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To cite this article: Kristopher J. Stahr & Daniel E. Shoup (2016) The Effects of Macrophyte Stem Density and Structural Complexity on Foraging Return of Invertivorous Juvenile Largemouth Bass, North American Journal of Fisheries Management, 36:4, 788-792, DOI: [10.1080/02755947.2016.1173142](https://doi.org/10.1080/02755947.2016.1173142)

To link to this article: <http://dx.doi.org/10.1080/02755947.2016.1173142>



Published online: 07 Jul 2016.



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MANAGEMENT BRIEF

The Effects of Macrophyte Stem Density and Structural Complexity on Foraging Return of Invertivorous Juvenile Largemouth Bass

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Abstract

Aquatic vegetation can impact juvenile fishes through multiple pathways. Previous studies have found that dense macrophytes can cause a trade-off of survival for Bluegills *Lepomis macrochirus*, with decreased foraging efficiency in macrophytes but also decreased predation risk. For juvenile Largemouth Bass *Micropterus salmoides*, this phenomenon has been proposed but never experimentally tested. In addition, little information exists on the effects of vegetation on juvenile Largemouth Bass prior to the shift to piscivory, a critical period in the recruitment process. Therefore, the objective of this study was to determine if aquatic vegetation reduces the foraging ability of invertivorous (pre-piscivorous) juvenile Largemouth Bass. Twenty-four invertivorous juvenile Largemouth Bass were tested individually at each of five stem densities (0, 125, 250, 500, and 1,000 stems/m²) of artificial macrophytes within 20.8-liter aquaria. Five treatments of a simple stem architecture (at all stem densities) and three complex stem architecture treatments (125, 250, and 500 stems/m²) were used within this experiment. Complex stem density treatments were created using a branched design which doubled the string abundance (number of strings) within the water relative to corresponding stem densities in simple vegetation treatments. Thirty chironomid larvae were used as prey during each 15-minute foraging bout. Foraging return (number of chironomid larvae consumed/15-minute foraging bout) was not significantly different among all stem treatments. Therefore, our results suggest the predator avoidance advantage aquatic macrophytes provide to juvenile Largemouth Bass does not come with a trade-off in foraging efficiency (up to 1,000 stems/m² vegetation density), at least when Largemouth Bass are pre-piscivorous.

Aquatic vegetation provides many vital functions in freshwater ecosystems including cycling nutrients, producing oxygen, harboring zooplankton and other invertebrates and reducing erosion among others (Carpenter and Lodge 1986). Aquatic vegetation is thought to play an integral role in the early life history of several fishes including Northern Pike *Esox lucius* (Casselman and Lewis 1996), Bluegill *Lepomis macrochirus* (Spotte 2007) and Largemouth Bass *Micropterus salmoides* (DeVries et al. 2009). Because of the importance of aquatic vegetation to these fishes (and others), considerable work has focused on understanding specific mechanisms regulating aquatic vegetation-fish interactions.

Bluegills typically suffer decreased foraging efficiency with increased vegetation levels, leading to a trade-off between increased predation risk in open water and decreased foraging efficiency in vegetated habitats (Werner and Hall 1988). Because juvenile Largemouth Bass, like Bluegills, use vegetation as refuge from predators (Stahr and Shoup 2015) a trade-off could also exist for Largemouth Bass. The idea that a predation-foraging trade-off also exists for Largemouth Bass is an idea that has frequently been invoked (e.g., Colle and Shireman 1980; Pothoven et al. 1999), but not experimentally tested. Understanding the role of macrophytes in the early life history of Largemouth Bass is especially important as it may provide management solutions that improve recruitment, which can be a limiting factor for many Largemouth Bass populations (Garvey et al. 2002).

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Received December 15, 2015; accepted March 23, 2016

Several field studies have inferred the effects of aquatic vegetation on Largemouth Bass recruitment (e.g., Colle et al. 1987; Bain and Boltz 1992; Bettoli et al. 1992; Hoyer and Canfield 1996; Pothoven et al. 1999). However, multiple environmental factors differed between high and low vegetation treatments in these studies (e.g., vegetation species present, macrophyte architecture, prey abundance, turbidity, competitor abundance, etc.) making it difficult to understand the ecological mechanism(s) linking vegetation with Largemouth Bass recruitment. In fact, some studies produced conflicting results (e.g., Colle and Shireman 1980; Bettoli et al. 1992; Cross et al. 1992; Strakosh et al. 2009), likely due to different environmental conditions among studies. One potential explanation for conflicting results in past studies could be the failure to consider the differences among vegetation species. Several studies (e.g., Durocher et al. 1984; Wiley et al. 1984; Bettoli et al. 1992; Miranda and Pugh 1997) that have evaluated the effects of macrophytes on juvenile Largemouth Bass foraging considered all macrophyte species together (e.g., total submersed macrophyte density, vegetation surface coverage, biomass), ignoring the possible effects individual to each species (root structure, leaf architecture, timing of growth, etc.). To truly understand how macrophytes affect fishes, one must consider how the fish themselves perceive and respond to aquatic vegetation.

