Managing Macrophytes to Improve Fish Growth: A Multi-lake Experiment

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ABSTRACT

Macrophyte harvesting often has been suggested as a way to improve fish growth and size structure in lakes with high densities of submergent macrophytes and stunted fish populations. However, previous experimental tests have provided no clear consensus on whether the technique works for management. We conducted a series of whole-lake manipulations to test the effects of macrophyte removal on growth of bluegill and largemouth bass. We selected four lakes in southern and central Wisconsin for experimental manipulation and nine others for controls. In August 1994, we removed macrophytes from approximately 20% of the littoral zone by cutting a series of evenly spaced, deep channels throughout each treatment lake. In the first year after manipulation, we observed substantially increased growth rates of some age classes of both bluegill and largemouth bass in treatment lakes relative to controls. Growth rates of other age classes were less responsive to manipulation. We observed increased bluegill and largemouth bass growth despite rapid regrowth of macrophytes in our treatment lakes. By May 1996, fewer than 25% of the channels remained. Our results suggest that harvesting macrophytes in a series of deep channels may be a valuable tool for integrated management of fish and macrophytes.

Many lakes and reservoirs across North America suffer from high densities of submergent macrophytes. The thick beds of vegetation that cover the littoral zone are perennial problems in some lakes and recent developments in others (Colle and Shireman 1980; Cooke et al. 1993). Excessive macrophyte growth often can be traced to the invasion of exotic macrophytes such as Eurasian milfoil (*Myriophyllum spicatum*) (Aiken et al. 1979) and hydrilla (Hydrilla *verticillata*) (Haller 1979). As these invaders spread, they displace the diverse community of native species and create a near-monoculture of dense macrophytes (Haller and Sutton 1975; Nichols 1994). Consequently, the aesthetic quality and recreational value of a lake can decline severely.

High densities of macrophytes also can harm the quality of a fishery (Wiley et al. 1984; Bettoli et al. 1992). Dense macrophytes can cause panfish and game fish to become stunted via two pathways. First, feeding rates generally are reduced in lakes with dense macrophytes (Crowder and Cooper 1982). Although prey abundance (either insect or fish) may increase as macrophyte density increases, macrophytes also reduce predator foraging efficiency by providing a refuge for prey. Therefore, feeding rate (determined by the combination of prey abundance and foraging efficiency) is maximized at intermediate macrophyte densities and reduced as densities increase beyond that point (Heck and Crowder 1991; Savino et al. 1992). Second, dense vegetation generally reduces foraging efficiency of piscivores and lowers predator-induced mortality rates of small fishes (Savino and Stein 1982; Gotceitas and Colgan 1989). This reduction in mortality leads to a greater population density and stronger competitive interactions among small fishes (Mittelbach 1988).

Macrophyte Harvesting as a Management Strategy

The potential for improving growth and size-structure of fishes by reducing macrophyte densities

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has long been recognized. As early as 1941, Swingle and Smith recommended macrophyte control as a strategy "for correcting conditions that produce stunted populations in impounded waters" (Swingle and Smith 1941:104). Since that time, the idea has been proposed and tested many times (reviewed in Engel 1995). However, in spite of this research the current status of macrophyte removal as a fishery management tool is unclear. One reason for the uncertainty is the lack of consensus from previous experiments. Even studies conducted with the same fish and macrophyte species have yielded variable results (e.g., Shireman et al. 1985; Cross et al. 1992; Bettoli et al. 1993), in part because experiments were conducted at different scales (e.g., aquaria, cages, experimental ponds) to examine different mechanisms of fish-macrophyte interactions. Furthermore, few studies have provided any practical advice on macrophyte removal. Thus, the logistic challenges of large-scale macrophyte manipulations have not been assessed.

