

Largemouth Bass Diets in Two Aquatic Plant Communities

ERIC D. DIBBLE AND S. L. HARREL¹

ABSTRACT

Differences in the architecture among aquatic plant beds provide a diverse structural habitat potentially important to foraging fishes. To examine potential effects that aquatic plants have on feeding largemouth bass (*Micropterus salmoides* Lacepede), we measured for differences in diets of adult (\bar{X} = 264 mm, TL) and juvenile (\bar{X} = 102 mm, TL) bass feeding in two aquatic plant species: common pondweed (*Potamogeton nodosus* Poiret) and Eurasian watermilfoil (*Myriophyllum spicatum* L.). We constructed enclosures (10 m diam) within a pond (0.2 ha) to serve as experimental replicates and to control for the treatment of plants and prey fishes. Macroinvertebrates were sampled in each enclosure to determine abundance across the plant treatments, yet no significant difference was noted in these densities. However, the diets of both juvenile and adult fish differed between the aquatic plants. Diets from the adult largemouth bass feeding in common pondweed constituted 86% macroinvertebrates and 14% prey fish, yet when feeding in Eurasian watermilfoil, diets constituted 25% macroinvertebrates and 75% prey fish. Similarly, diets of juvenile largemouth bass in pondweed consisted of 71% macroinvertebrates and 29% prey fish, whereas in Eurasian watermilfoil, 67% of their diets was prey fish and only 33% macroinvertebrates. These results suggested the architecture of a particular species of aquatic plant may contribute to differences in diets of adult and juvenile largemouth bass.

Key words: fish, *Myriophyllum spicatum*, *Potamogeton nodosus*, *Micropterus salmoides*, foraging, plant architecture, invertebrates.

INTRODUCTION

Morphological differences among aquatic plant species provide structural variety important to fish habitat. Aquatic plants serve as structural refugia that influences prey availability (Savino and Stein 1982) and provide substrate for the attachment of invertebrates that fish feed upon (Pardue 1973, Keast 1984). Differences in stem densities among aquatic plants can alter foraging efficiency of fish by increasing search times and decreasing capture rates of prey (Minello and Zimmerman 1983, Anderson 1984). In addition, orientation of underwater structure (i.e., configuration of stems and leaves) in aquatic habitat can influence available light, which may benefit feeding behaviors in fishes

(Helfman 1981, Diehl 1988, Johnson 1993). Examining differences among aquatic plants and their effect on foraging ecology of fishes is important, because factors that influence availability of food and protection from predators in aquatic habitat affect growth and survival of fishes (Mittelbach 1981, Savino and Stein 1992).

Recent studies suggest that micro-level responses by individual fish to refugia provided by aquatic plants can determine population dynamics of fishes present in a system by altering diets and growth (Adams and DeAngelis 1987, Diehl 1993, Diehl and Eklov 1995). System level measurements of aquatic plant habitats, such as % coverage and biomass, are common; however, measurements made at this scale may not be relevant to delineate critical mechanisms that ultimately influence dynamics of fish populations (Dibble et al. 1996b). Recently, methods have been developed to better quantify attributes of aquatic plants potentially important to fish populations (Dionne and Folt 1991, Lillie and Budd 1992, Wychara et al. 1993, Dibble et al. 1996a). Much of the emphasis has been theoretical and concerned with direct and indirect influences of stem density and habitat complexity on fish populations (Crowder and Cooper 1982, Sih 1987), yet little is known whether the variation of growth forms between macrophytes have a differential impact on the foraging efficiency of fishes.

To investigate the hypothesis that aquatic plants of two distinct morphologies have different effects on foraging fishes, we conducted an enclosure experiment in a pond and compared diets of adult and juvenile largemouth bass (*Micropterus salmoides* Lacepede) foraging within two aquatic plants. We used Eurasian watermilfoil (*Myriophyllum spicatum* L.) and common pondweed (*Potamogeton nodosus* Poiret) as our plant treatments because they exhibit different structural architecture (Dibble et al. 1996a). Eurasian watermilfoil with its branching stems containing featherlike whorled leaves and leaflets, contrasts with common pondweed with its more slender and erect stems containing wide alternate leaves. Eurasian watermilfoil is a prolific exotic species that frequently out-competes native plants endemic to many lakes (Haller and Sutton 1975, Madsen et al. 1991). Adult and juvenile largemouth bass were used in separate trials because structural habitats can exhibit differential effects that are dependent on the life stage of the fish (Savino and Stein 1989).