Few studies have identified how macrophyte complexity affect juvenile Largemouth Bass foraging success. Valley and Bremigan (2002) found that dense macrophytes negatively affected piscivorous juvenile Largemouth Bass foraging rates. In addition, Anderson (1984) noted a complex interaction between advanced juvenile Largemouth Bass feeding abilities (feeding on both fish and invertebrates) and vegetation levels, with increased foraging times but no reduction in capture success between high and low vegetation treatments. However, no studies have investigated how structural complexity of macrophytes can affect foraging return of purely invertivorous (pre-piscivorous) juvenile Largemouth Bass.

Overall, a more systematic approach is needed to explain the mechanisms driving field patterns that are the basis for Largemouth Bass-vegetation management strategies. Therefore, we conducted a controlled laboratory experiment to determine if invertivorous juvenile Largemouth Bass experience the decreased foraging efficiency at high vegetation levels previously observed with Bluegills. In addition, we sought to identify how macrophyte architecture (simple or branched/complex stems) affects foraging return of invertivorous juvenile Largemouth Bass.

METHODS

Twenty-four juvenile Largemouth Bass 37.3 ± 0.6 mm TL (mean \pm SE) were collected via seining from ponds and reservoirs near Stillwater, Oklahoma and housed in separate tanks at the Oklahoma State University Fisheries and Aquatic Ecology Wet Laboratory. Fish were fed to satiation daily a diet of frozen chironomid larvae (thawed prior to feeding).

All experiments were conducted within 20.8-liter aquaria ($40.6 \times 25.4 \times 20.3$ cm). Artificial submersed macrophytes were created using 2-mm diameter, green, floating, nylon string, similar to those used in previous Bluegill foraging studies (Gotceitas 1990; Savino et al. 1992; and Shoup et al. 2003). We uniformly affixed strings (25-cm long) to hardware mesh at the bottom of the aquarium, which was then covered with white aquarium sand. Stem densities of 0, 125, 250, 500 and 1,000 stems/m² were used within the experiment; resulting average interstitial spaces were 74.3, 57.3, 44.6, and 28.3 mm respectively. Stem densities were similar to previous studies investigating the effects of stem density on Bluegill foraging (Gotceitas 1990; Savino et al. 1992; Shoup et al. 2003).

Complex macrophyte treatments were also created with similar stem densities to those above but with a branched stem design. We created branched stems by tying two 12.5-cm pieces of string to each stem: one at the base and one at the mid-point of the stem (Figure 1). Therefore, the complex treatments had the same stem density as the simple treatments, but double the amount of strings within the water column (complexity). Complex treatments were made for stem densities of 125, 250 and 500 stems/m², which could then be compared to simple stem treatments of the same density (stem density effects) or compared to the next higher stem density (which had the same abundance of string within the water but arranged as simple stems rather than the branched complex design).

Thawed frozen chironomid larvae were used as prey for the experiment. Chironomid and other dipteran larvae are regularly consumed by juvenile Largemouth Bass prior to the shift to piscivory (Engel 1987; Long and Fisher 2000; Parkos and Wahl 2010; Middaugh et al. 2013), and availability of chironomid larvae has been theorized to play an integral role in the shift to piscivory itself (Brenden and Murphy 2002). In addition,

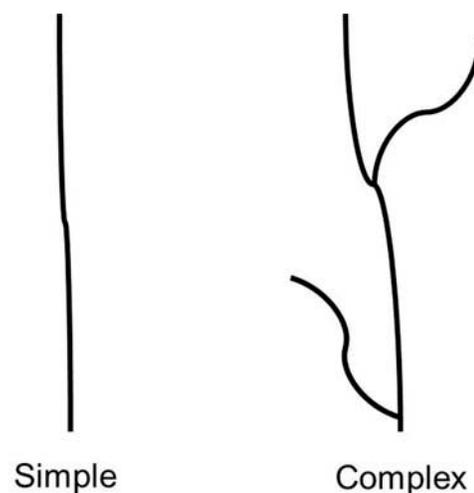


FIGURE 1. Example of the two stem architectures used for simple and complex vegetation treatments. The complex architecture results in the same stem density as the simple treatments, but with twice the string abundance.

chironomid larvae can be abundant in several types of aquatic vegetation (Dvořák and Best 1982; Chilton 1990; Van de Meutter et al. 2008). Frozen chironomid larvae have been used previously in experiments studying Bluegill foraging efficiency at different vegetation densities (Savino et al. 1992). Prior to the experiment we feed-trained juvenile Largemouth Bass on chironomid larvae until they fed readily in the presence of an observer.