Resolving the status of macrophyte removal as a management tool requires explicit consideration of the scale of experimentation (Levin 1992). To test whether macrophytes can be managed to improve fish growth, the experiment must be conducted on whole lakes. At this scale, all direct and indirect pathways between fish and macrophytes will be affected, and the overall effect of a manipulation can be investigated (Frost et al. 1988). Whole lakes also are the typical unit of management (Kitchell 1992). Therefore, whole-lake experiments can be used as field tests of potential management techniques.

Another important consideration in experimental design is the level of replication (McAllister and Peterman 1992). Replication provides the statistical power necessary to detect an effect, if the effect exists (Cohen 1988). Because the interaction between fish and macrophytes involves many potentially conflicting mechanisms, the possibility of a negative result (i.e., no effect of macrophyte manipulations) is strong. Replication is necessary to allow a conclusion of no effect to be interpreted as a lack of biological change and not a lack of statistical power (Peterman 1990).

A Multi-lake Experiment

In 1994, we initiated a replicated whole-lake experiment to test the hypothesis that submergent macrophytes can be managed to improve fish growth. Our experiment was conducted in southern and central Wisconsin, where Eurasian milfoil has become a nuisance and reduced the recreational value of many lakes (Nichols 1994). High macrophyte densities also have harmed growth rates of important fishes for the recreational fishery such as bluegill (*Lepomis macrochirus*) and largemouth bass (*Micropterus salmoides*), causing concern among anglers (Engel 1987).

The early stages of our experiment involved several planning exercises (Carpenter et al., in press). First, we chose a design that assigned experimental lakes into two groups. We designated one group of lakes to receive a uniform manipulation of littoral zone macrophytes and a second group of lakes to serve as unmanipulated controls. In subsequent analyses, we compared differences between pre- and postmanipulation growth rates of bluegill and largemouth bass in manipulated lakes to control lakes. We focused our analyses on growth responses because changes in fish density can be difficult to detect (Carpenter et al. 1995). Next, we developed a series of simulation models to predict fish growth responses to a range of manipulation intensities (Trebitz and Nibbelink 1996; Trebitz et al. 1997). These models indicated that clearing approximately 20% of the littoral zone of macrophytes would provide meaningful improvements in fish growth and size structure. Finally, we conducted a power analysis to determine the number of experimental lakes needed to detect these predicted responses (Carpenter et al. 1995). To detect changes in growth, the power analysis suggested that we would require at least three lakes per treatment (manipulated or control).

Lakes were selected for the experiment based on several criteria (Carpenter et al., in press). Using insights of state biologists and managers, we chose a set of 13 lakes (Table 1) with similar size structures of bluegill and largemouth bass ◆

Table 1 describes our study lakes in southern and central Wisconsin. Littoral zone area was calculated as the area between shore and the lower depth limit of macrophyte growth. The value for White Mound Lake was not available (NA). Sample sizes reported for bluegill (BG) and largemouth bass (LMB) are for all age classes combined.

Lake	County	Treatment	Area (ha)	% of area in littoral zone	Max. depth	Sample Size BG 1993	Sample Size BG 1995	Sample Size LMB 1993	Sample Size LMB 1995
Fish	Dane	Cut	102.0	54.5	19.0	112	103	172	24
Heidmann	Kewaunee	Cut	10.5	67.2	9.2	69	112	60	13
Silver	Watipaca	Cut	28.3	77.7	5.2	39	118	9	16
Tuma	Manitowoc	Cut	7.7	76.9	9.2	55	125	74	18
East Alaska	Kewaunee	Control	21.5	49.0	15.3	58	87	22	28
Harpt	Manitowoc	Control	12.6	40.0	7.3	56	115	66	25
Horseshoe	Manitowoc	Control	8.9	14.0	16.5	43	75	11	21
Kusel	Waushara	Control	32.0	76.0	8.9	38	106	94	36
Mauthe	Fond du Lac	Control	31.6	42.0	7.1	37	78	5	25
Napowan	Waushara	Control	20.7	87.0	5.5	42	89	36	54
Shea	Kewaunee	Control	13.0	72.0	7.3	73	110	25	6
Wingra	Dane	Control	140.0	89.0	4.3	34	124	47	45
White Mound	Sauk	Control	42.1	NA	8.5	68	114	109	50

(Olson 1996; Nibbelink and Carpenter, in press), macrophyte-dominated littoral zones (i.e., >90% coverage) with high densities of Eurasian milfoil, no history of winterkill (to avoid confounding effects; Tonn and Paszkowski 1986), and no other significant management actions (e.g., chemical rehabilitation, predator management, etc.).

