THE EFFECT OF VEGETATION ON THE ONTOGENY

TO PISCIVORY IN JUVENILE LARGEMOUTH BASS

By

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Abstract: Largemouth Bass (*Micropterus salmoides)* are an economically important gamefish species in North America and as such are a focal species for managers. A frequent bottleneck to their recruitment is overwinter survival in their first year of life. Early ontogeny to piscivory provides increased overwinter survival through growth and accumulation of lipids. This ontogeny is slowed by dense and complex vegetative habitats according to anecdotal field evidence. I chose to address two issues: 1) does vegetation density affect the foraging return of piscivorous juvenile Largemouth Bass? 2) Does vegetation density affect the timing of the ontogeny to piscivory in juvenile Largemouth Bass? To answer objective 1) I conducted foraging trials using piscivorous juvenile Largemouth Bass and Juvenile Fathead Minnows (*Pimephales promelas*) in eight treatments of varying simulated vegetation densities (0, 125, 250, 500, and 1,000 stems/m^2) and complexities (simple and complex). Piscivorous Largemouth Bass consumed the most Fathead Minnows in the 125 stems/m2 simple treatment and the least in the 0 stems/m2 treatment. Indicating that juvenile Largemouth Bass forage least efficiently on Fathead Minnows in habitats with no complexity. To answer objective 2) I conducted enclosure experiments across 5 weeks of the typical time frame (mid-summer) that juvenile Largemouth Bass would transition to piscivory. Thirty-two enclosures were constructed across two 0.10 hectare ponds and treated with four stem densities of simulated vegetation (0, 50, 250, and 500 stems/m^2). Three juvenile Largemouth Bass and 30 juvenile Bluegill (*Lepomis macrochirus*) were added to each enclosure. All fish were sampled twice per week. Largemouth bass growth was measured as total length (mm) and diets were collected via gastric lavage. Bluegill densities were manipulated to stay consistent. It was found that Largemouth Bass switched to piscivory during the second week in the 0, 50, and 500 stems/m^2 treatments but did not completely switch in the 250 stems/m^2 treatment. Growth mirrored this pattern where Largemouth Bass grew less in the 250 stems/m^2 treatment. Differing results in these two experiments suggest that vegetation density does affect the foraging rate and subsequent ontogeny to piscivory in juvenile Largemouth Bass. However, it has an interactive effect with available fish prey species.

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THE EFFECT OF VEGETATION DENSITY AND COMPLEXITY ON THE FORAGING

EFFICIENCY OF PISCIVOROUS JUVENILE LARGEMOUTH BASS

Introduction

Largemouth Bass, *Micropterus salmoides*, are a popular sportfish with a significant

economic impact in North America (Chen et al. 2003). As such, Largemouth Bass are often a

focal species for managers (Parkos and Wahl 2002). A common problem encountered when

managing Largemouth Bass is inconsistent recruitment (Jackson and Noble 2000; Maceina and

Bettoli 1998). There is a complex interaction of factors that affect recruitment of Largemouth

Bass including adult population size, spawn timing, growth rate, predation, and overwinter

survival (Post et al. 1998). Additional information is needed to understand the recruitment

process for this species.

Predation is a significant source of mortality for all juvenile fishes, including Largemouth

Bass (Post et al. 1998), that can reduce recruitment. Juvenile Largemouth Bass, like other

juvenile fishes, use aquatic vegetation to escape predation (Dibble and Harrel 1997; Miranda and

Hubbard 1994; Stahr and Shoup 2015). It is for this reason that managers frequently use

vegetation enhancement to increase juvenile Largemouth Bass survival (Allen and Tugend 2002;

Smart et al. 1996). Enhancement in this case often means either increasing vegetation in barren

aquascapes (Smart et al. 1996) or decreasing vegetation in overly dense areas of vegetation (Allen

and Tugend 2002). However, predation is not the only bottleneck preventing juvenile

Largemouth Bass from reaching their second year of life and management efforts designed to improve predator avoidance may compromise other recruitment-limiting factors such as growth.

Juvenile Largemouth Bass must also grow sufficiently to have energy reserves necessary to avoid starvation during winter (Miranda and Hubbard 1994). This is most likely to occur when juveniles make an early ontogenetic diet shift from eating invertebrates to more calorically-dense fish prey and begin accumulating lipids to sustain them over winter (Ludsin and DeVries 1997). A delay in the ontogeny to piscivory by juvenile Largemouth Bass can reduce overwinter survival and lead to reduced recruitment.

Anecdotal evidence suggests the presence of vegetation slows this switch to piscivory in Largemouth Bass and reduces growth (Bettoli et al. 1992; Miranda and Pugh 1997). However, the specific mechanisms that lead to this change in diet and increase in growth have not been studied for this species. Therefore, it is not clear if vegetation inhibits piscivory in juvenile Largemouth Bass directly by reducing foraging return when they pursue fish prey or if vegetation density affects the prey community such that the Largemouth Bass have lower prey abundance with the most common prey being larval fish when vegetation is removed.