METHODS AND MATERIALS

This experiment was conducted in a 0.2-ha pond at the U.S. Army Corps of Engineers Aquatic Ecosystem Research Facility (LAERF) located in Lewisville, Texas. The pond was lined with gravel (< 25 mm in diameter) and a plastic ground

¹Department of Wildlife and Fisheries, P.O. Box 9690, Mississippi State, MS 39762. Received for publication February 10, 1997 and in revised form July 1, 1997.

barrier to prevent incidental growth of rooted aquatic plants. Six circular enclosures (approximately 10 m in diameter) were constructed with PVC pipe and plastic shade cloth (mesh size < 0.5 mm). Water levels were maintained in the pond during each trial so all enclosures contained similar depths (range = 1.5 - 1.6 m).

For each plant treatment a single species was planted into three of the six enclosures, representing three replications of the treatment. Plant sprigs (10-15 cm tall) were transplanted from low-flow aquatic raceways where they were propagated into four small plastic pools (1.5 m diameter) positioned in the center of the enclosures. To control for equal plant coverage within the enclosure, plant sprigs were transplanted at similar density of 10 plants/m². Plants were allowed to grow and mature (top out at surface with flowers) before fish were stocked, and surface coverages were similar among all enclosures (approximately 80% of the surface area). A new plant treatment was planted before each trial was begun.

The day before each trial was run and prior to introduction of predators into the enclosures, interstitial configuration was measured within the plants by a diver. Length and frequency of interstices (gaps between stems and leaves) were measured along horizontal and vertical transects (approximately 1 m in length) within the plants (c.f., Dibble et al. 1996a). Transects were randomly placed within plants and replicated 12× for each plant treatment. Vertical transects started at the water surface in the upper plant strata and were run to the lower plant strata and substrate; horizontal transects were placed within the plants at mid strata (approximately 0.3 m depth). Interstitial frequency represented the total number of gaps between leaves and stems intercepted by vertical (f_v) and horizontal (f_h) transects. Interstitial length represented the mean length (mm) of all gaps between stems and leaves measured along vertical (l_v) and horizontal (l_h) transects. Significance in the difference of interstitial frequencies and lengths between plant treatments was determined with a one-way AOV (Statistix 1994).

We conducted the first trial in August (1993) using adult largemouth bass. Five largemouth bass (\bar{X} = 264, range 209-380 mm TL) were introduced into each enclosure containing a respective plant treatment. Prior to introduction into the experimental enclosures, the fish were kept approximately 7 d in aerated fiberglass holding tanks (3 m diameter) to allow complete digestion of stomach contents and assure active foraging when introduced into the enclosures. In September (1994) we ran a second trial using juvenile largemouth bass. We introduced 25 juveniles (\bar{X} = 102, range = 86-142 mm TL) into each enclosure. As in the previous year, these fish were held in a raceway containing no food items for a 2 d period prior to the experiment to assure empty stomachs and stimulate foraging.

Prey fish abundance was controlled across treatments in both experiments by introducing equal numbers into each enclosure. One hundred prey fishes comprised of 60 bluegill (*Lepomis macrochirus* Rafinesque) (\bar{X} = 32, range = 26-43 mm TL) and 40 largemouth bass (\bar{X} = 57, range = 48-62 mm TL) were introduced into each enclosure as prey for adult largemouth bass in the first trial. Because largemouth bass used in the juvenile trial were considerably smaller than largemouth bass used in the adult trial, we introduced smaller prey

fishes. Similar to the adult trial, 100 of these fishes were introduced into each enclosure and were comprised of 70 bluegill (\bar{X} = 29, range = 24- 41 mm TL) and 30 fathead minnows (*Pimephales promelas* Rafinesque) (< 60 mm). We observed no initial mortality after stocking prey fishes in the trials indicating availability was equal across plant treatments.