We used thirty chironomid larvae as prey in each experiment, based on preliminary trials indicating juvenile Largemouth Bass were always satiated below this level. The resulting chironomid larval density was comparable to previous studies with Bluegills (Savino et al. 1992). Chironomid larvae were counted and haphazardly added to each aquarium prior to the introduction of one juvenile Largemouth Bass. Chironomid larvae sank and dispersed throughout the tank with some landing on artificial vegetation stems and others sinking to the tank bottom. Chironomid larvae were, on average, 11.6 ± 0.2 mm long and 1.1 ± 0.1 mm wide. Largemouth Bass were starved 24 h prior to the start of the experiment to standardize hunger levels. Largemouth Bass were placed within plastic mesh cages ($50 \times 100 \times 100$ mm) and suspended within the experimental tank containing chironomid larvae to acclimate for one hour. Each fish was then released into the aquarium and allowed to forage for 15 minutes, at which time it was removed and the number of chironomid larvae remaining was counted and subtracted from 30 to determine the number of chironomids that had been consumed. We chose 15 minute trials because preliminary data indicated this is how long Largemouth Bass took to be satiated when feeding in tanks with large densities of chironomids and no vegetation. If the hypothesis that foraging return decreases as structural complexity increases is correct, this should result in fewer chironomids eaten in vegetated trials as Largemouth Bass would run out of time before being satiated.

Each Largemouth Bass was tested once in each vegetation treatment, resulting in a total of 192 treatment-trials. The treatment order administered to each Largemouth Bass was randomized to reduce the potential for learning to bias results throughout the course of the experiment. Additionally, in a given day one trial of all treatments was conducted concurrently (using different Largemouth Bass) to block potential temporal biases. Because 8 treatment tanks were used, a maximum of 3 block replications was carried out per day. To compare differences in foraging return between treatments (number of chironomid larvae consumed during trial), we specified a generalized linear model with vegetation density as a continuous fixed factor, stem design (simple, complex, or stems absent/control) as a categorical fixed factor, and random residuals (repeated measures) specifying Largemouth Bass as subjects with SAS Proc Glimmix (SAS Institute 2011). Because the response variable (number of chironomid larvae consumed) was a count variable, we specified a Poisson distribution. A significance level of 0.05 was used for all tests.

RESULTS

Juvenile Largemouth Bass foraging return was not affected by vegetation stem density ($F_{1, 164} = 1.36$, $P = 0.25$) or complexity ($F_{2, 46} = 0.32$, $P = 0.73$; Figure 2). There was also no significant interaction between vegetation stem density and complexity ($F_{1, 164} = 0.66$, $P = 0.42$). The mean number of chironomid larvae consumed was 11.84 (SE, 3.27) mm across all treatments. The mean number of chironomid larvae consumed ranged between 11.21 (SE, 0.66) within the 500 stems/m² complex treatment and 12.54 (SE, 0.65) within 250 stems/m² complex treatment.

DISCUSSION

Previous studies with other sunfish species found foraging return typically declines as vegetation density increases (Gotceitas 1990; Kieffer and Colgan 1991; Theel and Dibble 2008), however we found this did not occur for Largemouth Bass. It is possible that the lack of prey mobility in our study could contribute to these results. However, Savino et al. (1992) also used nonmoving prey and still found decreased foraging ability at higher macrophyte stem densities with Bluegills. In addition, chironomid larvae inherently have limited movement and activity as prey and thus live prey likely would not result in decreased captures. Therefore, our results suggest that invertivorous juvenile Largemouth Bass respond differently to dense vegetation than Bluegills in that Largemouth Bass may benefit from reduced predation mortality in vegetation (Stahr and Shoup 2015) with no trade-off in growth rate. Therefore, increasing vegetation could be an even