If the foraging efficiency of piscivorous juvenile Largemouth Bass is affected by dense or complex vegetation then they may suffer a tradeoff between foraging and predation refuge. Other species of juvenile fishes suffer from reduced foraging efficiency in dense or complex habitats, which forces them into a tradeoff between foraging efficiency and predator avoidance (Diehl and Eklöv 1995; Gotceitas 1990a; Gotceitas 1990b; Mittelbach 1981; Persson 1991; Pothoven et al. 1999; Shoup et al. 2003). Due to the effect aquatic vegetation has on these similar species, it has traditionally been assumed that juvenile Largemouth Bass suffer from this same trade-off (Colle and Shireman 1980; Pothoven et al. 1999). A recent laboratory study found that juvenile Largemouth Bass foraging on chironomid larvae did not suffer from a decrease in foraging

efficiency, even at high (1,000 stems/m^2) densities of vegetation (Stahr 2014). This suggest that juvenile Largemouth Bass may not face a trade-off between predator avoidance and foraging return, at least for pre-piscivorous individuals.

The purpose of this study is to test the effects of vegetation density and complexity on the foraging efficiency of piscivorous juvenile Largemouth Bass shortly after their transition to piscivory. This information is needed to determine if a predation risk-foraging return tradeoff exists for juvenile Largemouth Bass that inhabit vegetation and to see if the presence of vegetation reduces foraging of piscivorous juvenile Largemouth Bass such that it could account for a delay in the ontogeny to piscivory. Understanding the interaction between vegetation and Largemouth Bass recruitment (a function of both predation risk and foraging return) is important to guide management efforts to enhance recruitment of this species.

Methods

Foraging trials were conducted in the Oklahoma State University Fisheries and Aquatic Ecology Wet Laboratory from May 18, 2015 through July 19, 2015. Forty-seven juvenile Largemouth Bass were collected via seining from the Oklahoma State University Aquatic Ecology Research Ponds (OSU AERP) where they were spawned from adult Largemouth Bass that had been collected via electrofishing at Lake Carl Blackwell and Boomer Lake near Stillwater, Oklahoma. Largemouth Bass sizes ranged from 69 mm to 83 mm TL (mean = 75.2 mm $\pm$ 3.27 mm standard deviation). No fish as prey were provided to Largemouth Bass in the ponds, so all Largemouth Bass were pre-piscivorous at the time of collection. Juvenile Fathead Minnows, *Pimephales promelas*, were used as the forage species. The Fathead Minnows were approximately 25 mm in total length (mean = 25.5mm $\pm$ 2.43 standard deviation). The Fathead Minnows were large enough to be evasive yet small enough that multiple Fathead Minnows could be eaten in a 15 minute trial by a 75mm total length Largemouth Bass. This prey size is also

within the 25 – 30mm length range selected by 75 mm largemouth bass in size selectivity trials (Einfalt et al. 2015). Fathead Minnows were collected via seine from the OSU AERP where they were spawned from Fathead Minnow stock acquired from I.F. Anderson Farms, Lonoke, Arkansas.

Largemouth Bass were held in 200 gallon tanks and fed an ad libitum diet of thawed frozen chironomid larvae prior to acclimation to trial conditions. Fathead minnows were held in a 200 gallon tank and fed an ad libitum diet of pulverized commercial flake food. Largemouth Bass were given an 8 day acclimation period in 37.8 liter (50.8 cm x 27.9 cm x 33.0 cm) glass aquaria immediately preceding trials where they were fed appropriately sized Fathead Minnows to ensure their willingness to consume piscivorous prey items in isolated glass aquaria with an observer. Fathead Minnows were moved from their holding tank to the trial aquaria directly before a trial acclimation period was enacted.

Trials were conducted within 18.9 liter (43.2 cm x 22.9 cm x 27.9 cm) glass aquaria. Simulated vegetation was created within each aquarium using 2-mm diameter, 250-mm long, green, floating, nylon string that was affixed uniformly to hardware mesh buried under aquarium sand. Construction of simulated vegetation was modeled after similar previous research (Savino and Stein 1982; Gotceitas and Colgan 1987; Gotceitas and Colgan 1989; Shoup et al. 2003; Stahr 2014). Simulated vegetation was created at stem densities of 0 (control), 125, 250, 500, and 1,000 stems/m^2. I also created three simulated vegetation densities (125, 250, 500 stems/m^2) with a complex stem design made by tying two additional 125-mm long pieces of string to each main stem, effectively doubling the string abundance for each of these stem densities (Figure 1). Thus, in total there were eight treatments: control; 125, 250, 500, and 1,000 stems/m^2 with simple stems; and 125, 250, and 500 stems/m^2 with complex stems.

Prior to each trial, one juvenile Largemouth Bass and five juvenile Fathead Minnows were given a 24 hour acclimation period in a trial aquarium with a plastic mesh divider separating them on different sides. Each Largemouth Bass was tested once at each vegetation treatment level (i.e., repeated-measures design). Trials were run in groups with one Largemouth Bass assigned to each of the eight treatments each day to block potential temporal effects (i.e., created "trial blocks" of eight subjects being tested during the same eight days). Within trial blocks, the treatment order was randomly assigned to each Largemouth Bass using a Latin square crossover design. To initiate a trial, the plastic mesh divider from each tank was removed and Largemouth Bass were given 15 minutes to forage. At the end of the trial, the remaining Fathead Minnows were counted to discern the quantity of prey consumed.