We manipulated macrophytes in four study lakes (cut lakes) in August–September 1994 (Table 1). The other nine lakes served as unmanipulated controls (Table 1; control lakes outnumbered cut lakes because they could be monitored with little effort). In each cut lake, we removed macrophytes in a series of evenly spaced channels that extended from shore to the edge of the littoral zone. In addition to being the most practical method for macrophyte removal (Engel 1995), channels also increase the amount of vegetation-open water edge, which has been hypothesized to be an important zone of interaction in aquatic systems (Smith 1993; Jeppesen et al., in press). Channels were created with a mechanical harvester equipped with a 3-m-wide conventional cutting bar and a second custom-designed cutting bar that could cut a 2-m swath to a depth of 5 m. Macrophytes were cut just above the root crown (to slow regrowth), collected, and transported away from the lake to nearby agricultural fields. Due to variation in lake size and morphometry, the length, number, and width of channels, and the amount of effort varied among lakes (Table 2). However, the percentage of littoral zone cleared of macrophytes from each lake was close to our goal of 20%.

To investigate the effect of macrophyte harvesting on bluegill and largemouth bass growth, we analyzed changes in annual growth rates between 1993 and 1995 (1994 was the manipulation year and was not analyzed). We back-calculated 1993 and 1995 growth rates from scales collected by electrofishing all 13 lakes in spring 1994 (before the experiment began) and 1996, respectively. For each lake, we separated bluegill and largemouth bass populations by age class, and determined mean change in length (mm/yr) for the two years (analyses of growth using change in mass yielded similar results). Growth estimates for each age class were based on average sample sizes of 16.9 ± 1.3 ($\bar{X}$ ± 1 SE) for bluegill and 9.6 ± 1 for largemouth bass; sample sizes for each lake are given in Table 1. In cut lakes, changes in growth between 1993 and 1995 reflected a combination of annual variation in growing conditions and a response to harvesting. In control lakes, growth differences between the two years reflected only annual variation in growing conditions. Therefore, by comparing changes in growth between cut and control lakes (i.e., {95cut–93cut} v {95control–93control}), we could separate the effect of macrophyte harvesting from natural variation in growth (Stewart-Oaten et al. 1986). If the manipulation increased growth rates, then we expected to see growth improve in cut lakes more than in controls.