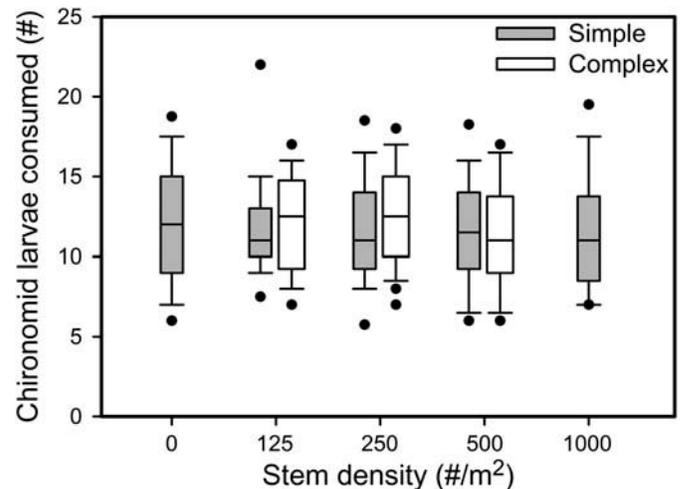


FIGURE 2. Box plot of chironomid larvae consumed by juvenile Largemouth Bass between stem densities (simulated with 2-mm nylon string) for both simple and complex treatments. Complex treatments had the same stem densities as simple treatments, but used twice as much string with two additional pieces of string attached to each stem to simulate branching. Horizontal line in box is the median, the box represents the interquartile range (25th–75th percentile), and whiskers represent 95% confidence intervals. Dots represent data falling outside the 5% confidence interval.

more valuable management approach for maximizing Largemouth Bass recruitment than previously recognized. Future research should examine if the patterns observed from our study (and other mesocosm studies) translate to larger, natural systems.

We found that both macrophyte complexity and density did not affect foraging return of prepiscivorous juvenile Largemouth Bass. Previous studies have noted reduced foraging return of invertivorous fishes in higher macrophyte complexities but not in higher stem densities (Dionne and Folt 1991; Warfe and Barmuta 2004). One explanation for these disparate results is that the growth form in our experiment may not have been complex enough to provoke a negative effect on foraging return of invertivorous juvenile Largemouth Bass. A complexity threshold may exist for juvenile Largemouth Bass; a hypothesis previously proposed for adult Largemouth Bass (Gotceitas and Colgan 1989). Alternatively, juvenile Largemouth Bass may not respond to structural complexity in the same way as other invertivores. Future experiments should focus on additional complex macrophyte growth forms to examine what level of structural complexity may be needed to negatively affect juvenile Largemouth Bass foraging return.

Our results are consistent with previous studies concluding that juvenile Largemouth Bass do not suffer from reduced growth rates in vegetation (Colle and Shireman 1980; Strakosh et al. 2009); however, other studies found juvenile Largemouth Bass growth rates increased when vegetation levels are reduced (Bettoli et al. 1992; Cross et al. 1992; Cailteux et al. 1998). Two likely explanations exist for the disparate results seen between these groups of studies. First, biotic responses to changes in vegetation may differ among systems. Macroinvertebrate abundance (Warfe and Barmuta 2004) and abundance of young-of-year fishes (including Largemouth Bass and their potential competitors) both increase as vegetation densities increases (Strakosh et al. 2009; Collingsworth and Kohler 2010). Therefore, as macrophyte abundance increases, juvenile Largemouth Bass growth could increase or decrease depending on which factors (i.e., food or competitor abundance) had the greatest increase in response to an increase in structural complexity. How these two factors vary as vegetation abundance changes may differ between systems. Second, reduced vegetation levels could cause an earlier shift to piscivory in Largemouth Bass (Bettoli et al. 1992), which in turn increases juvenile growth rates (Olson 1996). An earlier switch to piscivory is likely because reduced vegetation levels decrease invertebrate abundance (Diehl and Kornijów 1998), which would limit the availability of nonpiscine prey. Therefore, disparate results from previous studies may be a function of the life-history stage of the Largemouth Bass (prepiscivorous or piscivorous). Future research is needed to explain the results from these field-observed patterns correlating juvenile Largemouth Bass growth and vegetation; however, our results suggest that

inefficient invertebrate foraging by Largemouth Bass in dense vegetation is not the cause of these field patterns.

Despite the considerable work investigating Largemouth Bass recruitment, relatively little information exists concerning Largemouth Bass after the larval life stage but prior to the shift to piscivory. Our study is the first to evaluate how habitat complexity can affect Largemouth Bass at this critical life stage. By evaluating factors that could lead to a recruitment bottleneck at the juvenile life stage of Largemouth Bass, managers may be able to better predict Largemouth Bass recruitment patterns or develop management strategies that maximize recruitment of this species. Specifically, we provide evidence that increased vegetation abundance will not decrease the foraging ability of juvenile Largemouth Bass at the invertivorous stage of ontogeny (at least up to macrophyte stem density of 1,000 stems/m²). Therefore, enhancing vegetation coverage in lakes and reservoirs should be an effective management strategy for improving recruitment for Largemouth Bass by minimizing predation mortality (Stahr and Shoup 2015).

ACKNOWLEDGMENTS

We sincerely thank C. Broderius, E. Cartabiano, T. Hart, and T. Starks for help both in the field and the laboratory. We thank the Oklahoma Cooperative Fish and Wildlife Research Unit for the use of equipment. Funding for this project was provided by the Department of Natural Resource Ecology and Management, Oklahoma State University.

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