After a 3-d acclimation period for prey fishes and approximately 12 h prior to introduction of predator fish, the naturally established invertebrate populations were sampled during each trial to determine prey availability across plant treatments. Dip-nets and a modified Gerking plexiglass box sampler (150 × 300 mm) (Gerking 1957) were used to sample invertebrates. One net sample and three box samples (upper, middle, and lower strata) were collected in each replicate of both plant treatments, for a total of 12 invertebrate samples/treatment. Net samples were taken by placing the net on the bottom substrate and retrieving it quickly through the plants to the surface. Discrete samples were collected by clasp the box sampler around a section of plants, clipping protruding stems and leaves, and retrieving it. Samples were preserved in 70% ethanol and later processed by identifying and recording abundances of macroinvertebrates. Relative availability (%) of prey items was based on total numbers of each species of macroinvertebrate. Normality of macroinvertebrate data was assessed with a Wilk-Shapiro Rankit test and because data exhibited a non-normal distribution, significance of difference in these data was determined with the Kruskal-Wallis statistic (H) (Statistix 1994).

After largemouth bass were introduced into enclosures during each trial, they were allowed to feed for approximately 12 h prior to pond drainage. Fish were removed from each enclosure using a combination of dip-nets and seines. Electro-gear and rotenone were avoided so as not to bias diets and alter natural feeding behaviors by the fish. The pond took approximately 20 h to drain to the level where fish could be removed, thus accurate measurement of plant architecture effects on the diets during standing water levels and prior to pond drainage was unattainable. Diets here were based on items taken from stomachs from fish feeding during the total 32 hr period.

During adult trials, diets from the fish collected were immediately determined by stomach dissection conducted in the laboratory at LAERF. All largemouth bass collected during the juvenile trials were preserved in 10% formalin and transported to U.S. Army Corps of Engineers Waterways Experiment Station (WES), Vicksburg, Mississippi, where prey items were removed from stomachs and diets determined. Macroinvertebrates were identified by family or order, and prey fishes were delineated to species; however, unidentified species of fish that were partially digested were defined as *fish* sp. Prevalence of prey in diets was expressed as occurrence percentage and number of fish or invertebrate prey/stomach. The magnitude of treatment effect on diets within trials was measured with a Chi-square goodness of fit X^2 (Statistix 1994).

RESULTS AND DISCUSSION

Relative abundance of prey did not differ ($H = 0.004$, $P > 0.5$) across the two plant treatments (Table 1), however, diets of the adult and juvenile largemouth bass did ($X^2 = 265$, $P <$

TABLE 1. RELATIVE ABUNDANCE OF MACROINVERTEBRATES SAMPLED IN THE TWO AQUATIC PLANTS PRIOR TO ADULT AND JUVENILE TRIALS (DATA ARE POOLED FOR 3 ENCLOSURE REPLICATES).

Macroinvertebrate	Common Pondweed		Eurasian Watermilfoil	
	(No.)	(%)	(No.)	(%)
<i>Adult trial</i>				
Zygotera	52	52	84	70
Aeshnidae	12	12	9	7
Libellulidae	33	33	24	20
Baetidae ^a	—	—	—	—
Belostomatidae	4	4	3	3
Chironomidae ^a	—	—	—	—
<i>Juvenile trial</i>				
Zygotera	0	0	0	0
Aeshnidae	4	<1	4	<1
Libellulidae	7	<1	5	<1
Baetidae	0	0	1	<1
Belostomatidae ^a	—	—	—	—
Chironomidae	3,372	99	2,990	99

^aPrey items were not recorded from the sample because none were found in diets of the fish.

0.01 and $X^2 = 119.4$, $P < 0.001$, respectively). A total of 126 macroinvertebrates and 71 prey fishes were removed from stomachs of adult largemouth bass, and 189 macroinvertebrates and 102 prey fishes from the juveniles. Species composition of prey fishes eaten during the trials was comprised of approximately 89% bluegill, 7% largemouth bass, 4% fish sp. in the adult trial, and 41% bluegill, 36% fathead minnows, and 20% fish sp. during the juvenile trial.

