,</b> <b>0.00</b>	<b>-0.45,</b> <b>0.04</b>	+0.18, 1.00	-0.13, 1.00	<b>-0.49,</b> <b>0.02</b>	-0.38, 0.23	<b>-0.83,</b> <b>0.00</b>	-0.31, 1.00

<sup>a</sup> Statistics were performed on transformed data – ln (mean depth).

<sup>b</sup> Statistics were performed on transformed data – square root (arcsine(proportion plant metric)).

mersed cover ranged from 23–99%, and milfoil cover ranged from 0–90%. As expected, some of the nine macrophyte metrics were correlated, with 13 combinations being significant at  $p < 0.05$  (Table 2). In addition, mean depth in the 45 lakes was highly correlated with whole-lake % macrophyte cover ( $r = -0.75$ ,  $p < 0.001$ ) and edge ( $r = 0.61$ ,  $p < 0.001$ ; Table 2). Total phosphorus concentration was not significantly related to whole-lake or littoral macrophyte metrics ( $p = 0.2$ – $0.6$ ), with the exception of littoral % milfoil cover, for which there was a slight positive relationship ( $r^2 = 0.10$ ,  $p = 0.04$ ). Fish growth in the study lakes was variable across all age increments (Fig. 2), with coefficients of variation ranging from 28–47% for bluegill and 30–45% for large-mouth bass.

Non-linear quadratic regressions of 45 lakes, nine macrophyte metrics, two fish species, and four age increments did not result in the expected unimodal

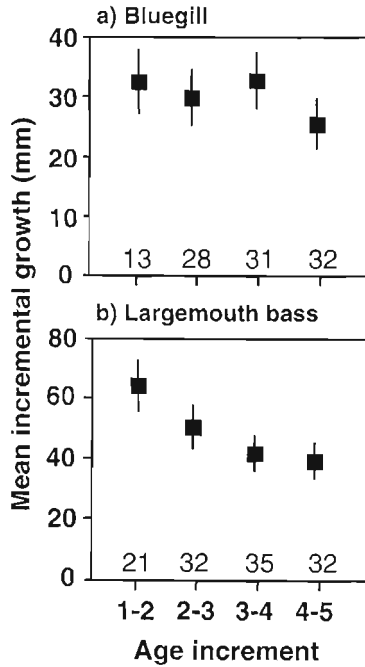


Fig. 2. Mean incremental fish growth and 95 % confidence intervals for a) bluegill and b) largemouth bass in the study lakes. Numbers above each age increment are the number of lakes (n) for that species-increment combination.

relationship between macrophytes and fish growth. In fact, none of the non-linear parameter estimates were different from zero. We did find linear relationships between fish growth and macrophyte metrics for some age-species combinations. For example, at the whole-lake scale, bluegill age 4–5 y growth significantly decreased with macrophyte % cover and dense macrophyte % cover (Fig. 3), for largemouth bass age 1–2 y, growth decreased with whole-lake macrophyte % cover and dense macrophyte % cover and increased with lake edge (Fig. 4 a–c), and at the littoral-zone scale, largemouth bass age 2–3 y growth decreased with increasing milfoil % cover (Fig. 4 d). However, the amount of variation explained by these macrophyte metrics was small ( $r^2 = 0.10–0.32$ ), suggesting that macrophytes may not account for a large amount of the variability in fish growth at the whole-lake scale.

For the above six significant univariate regressions, we next examined whether lake characteristics and additional macrophyte metrics could further explain variation in fish growth by either performing multiple regressions or by regressing residuals versus additional metrics and characteristics. For bluegill age 4–5 y growth, the amount of variation explained doubled by including an additional variable in multiple regression models (either lake area or litto-