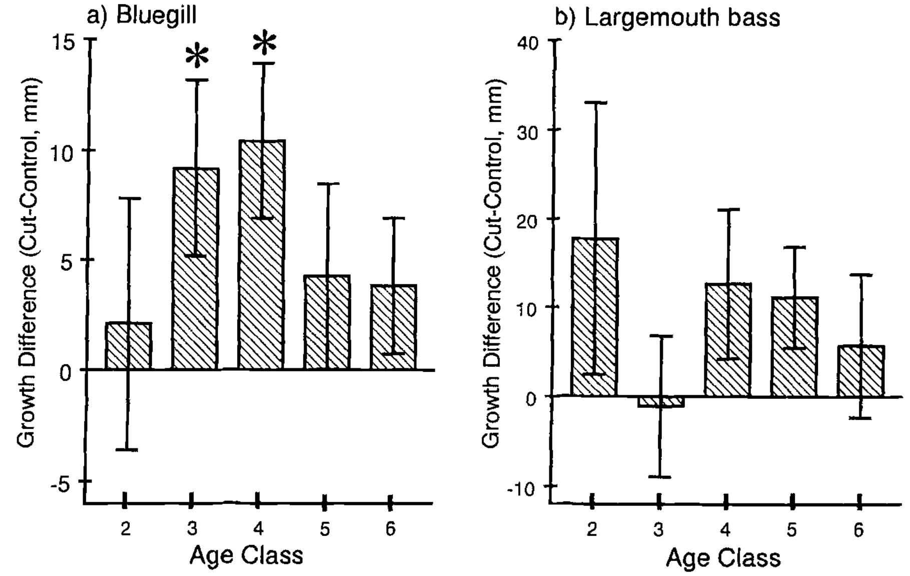

Figure 1 shows differences in growth rates between cut and control lakes for age 2–6 bluegill (a) and largemouth bass (b). Growth differences compare changes in growth rate in mm/yr between 1993 and 1995 in cut and control lakes. Error bars indicate pooled standard deviation. Asterisks indicate that a t-test was significantly different from 0 (p<0.05).

Table 2 summarizes macrophyte manipulations in four cut lakes. All manipulations were done between 8 August and 1 September 1994.

Lake	# of person hours for manipulation	Number of channels	Channel width (m)	Mean channel length (m)	Created edge (m)	% of littoral zone cleared
Fish	240	285	2	123.0	70,110	18.0
Heidmann	104	172	2	43.7	15,032	21.3
Silver	178	127	3	93.2	23,672	15.2
Tuma	121	108	2	46.5	10,044	17.0

Results

Fish Growth Responses

For bluegill, we observed increased growth rates after macrophyte harvesting (Fig. 1a). Interestingly, growth responses were age-dependent. Age-3 and -4 bluegill showed the strongest responses, and growth rates for both age classes were significantly higher in cut lakes relative to controls (Fig. 1a; age-3: t=2.29, df=11, p<0.05, age-4: t=2.98, df=11, p<0.05). Increases for these two age classes were driven by growth rate changes in both cut and control lakes. For example, growth rates of age-4 bluegill in cut lakes increased approximately 8 mm/yr (from 22.4 mm/yr to 30.9 mm/yr), whereas growth in control lakes decreased 2 mm/yr (from 28.6 mm/yr to 26.8 mm/yr). Consequently, there was a 10 mm/yr increase in growth of age-4 bluegill in cut lakes relative to controls. Other age classes also had improved growth rates in cut lakes, but these increases were not statistically significant.

Unlike bluegill, growth rates of largemouth bass did not respond consistently to macrophyte harvesting (Fig. 1b). Although growth rates of most age classes tended to increase in cut lakes (age-3 was the lone exception), these changes were not statistically significant (t-tests; p>0.10 for all largemouth bass age classes).

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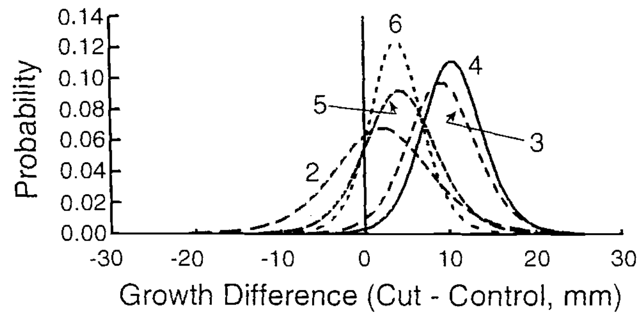
Dense macrophyte beds in the littoral zone of White Mound Lake, Wisconsin, harm the fishery and reduce the lake's recreational value.