Both size classes of largemouth bass fed on the larger invertebrate prey items in both plants (Table 2), although Chironomidae occurred most frequently (48%) in juvenile stomachs from common pondweed. In Eurasian watermilfoil, 54% of the macroinvertebrate prey were Libellulidae and 41% Chironomidae. Juvenile largemouth bass fed on Aeshnidae and Libellulidae in common pondweed and only on Libellulidae in Eurasian watermilfoil. Libellulidae and Aeshnidae constituted much of the macroinvertebrates eaten by adult largemouth bass in both plant treatments (Table 2).

It appeared that piscivory was more prevalent in Eurasian watermilfoil than in common pondweed. Macroinvertebrates were the most abundant prey items in the diets of largemouth bass feeding in common pondweed (Figure 1). Macroinvertebrates and fish numerically comprised 86% and 14% of the diet, respectively, in this treatment. However, diets of the adult largemouth bass measured in Eurasian watermilfoil consisted of 25% macroinvertebrates and 75% prey fishes. Similarly, juvenile largemouth bass fed more on macroinvertebrates (72%) than prey fishes (29%) in common pondweed and more on prey fishes (67%) than macroinvertebrates (33%) in Eurasian watermilfoil (Figure 1).

A variety of factors can contribute to differences in diets of fish feeding in aquatic plants. Decreases in total lake biomass and areal % coverage of aquatic plants can result in increases in piscivory due to temporarily altering the size of available refugia for prey fishes (Bettelli et al. 1992), whereas, increases can delay onset of piscivory in juvenile fishes (Colle

TABLE 2. PREVALENCE OF MACROINVERTEBRATES MEASURED IN DIETS OF THE ADULT AND JUVENILE LARGEMOUTH BASS SAMPLED IN THE TWO AQUATIC PLANT TREATMENTS (DATA WERE POOLED FOR 3 ENCLOSURE REPLICATES).

Macroinvertebrate	Common Pondweed		Eurasian Watermilfoil	
	(No.)	(%)	(No.)	(%)
<i>Adult trial</i>				
Zygotera	8	7	0	0
Aeshnidae	49	46	12	67
Libellulidae	37	35	6	33
Baetidae	0	0	0	0
Belostomatidae	13	12	0	0
Chironomidae	0	0	0	0
<i>Juvenile trial</i>				
Zygotera	3	2	1	2
Aeshnidae	38	23	1	2
Libellulidae	45	28	25	53
Baetidae	7	4	1	2
Belostomatidae	0	0	0	0
Chironomidae	69	43	19	40

and Shireman 1980). Biomass was not relevant to the scale at which this study was conducted and % coverage of plants was controlled and similar in all the experimental enclosures.

Differences in plant morphology may have been more relevant, because significant differences were measured in the frequency ($F = 25.82$, $P < 0.01$) and length ($F = 13.08$, $P < 0.01$) of vertical and horizontal interstices between plant treatments when the ponds were flooded. The frequency of both vertical and horizontal interstices was high and the mean length short in pondweed relative to watermilfoil (Table 3). Others have suggested that stem complexities and the size and orientation of interstitial spacing in aquatic habitats are important to fishes because they influence foraging efficiency (Lynch and Johnson 1989, Johnson 1993, Savino and Stein 1982, Anderson 1984, Diehl 1988).

TABLE 3. INTERSTITIAL MEASUREMENTS^a OF GAPS BETWEEN STEMS AND LEAVES OF THE TWO AQUATIC PLANTS (F_h = FREQUENCY OF HORIZONTAL INTERSTICES/M; L_h = LENGTH (MM) OF HORIZONTAL INTERSTICES; F_v = FREQUENCY OF VERTICAL INTERSTICES/M; L_v = LENGTH (MM) OF VERTICAL INTERSTICES). (DATA ARE POOLED FOR 4 LINE TRANSECTS TAKEN IN EACH ENCLOSURE REPLICATE).

Rep.	Common Pondweed				Eurasian Watermilfoil			
	f_h	l_h	f_v	l_v	f_h	l_h	f_v	l_v
<i>Adult trial</i>								
1	40.7	22.6	41.9	22.7	22.0	33.6	25.0	37.5
2	32.7	27.9	26.9	35.3	16.6	52.5	21.1	33.2
3	34.7	26.7	29.8	30.1	19.3	47.5	21.0	42.1
<i>Juvenile trial</i>								
1	43.0	19.8	12.9	32.5	13.3	35.9	14.3	39.9
2	39.6	15.0	22.7	28.5	11.8	44.5	8.9	54.9
3	44.7	17.1	23.3	25.3	6.1	76.9	6.9	88.4

^asignificant differences were measured in the frequency ($F = 25.82$, $P < 0.01$) and length ($F = 13.08$, $P < 0.01$) of vertical and horizontal interstices between plant treatments when the ponds were flooded.