Data were analyzed using a general linear mixed model with repeated measurements (individual Largemouth Bass treated as subjects) using SAS 9.4 Proc Glimmix (SAS 2014) to test the number of Fathead Minnows consumed among vegetation treatments and to test or account for carryover between treatments and temporal effects (trial block and run number, defined below). Carryover effects (i.e., the order in which treatments were administered; tested with a variable identifying the treatment tested on the previous day for each subject) were not significant ($F_{7,\,347} = 0.57$, $P = 0.777$) and were subsequently dropped from the model. A random variable was included in the model to account for the trial block (group of 8 subjects tested during the same 8 days) in which each fish was tested. A random variable was also included for run number (i.e., how many of the 8 trial days had already been experienced by the fish) to account for increased consumption that might occur due to Largemouth bass gaining proficiency with experience or eating more food as they grew during the time required to conduct the experiment (fish grew approximately 5% longer during the 8-day trial). A total of 47 Largemouth Bass were tested based on the results of a power analysis calculating the sample size needed to detect the

observed treatment differences with $\beta = 0.8$ (power needed when testing with $\alpha = 0.05$; Cohen 1998)

Results

The mean number of Fathead Minnows consumed per trial differed among treatments ($F_{7, 354} = 2.20$, $P = 0.034$, Figure 2). Fewer Fathead Minnows were consumed in the control treatment (mean = 1.75 fish consumed) than in the 125 stems/m^2 treatment (mean = 2.68 fish consumed; Tukey test P=0.029). No other pairwise treatment comparisons were significant (all Tukey values $P > 0.13$).

Discussion

The results of this experiment differed from field studies that found that removal of vegetation increased the frequency of piscivory in juvenile Largemouth Bass (Bettoli et al. 1992; Miranda and Pugh 1997). These previous studies suggested that the presence of vegetation inhibited foraging by piscivorous juvenile Largemouth Bass, similar to the results of previous studies of sunfish, *Lepomis spp.*, foraging in dense vegetation (Gotceitas 1990b; Kieffer and Colgan 1991; Savino et al. 1992; Theel and Dibble 2008). My results indicate that the presence of vegetation increases the foraging return of piscivorous juvenile Largemouth Bass relative to open water, even at densities as high as 1,000 stems/m^2. This suggests that aquatic vegetation enhancement should continue to be an integral tool in the management of Largemouth Bass populations as it provides a predation refuge for juveniles (Stahr and Shoup 2015) without sacrificing foraging return.

The disparity between previous field studies (Bettoli et al. 1992; Bettoli et al. 1993) and my experiment suggests that another factor besides habitat complexity effected the switch to piscivory when vegetation was removed in the field studies. This could be caused by several environmental changes that accompanied the vegetation removal. For example, the increase in

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piscivory observed in field studies could be due to changes in the piscine prey community.
During these studies the densities of *Lepomis spp.* decreased whereas Inland Silverside *Menidia beryllina* and Threadfin Shad *Dorosoma petenense* increased, which may have provided more appropriate-sized piscine prey for Largemouth Bass, depending on the hatching time of these different prey species. Alternatively, removal of vegetation likely reduced aquatic invertebrate abundance (Wiley et al. 1984; Cyr and Downing 1988; Rennie and Jackson 2005) and may therefore have caused juvenile Largemouth Bass to focus more on the more abundant piscine prey after vegetation removal. Regardless of the mechanism underlying the observed increase in piscivory of juvenile Largemouth Bass after vegetation removal, my results indicate that juveniles have a higher foraging return when foraging on piscine prey when some structural complexity exists.

It is possible that vegetation could reduce foraging by piscivorous Largemouth Bass at higher densities than those used in the current study. Although statistically significant differences were not found between any of the vegetation density or complexity treatments, Figure 2 shows slightly lower foraging rates at more complex treatments. This caution is further supported by results of Alexander et al (2015) who found larger (~87 mm TL) Largemouth Bass had greater consumption rates of guppies *Poecilia reticulata* as vegetation density increased to 1,800 stems/m^2 but consumption rates declined at densities of 2,700 stems/m^2. Also, adult Largemouth Bass foraging efficiency is reduced at vegetation densities as low as 170 stems/m^2 (Savino and Stein 1982; Stahr and Shoup 2015). Further research is needed to determine the size at which moderate vegetation densities begin to affect foraging return of Largemouth Bass. However, managers attempting to improve Largemouth Bass recruitment through vegetation enhancement should still attempt to manage for moderate vegetation densities to enhance survival of smaller individuals.

My results suggest that vegetation may benefit juvenile Largemouth Bass by improving their piscivorous foraging abilities relative to open water. These results, in combination with Stahr and Shoup (2015), suggest that vegetation stem densities as low as 170 stems/m^2 have the ability to reduce predation risk for juvenile Largemouth Bass while improving foraging efficiency in comparison to open water habitats. These findings suggest that piscivorous juvenile Largemouth Bass do not suffer from a tradeoff between foraging efficiency and predator avoidance in vegetated systems. As such, managing for moderate amounts of aquatic vegetation in systems with little or no vegetation should enhance recruitment of Largemouth Bass, provided there is adequate prey inhabiting the vegetation.