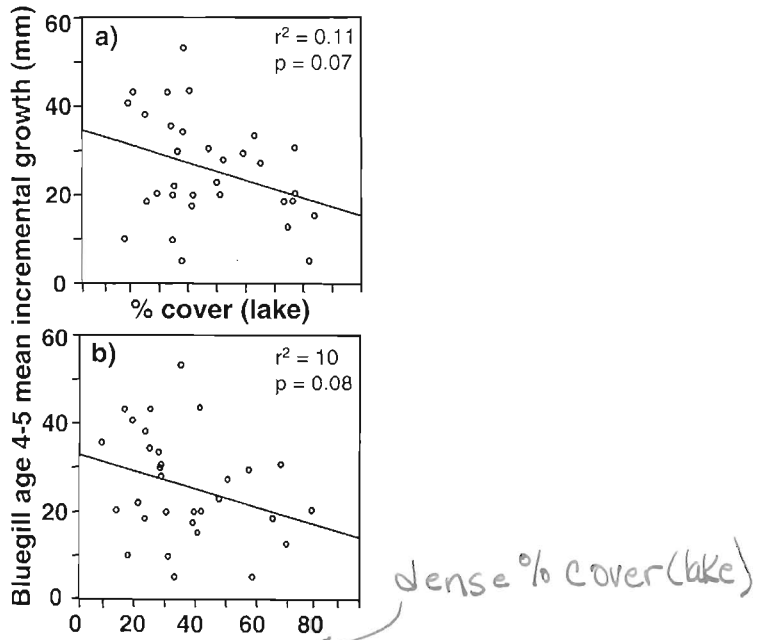


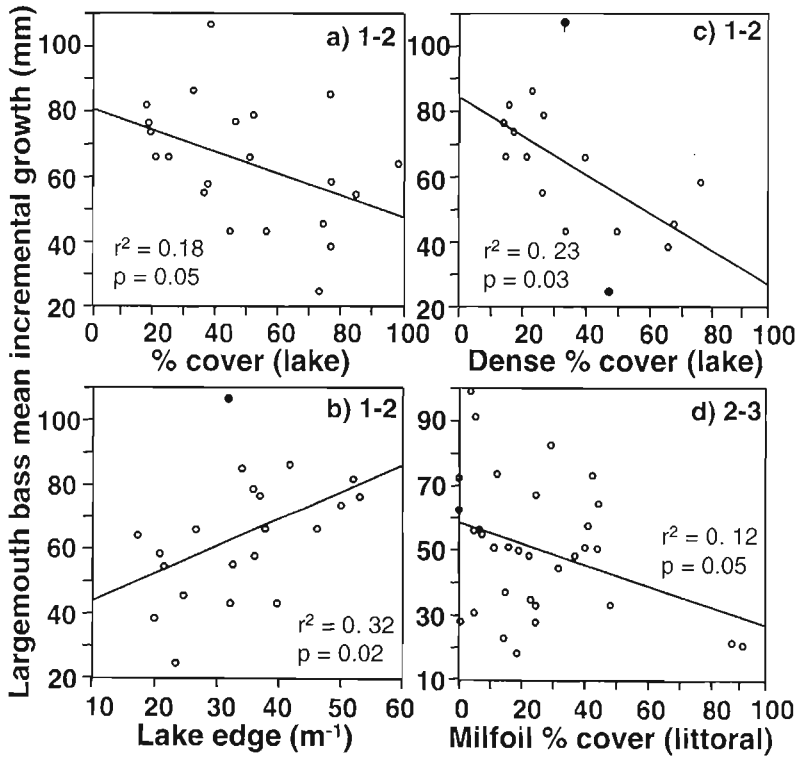
Fig. 3. Bluegill age 4–5 y mean incremental growth (n = 32) at the whole-lake scale versus a) macrophyte % cover and b) dense macrophyte % cover.

Table 3. Significant linear multiple regression results for bluegill (BG) age 4–5 y mean incremental growth (mm) versus whole-lake and littoral-zone macrophyte metrics and lake characteristics. Units for lake area = ha. ln = natural log, as = square root arcsine, prop = proportion, litt = littoral.

Model	Regression r <sup>2</sup>	Regression p value	Coefficients (a, b, c)	Coefficient p values
BG 4–5 = a + b (lake % cover) + c (ln(lake area)) + e	0.20	0.04	9.06, -0.19, 6.65	0.07, 0.08
BG 4–5 = a + b (lake % dense cover) + c (as(prop litt milfoil cover)) + e	0.19	0.05	29.73, -0.26, 16.35	0.03, 0.08
BG 4–5 = a + b (lake % dense cover) + c (ln(lake area)) + e	0.19	0.05	6.84, -0.20, 6.71	0.08, 0.08

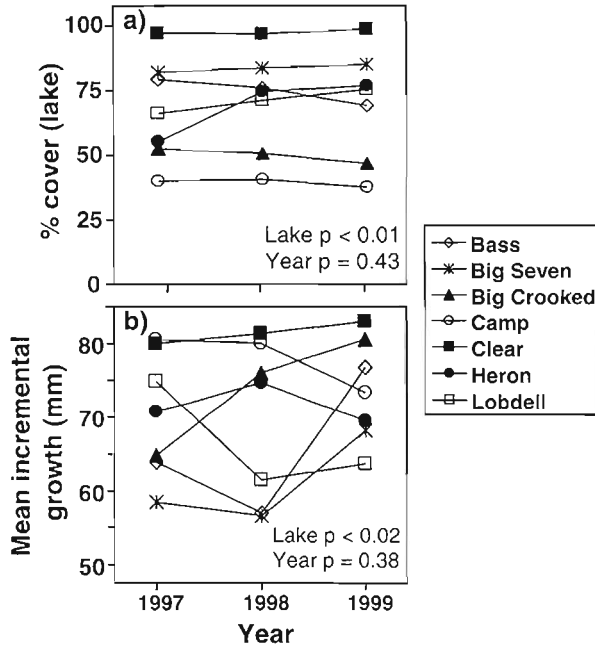
ral-zone milfoil % cover) (Table 3). However, the range of r<sup>2</sup> values was still relatively low (0.19–0.20) for these models. There were no significant regressions of residuals with other macrophyte metrics or lake characteristics.