To better understand and interpret the effects of macrophyte harvesting, we also analyzed changes in bluegill and largemouth bass growth from a Bayesian perspective (Ellison 1996). Conventional statistical analyses (e.g., t-tests) give the probability of rejecting the null hypothesis that the manipulation has no effect when the null is true (i.e., Type I error), providing a simple yes-no answer (Berger and Berry 1988). In contrast, a Bayesian analysis estimates probabilities for all possible outcomes (Gelman et al. 1995). Using a noninformative prior distribution (i.e., all outcomes have equal probability in the prior probability distribution), this analysis calculates posterior probability distributions from the difference in mean growth responses among cut and control lakes calculated between 1993 and 1995 and the pooled standard deviation. These distributions could then be interpreted directly as the probability of a specified effect (Gelman et al. 1995). Because the distribution describes all outcomes, the area under the curve sums to one. Therefore, combined probabilities for a range of outcomes could be determined. For example, the probability of growth increasing is equal to the area under the curve to the right of zero. Similarly, the probability of a desired (e.g., a 10-mm increase in growth) or undesired result (e.g., a decrease in growth) may be calculated directly.

Based on Bayesian analyses, growth rates of age-3 and -4 bluegill are almost certain to increase after macrophyte harvesting (Fig. 2a). The probability of growth increasing more in cut lakes than controls is very close to 1 for these 2 age classes. In addition, the probability of an increase in growth of at least 10 mm/year is 0.42 for age-3 and 0.55 for age-4. This response represents at least a 35% increase in growth from premanipulation growth rates of 27.5 ± 1.9 mm/yr ($\bar{X} \pm SE$) for age-3 and 22.4 ± 3.7 mm/yr for age-4. Growth rates of other age classes also are likely to increase in

a) Bluegill



b) Largemouth bass

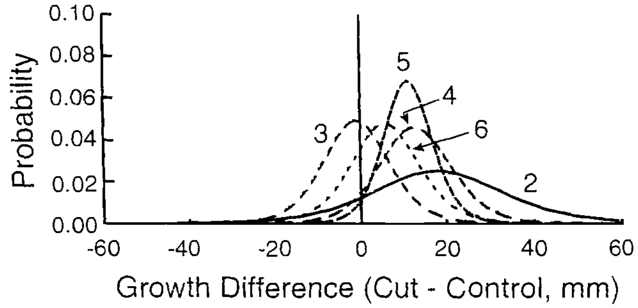


Figure 2 presents posterior probability distributions from a Bayesian analysis for growth differences of age 2–6 bluegill (a) and largemouth bass (b). X-axes represent possible differences between cut and control lakes (calculated as in Fig. 1). Y-axes represent probabilities of different outcomes. Residuals of data were checked for normality prior to analysis.

response to macrophyte harvesting (probability that growth increases more in cut lakes than controls is >0.6 for ages 2, 5, and 6). However, increases for these age classes are likely to be between 0 and 10 mm/yr (Fig. 2a).

For largemouth bass, Bayesian analyses indicate a high probability of growth rates increasing for age-4 and age-5 (Fig. 2b; probability of growth increasing more in cut lakes than controls is >0.9 for both age classes). Increases of 10 mm/yr from premanipulation growth rates of 41.7 ± 8.3 mm/yr for age-4 and 38.4 ± 3.0 mm/yr for age-5 are likely for both age classes (probability is >0.5 for both age classes). Ages 2 and 6 also are likely to grow better after harvesting, and increases of more than 20 mm/yr are possible for age-2 (probability =0.44). In contrast, growth rates of age-3 largemouth bass could increase or decrease with equal probability after harvesting. This result is expected when the manipulation has no effect, and growth rates vary among years.