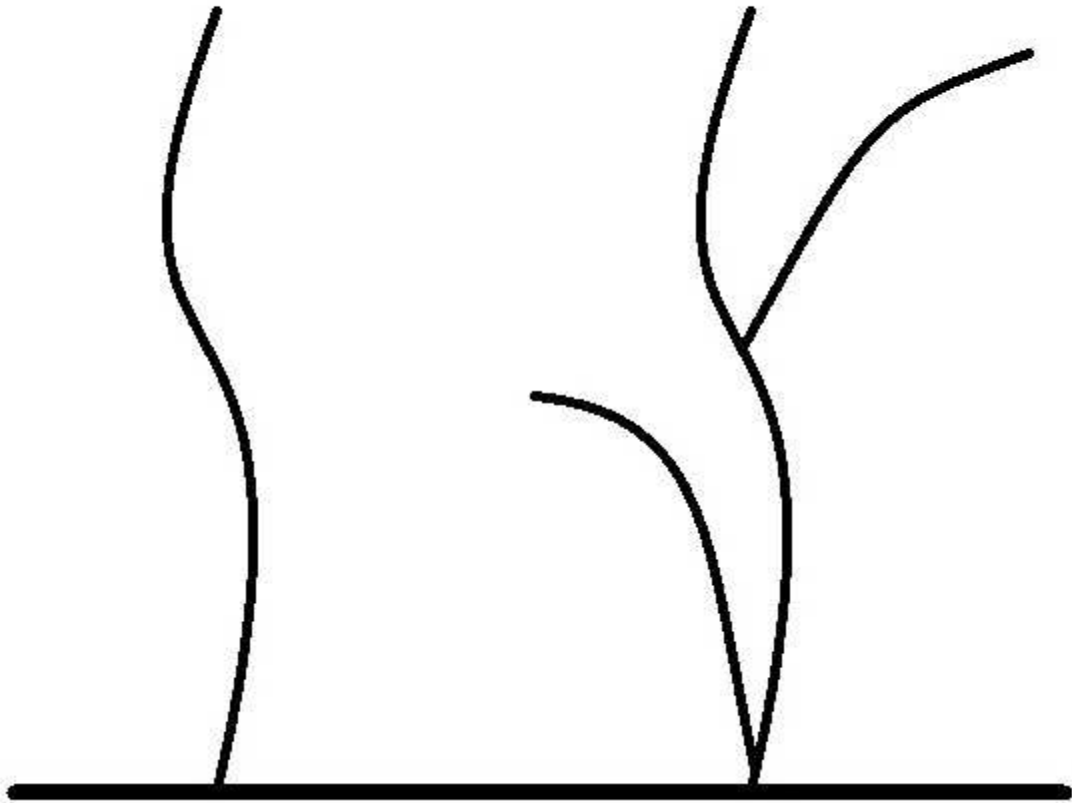**Simple**   **Complex**

Figure 1. Diagram of two levels of complexity used in creating simulated vegetation. Complex
treatments result in the same stem density as their simple counterparts but with twice the
abundance of string resulting in the same amount of string used as the next higher simple stem
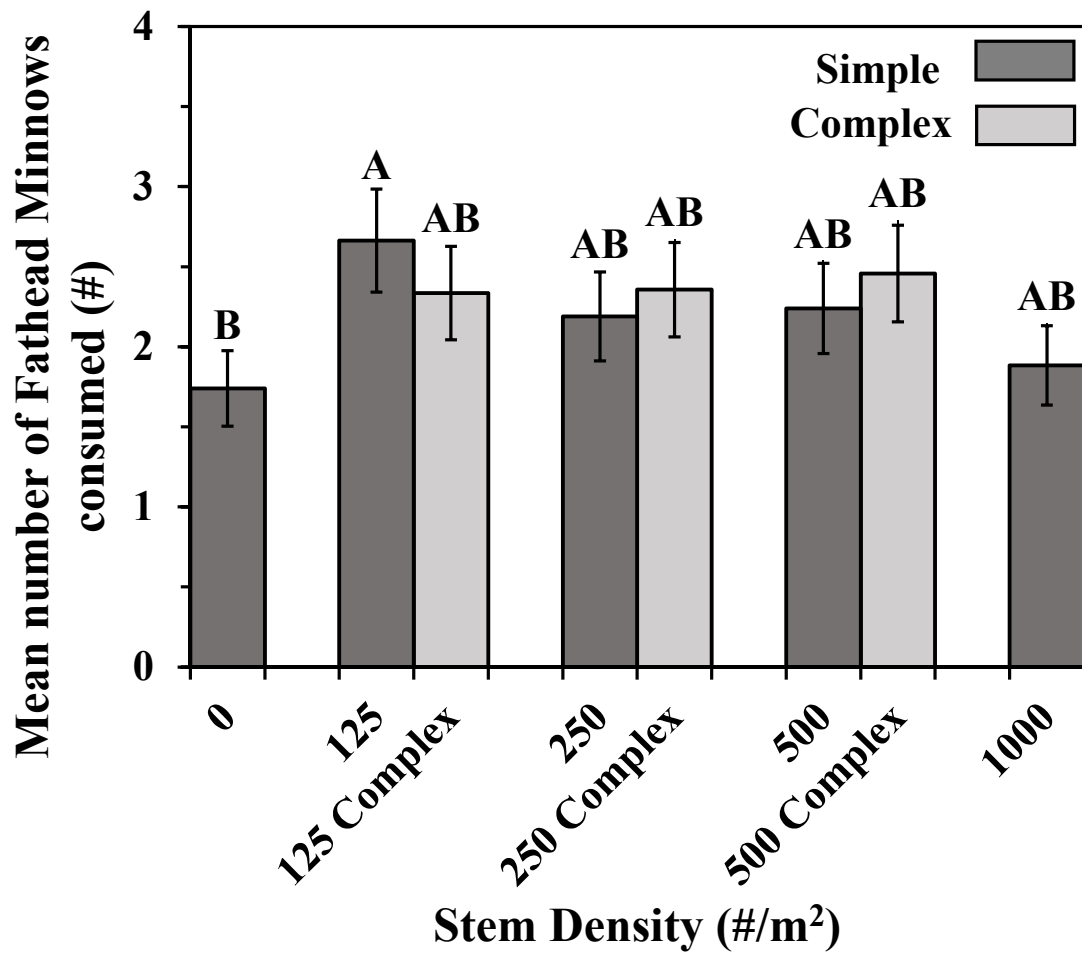treatment.