Both fish growth and macrophyte cover can vary within a lake among years as well as among lakes. Therefore, we used seven study lakes for which we had multiple years of both macrophyte cover and largemouth bass growth data to explore how temporal variability may have influenced our ability to detect patterns between fish growth and macrophyte metrics. For both macro-



**Fig. 4.** Largemouth bass mean incremental growth for a) age 1–2 y versus macrophyte % cover (lake), b) age 1–2 y versus lake edge, c) age 1–2 y versus dense macrophyte % cover (lake), and d) age 2–3 y versus milfoil % cover (littoral). Statistics for d) were performed on square root arcsine milfoil % cover. Filled circles in b and c are lakes that are statistical outliers. See Fig. 2. caption for sample sizes.

phyte % cover (lake) and largemouth bass growth, repeated measures analyses found time to be insignificant ( $p > 0.18$ ) and ANOVA analyses found variation among lakes more important than variation among years (Fig. 5). In fact, even though we know that three of these lakes had whole-lake macrophyte herbicide treatments in summer 1997 (Madsen et al. 2002), the lake mean square error for macrophyte % cover (lake) was 1153 as compared to the year mean square error of 20. In addition, although fish growth was more variable over time than macrophyte % cover (lake), year was not statistically significant for any age increment (Fig. 5 b). For example, for largemouth bass age 1–2 y growth, the lake mean square error was 154 as compared to the year mean square error of 34. The larger mean square errors associated with lakes than years for both macrophyte cover and fish growth support the idea that both measures vary more among lakes than within lakes across years. This result supports the idea that we can use macrophyte and fish survey data collected in



**Fig. 5.** Variability over time in a) macrophyte % cover (lake) and b) age 1–2 y large-mouth bass mean incremental growth for seven lakes with both fish growth and macrophyte data for multiple, corresponding years.

the same lake during different years to examine general trends between macrophyte cover and fish growth. We also examined the importance of temporal variation by regressing the residuals of the significant relationships between macrophyte % cover (lake) and fish growth versus the difference in years between the macrophyte survey year and the fish growth year. These regressions were insignificant ( $r^2 < 0.18$ ,  $p > 0.20$ ), which suggests that the number of years between the macrophyte survey year and the fish growth year does not explain additional variability in fish growth.

## Discussion

Using 45 thermally stratified north-temperate lakes, two fish species and nine macrophyte metrics across two spatial scales, we did not find evidence to support the hypothesis of an optimal intermediate macrophyte percent cover (or other metric) for fish growth. Rather, we found that growth for some age increments of bluegill and bass was negatively related to some whole-lake and littoral zone macrophyte metrics. However, it is important to recognize that al-

though these regressions were statistically significant, macrophyte metrics actually explained relatively little variation in fish growth ( $r^2 = 0.10 - 0.32$ ).

Bluegill and bass growth is strongly linked to water temperature and food availability (data we did not have for the 45 study lakes), which are in turn affected by many additional variables (e. g. bluegill and bass densities, predator and prey densities, lake morphometry, lake productivity; Diana 1995). Because these variables are also spatially and temporally variable, and may covary with macrophyte cover and fish growth, the relationship between macrophytes and fish growth at the whole-lake scale may be difficult to quantify (e. g. SHIMA & OSENBURG 2003). Although OSENBURG et al. (1988) found that growth rates of bluegill and pumpkinseed were influenced more by unique lake differences than by annual climate differences, we found that little additional variation in fish growth rates could be explained by lake mean depth, lake area, total alkalinity, or total phosphorus. Considering how many factors have the potential to affect fish growth in lakes, and how much each of those factors varies both within and among lakes, it is notable that we were able to demonstrate that some whole-lake and littoral zone macrophyte metrics can account for any variation in fish growth.

Although not unimodal, the statistically significant linear relationships we found make ecological sense. At the whole-lake scale, the negative relationships found between bluegill age 4–5 y growth and macrophyte % cover (lake) and dense macrophyte % cover (lake) (Fig. 3) are expected because as macrophyte % cover and density increases (and mean depth decreases), there may be less pelagic habitat available, leading to few large zooplankton for mature bluegill to feed on. Large zooplankton (mainly *Daphnia*) are a very profitable food source for adult bluegill, and variation in *Daphnia* abundance has been related to bluegill growth (MITTELBACH 1981, MITTELBACH & OSENBURG 1993). Similarly, the negative relationship we found between largemouth bass age 1–2 y and 2–3 y growth and whole-lake macrophyte % cover and dense macrophyte % cover (Fig. 4 a and c) may be because as macrophyte % cover and density increases, piscivorous bass foraging time may increase (DIBBLE et al. 1996), leading to decreased growth. Because mean depth in the 45 lakes was highly correlated with whole-lake % macrophyte cover, we examined whether any of the observed patterns between macrophyte metrics and fish growth were actually describing a depth effect. However, of the significant relationships, only bluegill age 4–5 y growth was significantly related to mean depth ( $r^2 = 0.12$ ,  $p = 0.05$ ). This result suggests that the observed relationships between fish growth and macrophyte metrics are not driven solely by lake mean depth.