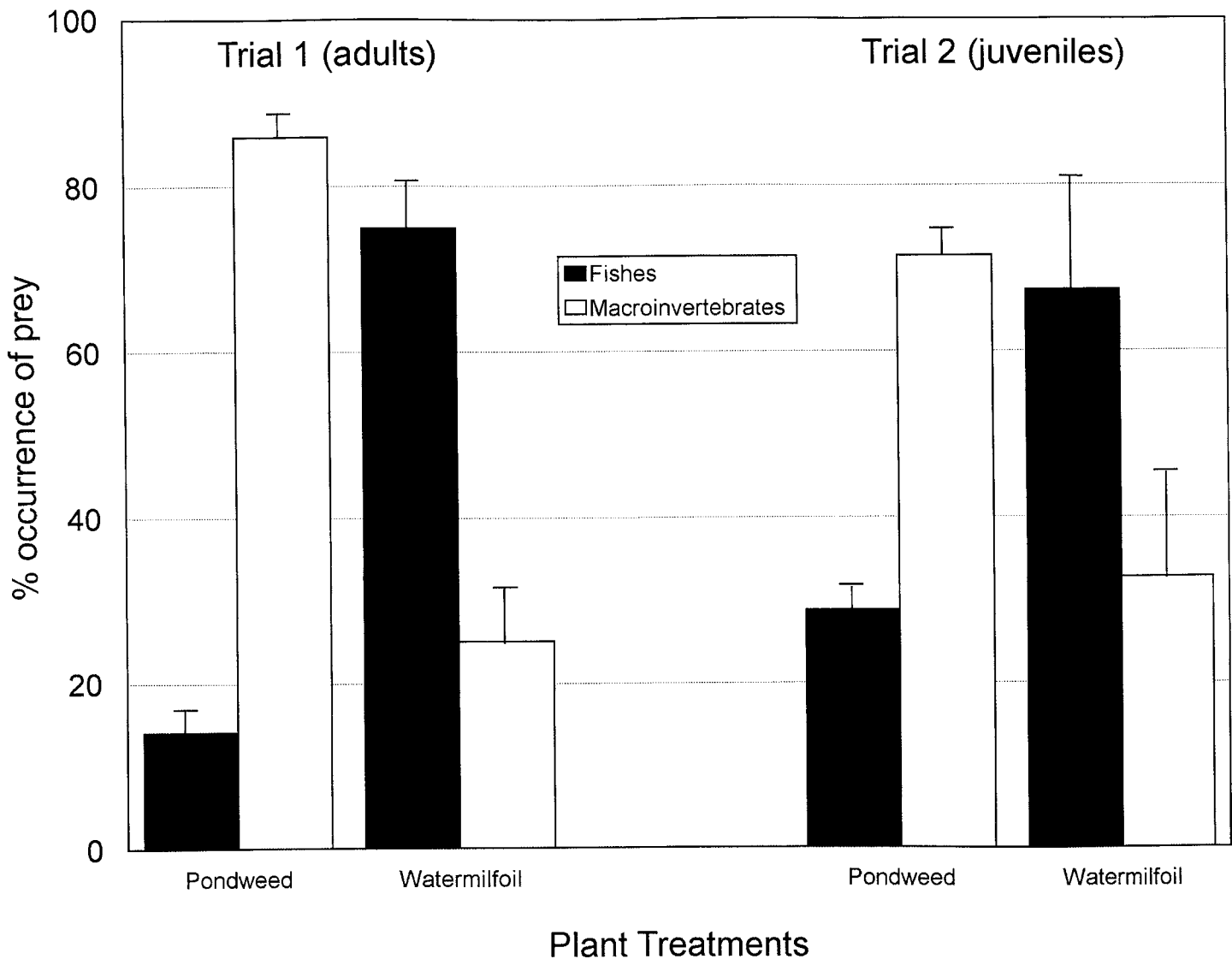


Figure 1. Difference in percent occurrence of total macroinvertebrates and prey fish measured in diets of the adult and juvenile largemouth bass among 3 replicated treatments containing Common pondweed (*Potamogeton nodosus*) and Eurasian watermilfoil (*Myriophyllum spicatum*). Bars indicate mean + one standard error.