Figure 2. Mean number of Fathead Minnows consumed at different simulated vegetation complexity levels. Simple stem densities were single strings of 2-mm diameter Nylon string. Complex treatments had a second string cut in half and tied to two locations on the main string making twice the amount of string as simple stems at the same stem density. Letters denote a Tukey-Kramer grouping. Means with different letters are significantly different at the $\alpha \leq 0.05$ level.

CHAPTER II

THE EFFECT OF VEGETATION DENSITY ON THE ONTOGENY TO PISCIVORY IN

JUVENILE LARGEMOUTH BASS

Introduction

Largemouth Bass, *Micropterus salmoides*, are an important game species in North

America (Chen et al. 2003). Largemouth Bass undergo an ontogenetic shift in feeding habits

from invertebrates to piscine prey during their first year of life (Ludsin and DeVries 1997;

Mittelbach and Persson 1998; Olson 1996; Werner and Gilliam 1984). The switch to piscivory

facilitates increased growth as fish are a greater source of energy than invertebrates (Keast and

Eadie 1985; Mittelbach and Persson 1998). With this increase in growth comes an increase in

available prey items, which further enhances growth (Mittelbach and Persson 1998). Growth is

also important as it facilitates an individual's ability to avoid predation (Hambright 1991) and

increases overwinter survival (Ludsin and DeVries 1997; Mittelbach and Persson 1998), which

are considered major bottlenecks in the Largemouth Bass recruitment process (Houde 1987;

Parkos and Wahl 2010). Therefore, understanding the factors that influence the timing of the

ontogenetic shift to piscivory is important in understanding recruitment dynamics of Largemouth

Bass.

Availability of fish prey that are small enough (approximately half the total length; Post

2003) for juvenile Largemouth Bass to consume is important to the switch to piscivory

(Mittelbach and Persson 1998). Availability can be affected by the prey community structure, hatch timing, and pre-piscivorous growth (Garvey and Stein 1998; Olson 1996. Johnson and Post 1996). These factors contribute to the wide range of size at ontogeny to piscivory for Largemouth Bass (30 – 140 mm total length, typically 40 – 60 mm total length; Bettoli et al. 1992; Brown et al. 2001; Huskey and Turingan 2001; Johnson and Post 1996; Mittelbach and Persson 1998; Olson 1996; Post 2003). Although ontogeny to piscivory may begin at these lengths, a steady supply of appropriately sized fish are required to maintain piscivory (Garvey and Stein 1998). Piscine prey community composition contributes to prolonged availability as some species of prey may quickly outgrow the gape limitations (e.g. Shad *Dorosoma spp.*; Hambright 1991) of juvenile Largemouth Bass while others spawn throughout the summer (e.g. Bluegill *Lepomis macrochirus*; Cargnelli and Gross 1996; Garvey et al. 2002; Santucci and Wahl 2003) providing a consistent supply of appropriately sized fish.

Habitat complexity may also influence the timing of ontogeny to piscivory for juvenile piscivores through reduced foraging efficiency, but it has not been adequately studied. Optimal foraging theory predicts that organisms will forage in a way that maximizes their net energy gain (MacArthur and Pianka 1966). Habitat complexity affects foraging rates and growth in many species of fish (Bettoli et al. 1992; Dibble and Harrel 1997; Miranda and Pugh 1997; Olson et al. 1998; Reid et al. 1999; Shoup et al. 2012; Stahr 2014; Stahr and Shoup 2015), so it may also lead to changes in diet if certain prey types require more energy to capture in certain environments (Mittelbach 1981) resulting in habitat-specific differences in diet (Dibble and Harrel 1997; Schramm and Zale 1985). Thus the prey actually selected in a given type of habitat will likely be a function of the way habitat complexity alters predator and prey behavior.