The variation in growth responses among age classes of both bluegill and largemouth bass is not surprising considering diets of both species are strongly size-dependent. Bluegill typically undergo a diet shift as a result of changes in predator-mediated habitat use (Mittelbach 1981). Up to 80 mm long, bluegill feed primarily on vegetation-dwelling invertebrates, whereas bluegill above 125 mm feed on zooplankton (Mittelbach 1981; Werner and Hall 1988). Between these two sizes, bluegill consume a combination of both prey types (Werner and Hall 1988) and, therefore, would be expected to benefit from an increase in the amount of edge between vegetation and open water. This size range corresponds closely to the two age classes that responded most strongly to our manipulation (age-3: $\bar{X}=92.8 \pm 5.6$ mm at the start of 1995; age-4: $\bar{X}=111.7 \pm 6.7$ mm). Largemouth bass diets also change with size. In our study lakes, largemouth bass switch from a diet of invertebrates to primarily bluegill at a length of 100 mm (Olson 1996). Because largemouth bass are gape-limited predators, they can consume only bluegill that are <40% their own length (Lawrence 1958; Timmons et al. 1980). The two age classes of largemouth bass that responded most strongly to macrophyte harvesting, age-4 and age-5, are capable of consuming bluegill up to 106 mm and 17 mm, respectively. Growth responses of bluegill suggest that fish of these sizes use channels. Therefore, our experiment suggests that harvesting macrophytes may lead to increased prey availability and growth of age-4 and -5 largemouth bass.

Macrophyte Regrowth

Macrophytes recovered quickly from harvesting. From aerial counts of channels, we estimated that an average of 23% of the original channels remained in May 1996, 21 months after our manipulation occurred (Fig. 3). Remaining channels also were much shorter in 1996, with the most significant regrowth occurring in shallow water (0–2 m). Channels persisted most strongly in Fish Lake, where Eurasian milfoil grows to depths of 2 m–5 m.

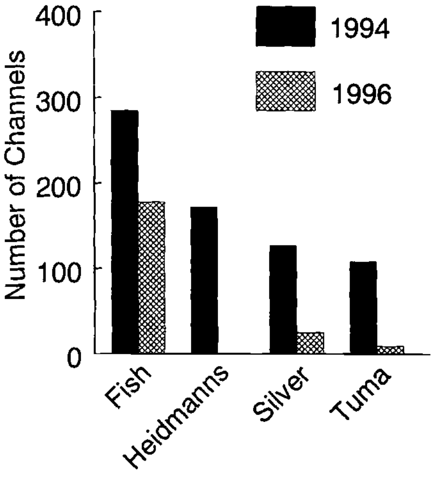


Figure 3 shows the number of channels in cut lakes. Channels were counted from aerial photos of each lake in 1994 (after harvesting) and 1996. No channels were visible in Heidmanns Lake in 1996.

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This aerial photo shows the spatial arrangement of channels after macrophyte harvesting.

Conclusions

Because macrophytes quickly returned to premanipulation densities, our experiment was a short-term perturbation. Our August 1994 manipulation of macrophytes lasted only through the 1995 growing season, and by summer 1996 the manipulation was essentially over in all but one lake. Nevertheless, we observed strong positive responses in growth rates of some age classes of both bluegill and largemouth bass. Although these increases were temporary, their effects will persist as an increase in bluegill and largemouth bass size structure for the lifetime of the affected age classes. We did not measure the longer-term effects of repeated macrophyte harvesting.

Results of this study suggest that macrophyte harvesting can be a useful technique for improving growth rates and size structures of panfish and game fish. Substantial increases in fish growth are possible with a manageable level of effort. In our experiment, harvesting macrophytes from 20% of the littoral zone was sufficient to temporarily increase growth rates of bluegill and largemouth bass. Models suggest that similar results should occur with macrophyte harvests of up to 40% of the littoral zone (Trebitz and Nibbelink 1996; Trebitz et al. 1997). In many lakes, mechanical harvesters are already used to control nuisance macrophytes. Our study suggests that changing the strategy of harvesting from clear-cutting the top meter of vegetation to selectively cutting deep channels throughout the lake may simultaneously improve the fishery and recreational value of a lake.

Acknowledgments

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References

Aiken, S. G., P. R. Newroth, and **I. Wile.** 1979. The biology of Canadian weeds. Myriophyllum spicatum. L. Can. J. Plant Sci. 59:201–215.

Berger, J. O., and **D. A. Berry.** 1988. Statistical analysis and the illusion of objectivity. Am. Sci. 76:159–165.