Although architectural changes in the macrophytes were not monitored during the drop in water level when we drained the pond, ingestion of prey items by the largemouth bass in both trails was significantly different between plant treatments. We observed differences between the two macrophytes when water levels changed, which reflected the quantitative measurements of the plants taken prior to pond drainage. As water levels dropped, common pondweed maintained and provided a more regular and spatially consistent habitat than the Eurasian watermilfoil, whereas the canopy of Eurasian watermilfoil collapsed more irregularly, forming large gaps, interspersed between submersed clumps of dense tangled stems and leaves. This irregular canopy formation is typical in monotypic beds of watermilfoil (Barko and Smart 1981) and it aggrandized as the water level decreased.

Our data suggest that aquatic plant architecture may have been responsible for the differences in the largemouth bass

diets. We hypothesize that foraging efficiency was altered differentially due to interference by stem and leaf configuration. Understanding how aquatic plants impact foraging efficiency of fishes at this level may not be directly relevant to the lake manager, however, indirectly it is relevant because it may mediate growth and survival, and ultimately affect dynamics in fish populations at a system level (Gutreuter and Anderson 1985 Adams and DeAngelis 1987). This study represents a preliminary step in evaluating morphological differences in aquatic plants at a scale important to individual fish, and future study is required to examine how these differences may impact fish populations at the community level.

ACKNOWLEDGMENTS

We would like to thank M. Belk, R. Drenner, K. Getsinger, K. Killgore, and S. Miranda for providing editorial comments

on the manuscript. We appreciate M. Crouch, G. Dick, J. Snow and other personnel at the U.S. Army Corps of Engineers Aquatic Ecosystem Research Facility, Lewisville, Texas for their technical assistance on the experiment. Additional appreciation goes to K. Gallow and K. Murphy for their help in the laboratory and field. Funding for this experiment was provided by the U.S. Army Corps of Engineers Aquatic Plant Control Research Program.