Based on the idea that edge habitat may increase prey vulnerability, thus providing for efficient foraging and increased growth (TREBITZ & NIBBELINK 1996), we examined whether the amount of open-water macrophyte edge habi-

that could help us to understand patterns in fish growth across lakes. The positive relationship between lake edge and bass age 1–2 y growth in the 45 study lakes (Fig. 4 b) supports earlier experimental evidence that found bass in enclosures with more edge habitat have higher capture success than those in enclosures with less edge habitat (SMITH 1993). Two field studies that cut channels in macrophytes with harvesters to increase the amount of macrophyte-open water edge habitat also found increased growth for some ages of largemouth bass (OLSON et al. 1998, UNMUTH et al. 1999) and bluegill (CROSS et al. 1992). In fact, similar to our study, these two field studies found that younger fish were more tightly linked to changes in macrophyte edge. Significant relationships involving smaller and younger bass are expected because growth slows as fish increase in size and age and because young piscivores are more tightly linked with the littoral zone (ANNETT et al. 1996): they use the macrophytes as a refuge from larger piscivores and they feed upon small bluegill that use macrophytes as a forage base before becoming pelagic zooplanktivores (MITTELBACH 1981, OLSON 1996, SHOUP et al. 2003).

We also examined whether quantifying macrophytes at the littoral-zone scale, as opposed to the whole-lake scale, and by growth form and species was important for understanding patterns in fish growth. In fact, we hypothesized that quantifying macrophyte % cover in these ways might be more powerful for understanding fish growth of species that depend on macrophytes in the littoral zone for refuge and forage. However, we found little evidence to support this idea; only one littoral zone macrophyte metric, milfoil % cover (littoral), was significantly related to fish growth for largemouth bass age 2–3 y.

We know that milfoil can decrease fish habitat by lowering oxygen concentrations, reducing the foraging efficiency of visual predators and supporting fewer macroinvertebrate prey than native macrophytes (KEAST 1984, LILLIE & BUDD 1992, ENGEL 1995, CHERUVELIL et al. 2002, VALLEY & BREMIGAN 2002 b). Therefore, we expect that as milfoil % cover (littoral) increases, fish growth may decrease. However, we found this result for only largemouth bass age 2–3 y, and this relationship was highly influenced by the two lakes with high milfoil % cover; removal of these two lakes resulted in no significant relationships between milfoil % cover (littoral) and fish growth. Therefore, without having additional lakes with high milfoil % cover, we cannot conclusively say whether milfoil % cover can explain patterns of fish growth across lakes. However, combined with results from previous studies conducted in milfoil-dominated systems, our results suggest that there may be a threshold milfoil % cover, above which milfoil has a negative impact on fish growth. Based on our sampling, ~ 5 % of Michigan lakes may be milfoil-dominated and thus have already reached this threshold.

Within-lake spatial scale may also be an important factor to consider when studying macrophyte-fish interactions at the whole-lake scale. For example,



because bluegill age 4–5 y growth was significantly related to both dense macrophyte % cover (lake) and milfoil % cover (littoral) by multiple regression, both the whole-lake and littoral zone scales may be important for explaining variability in fish growth. For example, the whole-lake scale may be most reflective of zooplankton availability for pelagic fish whereas the littoral zone scale may be most reflective of littoral fish interactions. This idea needs to be more explicitly tested, however, because in these 45 lakes, % milfoil cover (littoral) was highly correlated with whole-lake % milfoil cover ( $r = 0.93$ ,  $p < 0.001$ ). Thus we were not able to tease apart the importance of including both the littoral and whole-lake scales from the importance of including milfoil % cover at any spatial scale.

Although the significant linear relationships we found between fish growth and macrophyte metrics make ecological sense, we explored reasons why we did not find stronger relationships. For example, in addition to error in fish growth estimates and the spatial and temporal variation associated with other variables that are important for fish growth, our study examined these relationships across a twelve-year period (Table 1). Although this study period is large, our analyses of temporal variation found that for both macrophyte % cover (lake) and largemouth fish growth, among-lake variability is more important than within-lake variability through time. These large differences among lakes should supplant the within-lake temporal variation, thus allowing us to elucidate patterns across lakes. Therefore, the added variability due to the different sampling years for the fish growth and macrophyte metric data in our study should not have contributed largely to our inability to detect stronger relationships between fish growth and macrophyte metrics.

We also explored two main reasons why we may not have detected the expected unimodal relationship between macrophyte metrics and fish growth: 1) this relationship does not exist at the whole-lake scale in north-temperate lakes (at least not for *all* fish species and age or size classes), or 2) this relationship exists and we were not able to detect it with our study. Recall that the prediction of a unimodal relationship is based mainly on small-scale experiments that have measured macrophyte stem density and fish foraging or behavior, often of one fish species and fish age or size class. Therefore, this general relationship may not be applicable to the whole-lake scale or to all fish species and age or size classes when measuring macrophyte % cover and fish growth. Further, many of the field studies to date that have examined this relationship have included a single lake or reservoir, have sampled relatively few macrophyte transects or sampled a relatively small area within the ecosystem and extrapolated those levels to the whole-ecosystem level, or have studied reservoirs with very low % macrophyte cover. In fact, just one study was conducted on multiple whole-lakes in the north-temperate zone (HINCH & COLLINS 1993). Unfortunately, because this study measured macrophytes qualita-

tively, the results are not comparable to ours. Therefore, there is not adequate evidence in the literature or from our study to support the general idea of a unimodal relationship between fish growth and macrophytes at the whole-lake scale. Rather, results from whole-lake studies (OLSON et al. 1998, CROSS et al. 1992, UNMUTH et al. 1999, this study), seem to support the idea of negative linear relationships between fish growth and some macrophyte cover metrics for specific ages or sizes of particular fish species.