Bettoli, P. W., M. J. Maceina, R. L. Noble, and **R. K. Betsill.** 1992. Piscivory in largemouth bass as a function of aquatic vegetation abundance. N. Am. J. Fish. Manage. 12:509–516.

Bettoli, P. W., M. J. Maceina, R. L. Noble, and **R. K. Betsill.** 1993. Response of a reservoir fish community to aquatic vegetation removal. N. Am. J. Fish. Manage. 13:110–124.

Carpenter, S. R., and **eight coauthors.** 1995. Responses of bluegill to habitat manipulations: power to detect effects. N. Am. J. Fish. Manage. 15:519–527.

———. In press. Macrophyte structure and growth of bluegill (*Lepomis macrochirus*): design of a multi-lake experiment. *In* E. Jeppesen, K. Christoffersen, and M. Sondergaard, eds. The role of submerged macrophytes in structuring lakes. Springer-Verlag, Berlin.

Cohen, J. 1988. Statistical power analysis for the behavioral sciences, 2nd ed. L. Erlbaum Associates, Hillsdale, NJ.

Colle, D. E., and **J. V. Shireman.** 1980. Coefficients of condition for largemouth bass, bluegill, and redear sunfish in Hydrilla-infested lakes. Trans. Am. Fish. Soc. 109:521–531.

Cooke, G. D., E. B. Welch, S. A. Peterson, and **P. R. Newroth.** 1993. Lake and reservoir restoration. Lewis Publishers, Boca Raton, FL.

Cross, T. K., M. C. McInerny, and **R. A. Davis.** 1992. Macrophyte removal to enhance bluegill, largemouth bass, and northern pike populations. Section of Technical Services Investigational Report 415. Minnesota Department of Natural Resources, Division of Game and Fish, St. Paul.

Crowder, L. B., and **W. E. Cooper.** 1982. Habitat structural complexity and the interaction between bluegills and their prey. Ecology 63:1,802–1,813.

Ellison, A. M. 1996. An introduction to Bayesian inference for ecological research and environmental decision-making. Ecol. Appl. 6:1,036–1,046.

Engel, S. 1987. The impact of submerged macrophytes on largemouth bass and bluegills. Lake Reserv. Manage. 3:227–234.

———. 1995. Eurasian watermilfoil as a fishery management tool. Fisheries 20(3):20–27.

Frost, T. M., D. L. DeAngelis, S. M. Bartell, D. J. Hall, and **S. H. Hurlbert.** 1988. Scale in the design and interpretation of aquatic community research. Pages 229–258 *in* S. R. Carpenter, ed. Complex interactions in lake communities. Springer-Verlag, New York.

Gelman, A., J. B. Carlin, H. S. Stern, and **D. B. Rubin.** 1995. Bayesian data analysis. Chapman and Hall, New York.

Gotceitas, V., and **P. Colgan.** 1989. Predator foraging success and habitat complexity: quantitative test of the threshold hypothesis. Oecologia 80:158–166.

Haller, W. T. 1979. Aquatic weeds in Florida. Pages 1–14 *in* J. V. Shireman, ed. Proceedings of the Grass Carp Conference. University of Florida, Gainesville.

Haller, W. T., and **D. L. Sutton.** 1975. Community structure and competition between hydrilla and vallisneria. Hyacinth Control Journal 13:48–50.

Heck, K. L., and **L. B. Crowder.** 1991. Habitat structure and predator-prey interactions in vegetated aquatic systems. Pages 281–299 *in* S. S. Ball, E. D. McCoy, and H. R. Mushinsky, eds. Habitat structure: the physical arrangement of objects in space. Chapman and Hall, London.

Jeppesen, E., K. Christoffersen, and **M. Sondergaard,** eds. In press. The role of submerged macrophytes in structuring lakes. Springer-Verlag, Berlin.

Kitchell, J. F., ed. 1992. Food web management: a case study of Lake Mendota. Springer-Verlag, New York.