LITERATURE CITED

- Adams, S. M. and D. L. DeAngelis. 1987. Indirect effects of early bass-shad interaction on predator population structure and food web dynamics. Pages 103-117. *in* W. C. Kerfoot and A. Sih, editors. *Predation: Direct and Indirect Impacts on Aquatic Communities*. University Press of New England, Hanover, NH. 386 pp.
- Anderson, O. 1984. Optimal foraging by largemouth bass in structured environments. *Ecology* 65: 351-861.
- Barko, J. W. and R. M. Smart. 1981. Comparative influences of light and temperature on the growth and metabolism of selected submersed freshwater macrophytes. *Ecological Monographs* 51: 219-235.
- Bettolli, P. W., M. J. Maceina, R. L. Noble, and R. K. Betsill. 1992. Piscivory in largemouth bass as function of aquatic vegetation abundance. *North American Journal of Fisheries Management*. 12: 509-516.
- Colle, D. E. and J. V. Shireman. 1980. Coefficients of condition of largemouth bass, bluegill, and redear sunfish in hydrilla-infested lakes. *Transactions of the American Society* 109: 521-531.
- Crowder, L. B. and W. E. Cooper. 1982. Habitat structural complexity and the interaction between bluegill and their prey. *Ecology* 63: 1802-1813.
- Dibble, E. D., G. Dick, and K. J. Killgore. 1996a. Measurement of plant architecture in seven aquatic plants. *Journal of Freshwater Ecology* 11: 311-318.
- Dibble, E. D., K. J. Killgore and S. L. Harrel. 1996b. Assessment of fish-plant interactions. *in* L. E. Miranda and D. R. DeVries, editors. *Multidimensional Approaches to Reservoir Fisheries Management*. American Fisheries Society, Symposium 16, Bethesda, Maryland. 463 pp.
- Diehl, S. 1988. Foraging efficiency of 3 fresh-water fishes: effects of structural complexity and light. *Oikos* 53: 207-214.
- Diehl, S. 1993. Effects of habitat structure on resource availability, diet and growth of benthivorous perch, *Perca fluviatilis*. *Oikos* 67: 403-414.
- Diehl, S. and P. Eklov. 1995. Prey refuges affecting interactions between piscivorous perch and juvenile perch and roach. *Ecology* 76: 70-81.
- Dionne, M. and C. L. Folt. 1991. An experimental analysis of macrophyte growth as fish foraging habitat. *Canadian Journal of Fisheries and Aquatic Sciences*. 48: 123-131.
- Gerking, S. D. 1957. A method of sampling the littoral macrofauna and its application. *Ecology* 38: 219-225.
- Gotceitas, V. and P. Colgan. 1987. Selection between densities of artificial vegetation by young bluegills avoiding predation. *Transactions of the American Fisheries Society* 116: 40-49.
- Gutreuter, S. J. and R. O. Anderson. 1985. Importance of body size to the recruitment process in largemouth bass populations. *Transactions of the American Fisheries Society* 114: 317-327.
- Haller, W. T. and D. L. Sutton. 1975. Community structure and competition between *Hydrilla* and *Vallisneria*. *Hyacinth Control Journal* 13: 48-50.
- Helfman, G. S. 1981. The advantage to fishes of hovering in shade. *Copeia* 1981: 392-400.
- Johnson, S. L. 1993. Cover choice by bluegills: orientation of underwater structure and light intensity. *Transactions of the American Fisheries Society* 122: 148-154.
- Keast, A. 1984. The introduced aquatic macrophyte, *Myriophyllum spicatum*, as habitat for fish and their invertebrate prey. *Canadian Journal of Zoology* 62: 1289-1303.
- Lillie, R. A. and J. Budd. 1992. Habitat architecture of *Myriophyllum spicatum* L. as an index to habitat quality for fish and macroinvertebrates. *Journal of Freshwater Ecology* 4: 113-121.
- Lynch, W. E., Jr. and D. L. Johnson. 1989. Influences of interstice size, shade, and predators on the use of artificial structures by bluegills. *North American Journal of Fisheries Management* 9: 219-225.
- Madsen, J. D., J. W. Sutherland, J. A. Bloomfield, L. W. Eichler, and C. W. Boylen. 1991. The decline of native vegetation under dense Eurasian watermilfoil canopies. *Journal of Aquatic Plant Management* 29: 94-99.
- Minello, T. J. and R. J. Zimmerman. 1983. Fish predation on juvenile brown shrimp, *Penaeus aztecus* Ives: the effect of simulated *Spartina* structure on predation rates. *Journal of Experimental Marine Biology and Ecology* 72: 211-231.
- Mittelbach, G. G. 1981. Foraging efficiency and body size: a study of optimal diet and habitat use by bluegills. *Ecology* 62: 1370-1386.
- Pardue, G. B. 1973. Production response of the bluegill sunfish *Lepomis macrochirus* to added attachment surface for fish-food organisms. *Transactions of the American Fisheries Society* 102: 622-626.
- Savino, J. F. and R. A. Stein. 1982. Predator-prey interaction between largemouth bass and bluegills as influenced by simulated, submerged vegetation. *Transactions of the American Fisheries Society* 111: 225-266.
- Savino, J. F. and R. A. Stein. 1989. Behavioural interactions between fish predators and their prey: effects of plant density. *Animal Behavior* 37: 311-321.
- Savino, J. F. and R. A. Stein. 1992. Bluegill growth as modified by plant-density: an exploration of underlying mechanisms. *Oecologia* 89: 153-160.
- Sih, A. 1987. Predators and prey lifestyles: an evolutionary and ecological overview. *in* W. C. Kerfoot and A. Sih, editors. *Predation: Direct and Indirect Impacts on Aquatic Communities*. University Press of New England, Hanover, NH. 386 pp.
- Statistix. 1994. Statistix Analytical Software. Version 4.0: User's Manual. Tallahassee, FL.
- Wyckera, U., R. Zoufal, P. Christof-Dirry, and G. A. Janauer. 1993. Structure and environmental factors in macrophyte stands. *Journal of Aquatic Plant Management* 31: 118-122.