If in fact this unimodal relationship exists, we might have failed to detect this pattern between fish growth and macrophyte metrics because, although lake macrophyte cover in our 45 study lakes had a large range (18–99%), our stratified random sampling design resulted in few lakes at either extreme. It is at just such extremes that some past studies have found decreases in fish growth (e.g., BROWN & MACEINA 2002), thus leading to the idea of an intermediate optimum macrophyte density or cover for fish growth. This leads us to question what the ecological relationship would look like if we had sampled additional lakes at the two extremes of macrophyte cover, especially lakes with very low macrophyte % cover. We might expect a threshold effect, below which foraging habitat for prey fish and refuge from predators reaches such low levels that prey fish experience extremely low growth and abundance leading to a reduction in predator fish growth. Therefore, if growth decreases at the low end of the macrophyte cover range, there may still be an optimum intermediate macrophyte cover for fish growth that we did not detect. We could not address this possibility with our data because we did not have lakes with very low % cover, even though we chose lakes with large ranges of lake morphometry, water chemistry and water clarity.

Given our stratified sample design, we can speculate as to how common lakes are in the north temperate region that have very low macrophyte cover (<20%). Recall that mean depth is highly negatively correlated with macrophyte % cover ( $r = -0.75$ ,  $p < 0.001$ ). If we compare our study lakes to 626 large (>20 h) public lakes in Michigan, our mean depth range includes ~78% of these lakes. In fact, just 15% of these large public Michigan lakes are extremely shallow (mean depth <2.0 m). Therefore, if the unimodal relationship between macrophytes and fish growth identified by experiments does in fact exist at the whole-lake scale, it may not be particularly relevant to the majority of north-temperate lakes. We could then ask: are lakes with very low macrophyte cover ones in which we might expect macrophytes to play an important role in driving fish growth? Lakes at the very low end of macrophyte % cover are likely very shallow lakes in a turbid state with high resuspension or with very low productivity (e.g., JEPPESEN et al. 2000), high flow-through systems such as reservoirs, or very large, deep lakes with small or no littoral zones. We might expect that fish growth in these three types of systems would be influenced less by macrophytes in general and more by physical features such as

water flow, oxygen levels or temperature levels (GASITH & HOYER 1998). Therefore, if low fish growth exists in lakes with very low macrophyte cover, and leads to a unimodal relationship between macrophyte cover and fish growth such as that identified by experiments, this relationship may reflect effects driven by characteristics confounded with macrophyte cover rather than macrophyte cover itself. Future research that includes lakes with very low macrophyte cover (<20%), including whole-lake experiments that reduce macrophyte cover across a wide gradient and measure the response of fish growth, is necessary to answer such questions.

Our study demonstrates the potential of using baseline field data to test important questions. In addition, the results of our study are relevant because a more thorough understanding of the relationships between macrophytes and fish growth can help us achieve more holistic lake management. Lake managers are often confronted with the problem of managing lakes for multiple uses and user groups, some of which are at odds with one another. For example, typically, lake managers have been either fisheries managers or macrophyte managers, and they have worked independently. Often, macrophyte managers are pressured by boaters and swimmers to remove macrophytes whereas anglers press for macrophyte enhancement. This dichotomy is evidenced by the lack of integration between the two professional societies relevant to these management activities: the American Fisheries Society (AFS) and the Aquatic Plant Management Society (APMS). More recently, as the relationships between fish and macrophytes have been made increasingly clear, these managers have come to recognize each others' importance and have begun to work together. Evidence of this realization can be seen published works such as TREBITZ & NIBBELINK (1996), CARPENTER et al. (1998), and OLSON et al. (1998) in which a large group of researchers and managers studied how to manage macrophytes to benefit fish growth. However, integration of research and management of fish and macrophytes is far from complete: an abstract and title search of 2003 presentations at annual meetings using the keywords fish, macrophyte, and plant resulted in 1% (12/1181) of AFS talks on research that included macrophytes (American Fisheries Society 2003) and 5% (3/62) of APMS talks on research that included fish (Aquatic Plant Management Society 2003). Therefore, it is only through additional collaborative research examining macrophytes and fish growth, and the dissemination of results to all audiences, that we can achieve better ecological understanding of the relationship between whole-lake macrophyte cover and fish growth and a more holistic lake management of north temperate lakes.