Lawrence, J. M. 1958. Estimated sizes of various forage fishes largemouth bass can swallow. Proc. Ann. Conf. SE Assoc. Game Fish Comm. 11:220–225.

Levin, S. A. 1992. The problem of pattern and scale in ecology. Ecology 73:1,943–1,967.

Mittelbach, G. G. 1981. Foraging efficiency and body size: a study of optimal diet and habitat use by bluegills. Ecology 62:1,370–1,386.

———. 1988. Competition among refuging sunfishes and effects of fish density on littoral zone invertebrates. Ecology 69:614–623.

McAllister, M. K., and **R. M. Peterman**. 1992. Experimental design in the management of fisheries: a review. N. Am. J. Fish. Manage. 12:1–18.

Nibbelink, N. P., and **S. R. Carpenter**. In press. Interlake variation in growth and size structure of bluegill: inverse analysis of an individual-based model. Can. J. Fish. Aquat. Sci.

Nichols, S. A. 1994. Evaluation of invasions and declines of submersed macrophytes for the Upper Great Lakes region. Lake Reserv. Manage. 10:29–33.

Olson, M. H. 1996. Predator-prey interactions in size-structured fish communities: implications of prey growth. Oecologia 108:757–763.

Peterman, R. M. 1990. Statistical power analysis can improve fisheries research and management. Can. J. Fish. Aquat. Sci. 47:2–15.

Savino, J. F., **E. A. Marschall**, and **R. A. Stein**. 1992. Bluegill growth as modified by plant density: an exploration of underlying mechanisms. Oecologia 89:153–160.

Savino, J. F., and **R. A. Stein**. 1982. Predator-prey interaction between largemouth bass and bluegills as influenced by simulated, submersed vegetation. Trans. Am. Fish. Soc. 111:255–266.

Shireman, J. V., **M. V. Hoyer**, **M. J. Maceina**, and **D. E. Canfield, Jr.** 1985. The water quality and fishery of Lake Baldwin, Florida, four years after macrophyte removal by grass carp. Lake Reserv. Manage. 1:201–206.

Smith, K. D. 1993. Vegetation-open water interface and the predator-prey interaction between largemouth bass and bluegills. Doctoral dissertation. University of Michigan, Ann Arbor.

Stewart-Oaten, A., **W. W. Murdoch**, and **K. R. Parker**. 1986. Environmental impact assessment: "pseudoreplication" in time? Ecology 67:929–940.

Swingle, H. S., and **E. V. Smith**. 1941. The management of ponds with stunted fish populations. Trans. Am. Fish. Soc. 71:102–105.

Timmons, T. J., **W. J. Shelton**, and **W. D. Davies**. 1980. Differential growth of largemouth bass in West Point Reservoir, Alabama-Georgia. Trans. Am. Fish. Soc. 1098:176–186.

Tonn, W. M., and **C. A. Paszkowski**. 1986. Size-limited predation, winter-kill, and the organization of Umbra-Perca assemblages. Can. J. Fish. Aquat. Sci. 43:194–202.

Trebitz, A. S., and **N. P. Nibbelink**. 1996. Effect of pattern of vegetation removal on growth of bluegill: a simple model. Can. J. Fish. Aquat. Sci. 53:1,844–1,851.

Trebitz, A. S., and **11 coauthors**. 1997. A model of bluegill-largemouth bass interactions in relation to aquatic vegetation and its management. Ecol. Model. 94:139–156.

Werner, E. E., and **D. J. Hall**. 1988. Ontogenetic habitat shifts in bluegill: the foraging rate-predation risk trade-off. Ecology 69:1,352–1,366.

Wiley, M. J., **R. W. Gorden**, **S. W. Waite**, and **T. Powless**. 1984. The relationship between aquatic macrophytes and sport-fish production in Illinois ponds: a simple model. N. Am. J. Fish. Manage. 4:111–119.