Complex habitats, such as vegetation, likely delay the ontogeny to piscivory in Largemouth Bass because highly mobile fish prey may be more difficult to capture in these complex habitats. Juvenile Largemouth Bass primarily prey on zooplankton, macroinvertebrates,

and fish (Galarowicz and Wahl 2005; Graeb et al. 2006). Zooplankton are often the most abundant and easily captured (Graeb et al. 2005; Mittelbach 1981) prey item, but their small size requires the consumption of large quantities to meet predator energetic needs (Cummins and Wuycheck 1971). Macroinvertebrate prey items are less abundant and more mobile than zooplankton, making them somewhat harder to consume (Graeb et al. 2005; Mittelbach 1981). However, macroinvertebrates are larger in size and therefore provide a better energy return than zooplankton, which may help offset the additional effort required to capture them (Cummins and Wuycheck 1971). Piscine prey are the least abundant and most difficult to capture (Graeb et al. 2005), but they are also the most energetically valuable (Cummins and Wuycheck 1971; Miranda and Muncy 1989). Dense vegetation affects the ability of Largemouth Bass to find and capture prey primarily by obstructing vision (Breck 1993) and hampering maneuverability (Savino and Stein 1982). Therefore, it is logical that an increase in habitat complexity would have a disproportionately large effect on the foraging of juvenile Largemouth Bass when they are feeding on fast moving or highly maneuverable fish prey relative to when they are feeding on slower moving and less maneuverable zooplankton or macroinvertebrates.

Of all the factors influencing the timing of the ontogenetic shift to piscivory in Largemouth Bass, vegetation density is the least studied. Earlier ontogeny to piscivory in Largemouth Bass has been correlated with the removal of complex vegetation (Bettoli et al. 1992); however, vegetation removal can affect the fish community by altering the abundance of prey and competitors, both of which can also affect the ontogeny to piscivory (Bettoli et al. 1992; Brown et al. 2001; Garvey and Stein 1998b; Huskey and Turingan 2001). In laboratory studies, adult Largemouth Bass have reduced foraging return when feeding on fish prey in vegetated habitats (Gotceitas and Colgan 1987; Gotceitas and Colgan 1989; Savino and Stein 1982; Stahr 2014; Stahr and Shoup 2015). However, juvenile Largemouth Bass foraging rates are unaffected by the presence of vegetation when feeding on non-mobile invertebrate prey (e.g. chironomid

larvae; Stahr 2014) and increase in the presence of moderate vegetation when foraging on piscine prey (Chapter 1). Therefore, it is unclear whether vegetation is likely to affect the timing of the ontogeny of piscivory in juvenile Largemouth Bass. The purpose of this experiment was to determine how vegetation density affects the ontogeny to piscivory and growth of juvenile Largemouth Bass. To do so, we used enclosures that combined the control of a laboratory experiment with the applicability of a field study by controlling vegetation densities and piscine prey densities for juvenile Largemouth Bass during the summer months when they would naturally transition to piscivory.

Methods

Set up

To determine the effect of vegetation density on the timing of ontogeny to piscivory in juvenile Largemouth Bass, juvenile Largemouth Bass diets and growth were monitored over a five-week experiment during a timeframe when they would typically switch to piscivory (mid-summer). Square enclosures ($1 m^2$) with vegetation densities of 0, 50, 250, and 500 stems/m^2 (hereafter referred to as control, low, medium, and high) were constructed as experimental replicates. Enclosures were constructed from plastic mesh (3.3-mm bar mesh, approximately 7-mm diameter openings) attached to a u-post frame with the mesh buried approximately 15 cm in the pond bottom. Enclosures were set up in four rows of four enclosures within two 0.10-ha ponds at the Oklahoma State University Aquatic Ecology Research Ponds (i.e., 16 enclosures per pond). Enclosures were arranged with a Latin square design with one of each of the four vegetation densities per row. Row number and pond were treated as random blocking variables in the analysis.

Vegetation was simulated in the enclosures by affixing 3-mm diameter yellow twisted polypropylene rope to 1-m^2 mats of galvanized steel hexagonal poultry netting, with the poultry

netting affixed to the substrate with garden staples. For continuity, control treatments also received poultry netting even though no simulated vegetation was attached. Once the enclosures were built and vegetation mats installed, the ponds were filled to a depth of 0.6 m ($\pm$ 0.05 m) with water from Lake Carl Blackwell filtered through an 800 μm mesh. This left approximately 20 cm of plastic mesh extending above the water surface. The ponds held water (but no fish) prior to enclosure construction and were only partially drained during enclosure construction such that invertebrates were present at the time of refilling. Ponds were allowed to sit for one week while zooplankton and invertebrates populations adjusted to the changes in water level. After one week, three juvenile Largemouth Bass (mean = 40 mm total length, $\pm$ 1.9 SD) were stocked in each enclosure as the subjects of the experiment. Although this is a greater density than the lake-wide averages commonly reported for juvenile Largemouth Bass (0.02 fish/m^2 – 0.53fish/m^2) (Bettoli et al. 1992; Bettoli et al. 1993; Maceina et al. 1993; Strakosh et al. 2009; Valley and Bremigan 2002) it is less than the densities (i.e. up to 15 fish/m^2) reported at specific sites with complex habitat (Hayse and Wissing 1996). Each largemouth bass was given a different fin clip so the three fish in the same enclosure could be individually identified. Enclosures were also stocked at a density of 30 fish/m^2 with juvenile Bluegills that were approximately 30 % of the length of the juvenile Largemouth Bass as a source of fish prey (Post 2003). A density of 30 Bluegills/m^2 was chosen to provide adequate numbers of prey (10 prey fish per predator) while providing a realistic density for vegetated habitats (0.2 to 108 Age-0 Bluegills/m^2 ; Hayse and Wissing 1996).