### Acknowledgements

Financial Support was provided by EPA Star Fellowship number U-91595801-2 to K. Spence Cheruvellil at Michigan State University (MSU), a MI-DNR Fisheries Division

to M. T. Bremigan and N. Nate at MSU, and a MSU Agricultural Experiment Station Disciplinary Research Grant to P. A. Soranno, K. Spence Cheruvilil, and M. T. Bremigan. We thank our anonymous reviewers and AARON JUBAR, SHERRY MARTIN, and TYLER WAGNER for their thoughtful and helpful comments on this manuscript. We thank JIM BRECK for his help with historic fish growth data collection, and MICHAEL BELLIGAN for his help with the GIS work on this project. We thank TERESA GRATTAN, KEVIN HOFFMAN, ROB HOWE, PETE HRODEY, AARON JUBAR, TAMARA BRUNGER LIPSEY, ABBY MAHAN, SHERRY MARTIN, CASSIE MEIER, VERN MOORE, STACY NELSON, KRISTY ROGERS, JOHN WHITLOCK and SARAH WILLS for help field sampling. We thank KURT GETSINGER, JOHN MADSEN, LINDA NELSON, CHETTA OWENS, DIAN SMITH and MIKE STEWART, US Army Engineer Research and Development Center, for sharing some macrophyte data and their endless expertise. This study complies with the current laws of the United States.

## References

- ADAMS, S. M. & DEANGELSI, D. L. (1987): Indirect effects of early bass-shad interactions on predator population structure and food web dynamics. – In: KERFOOT, W. C. & SIH, A. (eds): *Predation. Direct and indirect impacts on aquatic communities.* – University Press of New England, NH, pp. 103–117.
- ALBERT, D. A. (1995): *Regional landscape ecosystems of Michigan, Minnesota, and Wisconsin: a working map and classification (fourth revision: July 1994).* – USDA, Forest Service, General Technical Report NC-178, St. Paul.
- American Fisheries Society (2003): Database of all Quebec City 2003 presentations. <http://portaltools.fisheries.org/2003Abs/afsform.cfm>. Cited 28 May 2004.
- ANDERSON, O. (1984): Optimal foraging by largemouth bass in structured environments. – *Ecology* **65**: 851–861.
- ANNETT, C., HUNT, J. & DIBBLE, E. D. (1996): The compleat bass: Habitat use patterns of all stages of the life cycle of largemouth bass. – *Amer. Fish. Soc. Symp.* **16**: 306–314.
- Aquatic Plant Management Society (2003): Abstracts of the 43rd annual meeting held July 20–23, 2003 in Portland, ME 2003. <http://www.apms.org/2003/abstracts.pdf>. Cited 28 May 2004.
- BETTOLI, P. W., MACEINA, M. J., NOBLE, R. L. & BETSILL, R. K. (1992): Piscivory in largemouth bass as a function of aquatic vegetation abundance. – *North Amer. J. Fish. Managem.* **12**: 509–516.
- BROWN, A. B. (1986): Modifying reservoir fish habitat with artificial structures. – In: HALL, G. E. & VAN DEN AVYLE, M. J. (eds): *Reservoir fisheries management: strategies for the 80's.* – Amer. Fish. Soc. Southern Division, Reservoir Committee, Bethesda, MD, pp. 98–102.
- BROWN, S. J. & MACEINA, M. J. (2002): The influence of disparate levels of submersed aquatic vegetation on largemouth bass population characteristics in a Georgia reservoir. – *J. Aquat. Plant Managem.* **40**: 28–35.
- CARPENTER, S. R. (1989): Replication and treatment strength in whole-lake experiments. – *Ecology* **70**: 453–463.

- CARPENTER, S. R., OLSON, M., CUNNINGHAM, P., GAFNY, S., NIBBELINK, N., PELLET, T., STORLIE, C., TREBITZ, A. & WILSON, K. (1998): Macrophyte structure and growth of bluegill (*Lepomis macrochirus*): Design of a multi-lake experiment. – In: JEPPESEN, E., SONDERGAARD, M., SONDERGAARD, M. & CHRISTOFFERSEN, K. (eds): The structuring role of submerged macrophytes in lakes. – Springer, New York, NY. pp. 217–226.
- CASSELMAN, J. M. (1983): Age and growth assessment of fish from their calcified structures—techniques and tools. – NOAA Technical Report NMFS **8**: 1–17.
- CHERUVELIL, K. S., SORANNO, P. A., MADSEN, J. D. & ROBERSON, M. J. (2002): Plant architecture and epiphytic macroinvertebrate communities: the role of an exotic dissected macrophyte. – J. North Amer. Benthol. Soc. **21**: 261–277.
- COLLE, D. E. & SHIREMAN, J. V. (1980): Coefficients of condition for largemouth bass, bluegill, and redear sunfish in hydrilla-infested lakes. – Trans. Amer. Fish. Soc. **109**: 521–531.
- CROSS, T. K., MCINERNEY, M. & DAVIS, R. (1992): Macrophyte removal to enhance bluegill, largemouth bass, and northern pike populations. – MN-DNR, Investigational Report No. 415.
- CROWDER, L. B. & COOPER, W. E. (1982): Habitat structural complexity and the interaction between bluegills and their prey. – Ecology **63**: 1802–1813.
- DIANA, J. S. (1995): Biology and Ecology of Fishes. Biological Sciences Press. Carmel, IA.
- DIBBLE, E. D., KILLGORE, K. J. & HARREL, S. L. (1996): Assessment of fish-plant interactions. – Amer. Fish. Soc. Symp. **16**: 357–372.
- DUROCHER, P. P., PROVINE, W. C. & KRAAI, J. E. (1984): Relationship between abundance of largemouth bass and submerged vegetation in Texas reservoirs. – North Amer. J. Fish. Managem. **4**: 84–88.
- ENGEL, S. (1995): Eurasian watermilfoil as a fishery management tool. – Fisheries **20**: 20–24.
- GASITH, A. & HOYER, M. V. (1998): Structuring role of macrophytes in lakes: Changing influence along lake size and depth gradients. – In: JEPPESEN, E., SONDERGAARD, M., SONDERGAARD, M. & CHRISTOFFERSEN, K. (eds): The structuring role of submerged macrophytes in lakes. – Springer, New York, NY. pp. 381–392.
- GOTCEITAS, V. & COLGAN, P. (1987): Selection between densities of artificial vegetation by young bluegills avoiding predation. – Trans. Amer. Fish. Soc. **116**: 40–49.
- GRAHAM, M. H. (2003): Confronting multicollinearity in ecological multiple regression. – Ecology **84**: 2809–2815.
- GRANT, S. C. H. & TONN, W. M. (2002): Effects of nutrient enrichment on recruitment of age-0 fathead minnows (*Pimephales promelas*): potential impacts of environmental change on the Boreal Plains. – Can. J. Fish. Aquat. Sci. **59**: 759–767.
- HAKANSON, L. & BOULION, V. V. (2001): Regularities in primary production, Secchi depth and fish yield and a new system to define trophic and humic state indices for lake ecosystems. – Internat. Rev. Hydrobiol. **86**: 23–62.
- HINCH, S. G. & COLLINS, N. C. (1993): Relationships of littoral fish abundance to water chemistry and macrophyte variables in Central Ontario lakes. – Can. J. Fish. Aquat. Sci. **50**: 1870–1878.
- JEFFRIES, M. (1993): Invertebrates colonization of artificial pondweeds of differing fractal dimension. – Oikos **67**: 142–148.

- JEPPESEN, E., JENSEN, J. P. SONDERGAARD, M., LAURIDSEN, T. & LANDKILDEHUS, F. (2000): Trophic structure, species richness and biodiversity in Danish lakes: change along a phosphorus gradient. – *Freshwat. Biol.* **45**: 201–218.
- KEAST, A. (1984): The introduced aquatic macrophyte, *Myriophyllum spicatum*, as habitat for fish and their invertebrate prey. – *Can. J. Zool.* **62**: 1289–1303.
- LILLIE, R. A. & BUDD, J. (1992): Habitat architecture of *Myriophyllum spicatum* L. as an index to habitat quality for fish and macroinvertebrates. – *J. Freshwat. Ecol.* **7**: 113–125.
- LONG, J. M. & FISHER, W. L. (2001): Precision and bias of largemouth, smallmouth, and spotted bass age estimated from scales, whole otoliths, and sectioned otoliths. – *North Amer. J. Fish. Managem.* **21**: 636–645.
- MACEINA, M. J. (1996): Largemouth bass abundance and aquatic vegetation in Florida lakes: an alternative interpretation. – *J. Aquat. Plant Managem.* **34**: 43–47.
- MACEINA, M. J., BETTOLI, P. W., KLUSSMANN, W. G., BETSILL, R. K. & NOBLE, R. L. (1991): Effect of aquatic macrophyte removal on recruitment and growth of black crappies and white crappies in Lake Conroe Texas. – *North Amer. J. Fish. Managem.* **11**: 556–563.
- MADENJIAN, C. P. & CARPENTER, S. R. (1991): Individual-based model for growth of young-of-the-year walleye: a piece of the recruitment puzzle. – *Ecol. Appl.* **1**: 268–279.
- MADSEN, J. D. (1999): Point intercept and line intercept methods for aquatic plant management. – APCRP Tech. Rep. TN APCRP-MI–02. USAE RDC, Vicksburg, MS.
- (1997): Methods for management of nonindigenous aquatic plants. – In: LUKEN, J. O. & THIERET, J. W. (eds): *Assessment and management of plant invasions*. – Springer, New York, NY. pp. 145–171.
- MADSEN, J. D., GETSINGER, K. D., STEWART, R. M. & OWENS, C. S. (2002): Whole lake fluridone treatments for selective control of Eurasian watermilfoil: II. Impacts on submersed plant communities. – *Lake Reserv. Managem.* **18**: 191–200.
- MENZEL, D. W. & CORWIN, N. (1965): The measurement of total phosphorus in sea-water based on the liberation of organically bound fractions by persulfate oxidation. – *Limnol. Oceanogr.* **10**: 280–282.
- Michigan Sea Grant (2003): Zebra mussel infestation monitoring program database: Michigan inland lakes 1992–2003. <http://www.miseagrant.org/ans/lakes.html>. Cited 28 May 2004.
- MIRANDA, L. E. & PUGH, L. L. (1997): Relationship between coverage and abundance, size, and diet of juvenile largemouth bass in winter. – *North Amer. Fish. Managem.* **17**: 601–609.
- MITTELBACH, G. G. (1981): Foraging efficiency and body size: a study of optimal diet and habitat use by bluegills. – *Ecology* **62**: 1370–1386.
- MITTELBACH, G. G. & OSENBURG, C. W. (1993): Stage-structured interactions in bluegill: consequences of adult resource variation. – *Ecology* **74**: 2381–2394.
- MURPHY, J. & RILEY, L. P. (1962): A modified single solution method for the determination of phosphate in natural waters. – *Anal. Chim. Acta.* **27**: 31–36.
- NUSCH, E. A. (1980): Comparison of different methods for chlorophyll and phaeopigment determination. – *Arch. Hydrobiol. Beih. Ergebn. Limnol.* **14**: 14–36.
- OLSON, M. H. (1996): Ontogenetic niche shifts in largemouth bass: variability and consequences for first-year growth. – *Ecology* **77**: 179–190.