All enclosures were sampled within a three hour period after sunrise twice/week using a frame net designed specifically to sample the 1-m^2 enclosures. The frame net was constructed from 3.8-cm diameter polyvinyl chloride pipe that formed a 1-m^2 square frame with 1-m long handles. A 1.6-mm mesh net was attached to the frame. To sample, I ran the leading edge of the frame across the bottom of the enclosure from one side to the other then lifted the frame net,

keeping it in contact with the far side as it was raised. Frame-net samples were repeatedly taken until three consecutive samples came back empty. All sampled Largemouth Bass were measured (mm, TL) and their stomach contents collected via gastric lavage (Culp et al. 1988). Lavaging was performed with a 3-ml veterinary-grade syringe with a dulled tip filled with water that was placed in the stomach via the esophagus. The plunger was depressed and stomach contents were flushed onto a 300-μm mesh screen and preserved in scintillation vials with 70% ethanol to be analyzed later in the laboratory. Preliminary data indicated the method was effective at removing all prey items and resulted in minimal mortality.

To maintain consistent fish prey levels, additional Bluegills were added to each enclosure after sampling to bring the density back to 30 fish/m^2. Zooplankton and macro-invertebrate densities were not adjusted because the openings in the enclosure allowed recolonization from the pond. Any dead Largemouth Bass that were observed were replaced with similar sized fish. Upon completion of the experiment the vegetation mats were removed and each pond was drained to allow an accurate count of Largemouth Bass left in each enclosure. Any Largemouth Bass not present in the final sample upon draining the ponds were assumed to have died immediately after the last date it had been sampled.

Data analysis

Stomach contents from each Largemouth Bass were identified to the lowest possible taxonomic level. Each diet item was measured using the imaging software ImageJ®. The length (mm) of each diet item was converted to a pre-digested mass (mg) using the regression equation $M = aL^b$ where M is equal to mass in milligrams, L is equal to length in millimeters, and a and b are organism-specific length-mass relationship constants derived from the literature (Benke et al. 1999; Culver et al. 1985; Smock 1980). After conversion to mass, diet items were classified into

four broad taxonomic groups; fish, insects, zooplankton, and other. The "other" group included rare diet items such as an amphipod, a bivalve, a spider, and all unidentifiable diet items.

Piscivory was identified using three metrics: 1) the mass of fish prey found in the diet on each date, 2) the number of uneaten Bluegills sampled on each date divided by the number of Largemouth Bass remaining in the enclosure was used as an indirect metric of piscivory and 3) the number of fish with piscine prey in the diet as well as fish with empty stomachs was used as a more direct measure of piscivory. I chose to include empty stomachs as in indicator of piscivory in the third index because the frequency of empty stomachs increases as Largemouth Bass make the shift to piscivory (Wallus and Simon 2008). Growth was analyzed as cumulative absolute growth (TL, mm) from the start of the experiment.

Vegetation density, date, and their interaction were tested as fixed effects within generalized linear statistical models to predict piscivory (mass of fish prey in diets, ratio of uneaten Bluegills to Largemouth, and frequency of piscivorous diets + empty stomachs) and Largemouth Bass growth (instantaneous growth rate). The model testing the mass of pre-digested weight for each taxonomic group consumed by Largemouth Bass was analyzed with MANOVA in SAS proc Mixed (SAS 2014; Khattree and Naik 1999). The models testing the ratio of uneaten Bluegills to Largemouth Bass and Largemouth Bass growth assumed a normal distribution and was tested with SAS Proc Mixed (SAS 2014). The model testing the frequency of piscivorous diets + empty stomachs specified a binomial distribution and was tested with SAS Proc Glimmix (SAS 2014). For all models, pond and rows within pond were used as random blocking variables and enclosures were specified as subjects on which repeated measurements were taken. Remaining density of Largemouth Bass was used as random blocking variables in growth and piscivory models but not the uneaten Bluegills/predator model as remaining Largemouth Bass was used to create the response metric. Response variables for the models testing the number of

remaining Bluegills/Largemouth and growth were ln(X+1) transformed to normalize their
residuals.

Results

The total mass of items within diets had a significant date x taxa interaction ($F_{12, 921}$ =
4.64, P < 0.001; Figure 3) indicating different amounts of some taxa were eaten on different
dates, but these differences in consumption did not differ between vegetation treatments.
Largemouth Bass ate more insects than any other prey type early in the experiment (First two
sampling dates) and transitioned to eating mostly fish prey by the final date of the experiment (no
significant differences among prey types on third and fourth sampling dates and significantly
more fish consumed than any other prey type but insects on final sampling data). The mass of
fish prey and insect prey consumed did not differ on any dates, but insect consumption was
greater than zooplankton and other prey consumption on 7/16 – 7/17 (both comparisons P < 0.03)
and fish prey consumption was greater than the consumption of zooplankton and other prey on
8/6 – 8/7 (both comparisons P = 0.04). No other pairwise comparisons of taxa within dates were
significantly different.