- OLSON, M. H., CARPENTER, S. R., CUNNINGHAM, P., GAFNY S., HERWIG, B. R., NIBBELINK, N. P., PELLETT, T., STORLIE, C., TREBITZ, A. S. & WILSON, K. A. (1998): Managing macrophytes to improve fish growth: a multi-lake experiment. – *Fisheries* **23**: 6–12.
- OSENBERG, C. W. & MITTELBACH, G. G. (1989): Effects of body size on the predator-prey interaction between pumpkinseed sunfish and gastropods. – *Ecol. Monogr.* **59**: 405–432.
- OSENBERG, C. W., WERNER, E. E., MITTELBACH, G. C. & HALL, D. J. (1988): Growth patterns in bluegill (*Lepomis macrochirus*) and pumpkinseed (*L. gibbosus*) sunfish: Environmental variation and the importance of ontogenetic niche shifts. – *Can. J. Fish. Aquat. Sci.* **45**: 17–26.
- REGIER, H. A. (1962): Validation of the scale method for estimating age and growth of bluegills. – *Trans. Amer. Fish. Soc.* **91**: 362–374.
- SAVINO, J. F. & STEIN, R. A. (1982): Predator-prey interaction between largemouth bass and bluegills as influenced by simulated, submersed vegetation. – *Trans. Amer. Fish. Soc.* **111**: 255–266.
- SHIMA, J. S. & OSENBERG, C. W. (2003): Cryptic density dependence: Effects of covariation between density and site quality in reef fish. – *Ecology* **84**: 46–52.
- SHOUP, D. E., CARLSON, R. E. & HEATH, R. T. (2003): Effects of predation risk and foraging return on the diel use of vegetated habitat by two size-classes of bluegills. – *Trans. Amer. Fish. Soc.* **132**: 590–597.
- SMITH, K. D. (1993): Vegetation-open water interface and the predator-prey interaction between largemouth bass and bluegills: A field experiment. – MI-DNR Fisheries Research Report No. 2000.
- STEMBERGER, R. S. & LAZORCHAK, J. M. (1994): Zooplankton assemblage responses to disturbance gradients. – *Can. J. Fish. Aquat. Sci.* **51**: 2435–2447.
- TREBITZ, A. S. & NIBBELINK, N. (1996): Effect of pattern of vegetation removal on growth of bluegill: a simple model. – *Can. J. Fish. Aquat. Sci.* **53**: 1844–1851.
- TUGEND, K. I., ALLEN, M. S. & WEBB, M. (2002): Use of artificial habitat structures in U. S. lakes and reservoirs: a survey from the Southern Division, AFS Reservoir Committee. – *Fisheries* **27**: 22–27.
- UNMUTH, J. M. L., HANSEN, M. J. & PELLETT, T. D. (1999): Effects of mechanical harvesting of Eurasian watermilfoil on largemouth bass and bluegill populations in Fish Lake, Wisconsin. – *North Amer. J. Fish. Managem.* **19**: 1089–1099.
- VALLEY, R. D. & BREMIGAN, M. T. (2002 a): Effects of selective removal of Eurasian watermilfoil on age-0 largemouth bass piscivory and growth in southern Michigan lakes. – *J. Aquat. Plant Managem.* **40**: 79–87.
- (2002 b): Effects of macrophyte bed architecture on largemouth bass foraging: implications of exotic macrophyte invasions. – *Trans. Amer. Fish. Soc.* **131**: 234–244.
- WRENN, W. B., LOWERY, D. R., MACEINA, M. J. & REEVES, W. C. (1996): Relationships between largemouth bass and aquatic plants in Guntersville reservoir, Alabama. – *Amer. Fish. Soc. Symp.* **16**: 382–39.