The number of uneaten Bluegills/Largemouth Bass had a significant vegetation density x
date interaction ($F_{24, 769}$ = 1.65, P = 0.03), indicating that the transition to eating fish occurred at
different times in the different vegetation treatments. Significantly fewer Bluegills were left
uneaten in the control, low, and high stem density treatments as early as 7/21 – 7/22. There was
no discernable transition to piscivory in the medium stem density indicating that ontogeny to
piscivory did not fully occur (Figure 4). The number of Largemouth Bass with Bluegills in their
stomachs or empty stomachs was highly variable and did not differ among any of the four
treatments ($F_{3, 950}$ = 0.04, P = 0.99).

Cumulative absolute growth of Largemouth Bass was greater in the control, low, and high vegetation treatment than in the medium treatment ($F_{3, 408} = 4.51$, $P < 0.01$; Figure 5). Growth also increased during the experiment ($F_{1, 408} = 348.42$, $P < 0.01$), but there was no vegetation density x date interaction, indicating the observed vegetation-density effects on growth were consistent throughout the experiment.

Discussion

I found evidence that the ontogeny to piscivory happened around the same time in the control, low, and high stem density treatments (i.e., Bluegill consumption increased around the same sample dates in these treatments). A significant change in Bluegill consumption never occurred in the medium stem density. I also found Largemouth Bass grew slowest at the medium vegetation level, further suggesting that ontogeny to piscivory was delayed at the medium vegetation level. In natural systems, the early ontogeny to piscivory observed in the control, low, and high vegetation levels could be even more pronounced as the predator gains a size advantage over a greater proportion of the prey community when additional prey species that were too large to consume during early ontogeny begin to fall within the gape limits of the growing predators (Phillips et al. 1995; Post 2003). Ultimately, this early shift to piscivory and the related increase in growth would allow the predator to accumulate lipids necessary for overwinter survival (Ludsin and DeVries 1997).

The pattern that I found relating vegetation density to the timing of piscivory is in conflict with field studies that suggests vegetation slows the ontogeny to piscivory in Largemouth Bass (Bettoli et al. 1992; Miranda and Pugh 1997). Several factors could have caused these differences between field studies and the current study. First, the field studies did not include control over the prey fish community, which changed over the course of the study (Bettoli et al. 1993). Thus, changes detected in the field studies could be driven by changes in the piscine prey

community rather than by the vegetation density directly affecting Largemouth Bass foraging decisions. Second, the reduction in vegetative environments in the field study likely reduced the abundance of invertebrates (Cyr and Downing 1988; Rennie and Jackson 2005; Wiley et al. 1984), forcing Largemouth Bass to switch to piscivory due to lack of other food options. Third, the use of a single fish prey species (Bluegill) may have driven the pattern seen in my study. Had multiple fish prey species been available, the delay in the timing of piscivory in the medium vegetation density may not have been as profound because different piscine prey types may be easier to capture at different vegetation densities.

One possible explanation for the high degree of piscivory in the control, low, and high vegetation treatments but not the medium vegetation treatment is that juvenile Largemouth Bass, like adult Largemouth Bass (Savino and Stein 1982; Savino and Stein 1989), utilize different predation techniques in different densities of vegetation. Adults employ a searching technique at low (< 250 stems/m^2) densities of vegetation. However, when their foraging rate is diminished by their inability to maneuver at higher (> 250 stems/m^2) vegetation densities, they adopt a lie-in-wait strategy (Savino and Stein 1982). It is possible that there is a transitional phase for juvenile Largemouth Bass where vegetation is too dense to employ a searching technique yet not dense enough to provide enough concealment to effectively employ a lie-in-wait technique. A threshold of 516 stems/m^2 is needed before Bluegill specifically select a patch of vegetation as a predation refuge (Gotceitas and Colgan 1987). Therefore, it is possible that the juvenile Largemouth Bass' searching ability was slowed in the medium treatment (250 stems/m^2) while juvenile Bluegill were still predator-cautious at this density (likely hiding rather than searching for food as they might do at stem densities > 516 stems/m^2), making an ambush strategy less effective than at higher vegetation densities. In high vegetation densities (500 stems/m^2), Bluegill may feel safer from predation and resume their own foraging behaviors, which would increase their encounter rates with juvenile Largemouth Bass using a lie-in-wait strategy.

Different results might have been found if different fish prey were used in this experiment because different prey may exhibit different anti-predatory behaviors (Schramm and Zale 1985). Juvenile piscivorous Largemouth Bass foraged more efficiently on Fathead Minnows *Pimephales promelas* at moderate (125 stems/m^2) vegetation densities than in open water (Chapter 1). The different pattern of consumption between the current study and previous laboratory work suggests that prey community and habitat complexity may interact to effect ontogeny to piscivory in juvenile Largemouth Bass.

My results in combination with previous lab (Chapter 1) and field (Bettoli et al. 1992; Miranda and Pugh 1997) work indicate that vegetation density is an important factor determining the ontogeny to piscivory in juvenile Largemouth Bass, but that its effects may differ with different piscine prey communities. As such, further research is needed to determine how prey assemblage interacts with vegetation density to affect the ontogeny to piscivory in juvenile Largemouth Bass. However, it is clear that structural complexity can affect the timing of the ontogeny to piscivory in Largemouth Bass, so changes in vegetation levels in lakes and reservoirs may have profound effects on Largemouth Bass year-class strength.
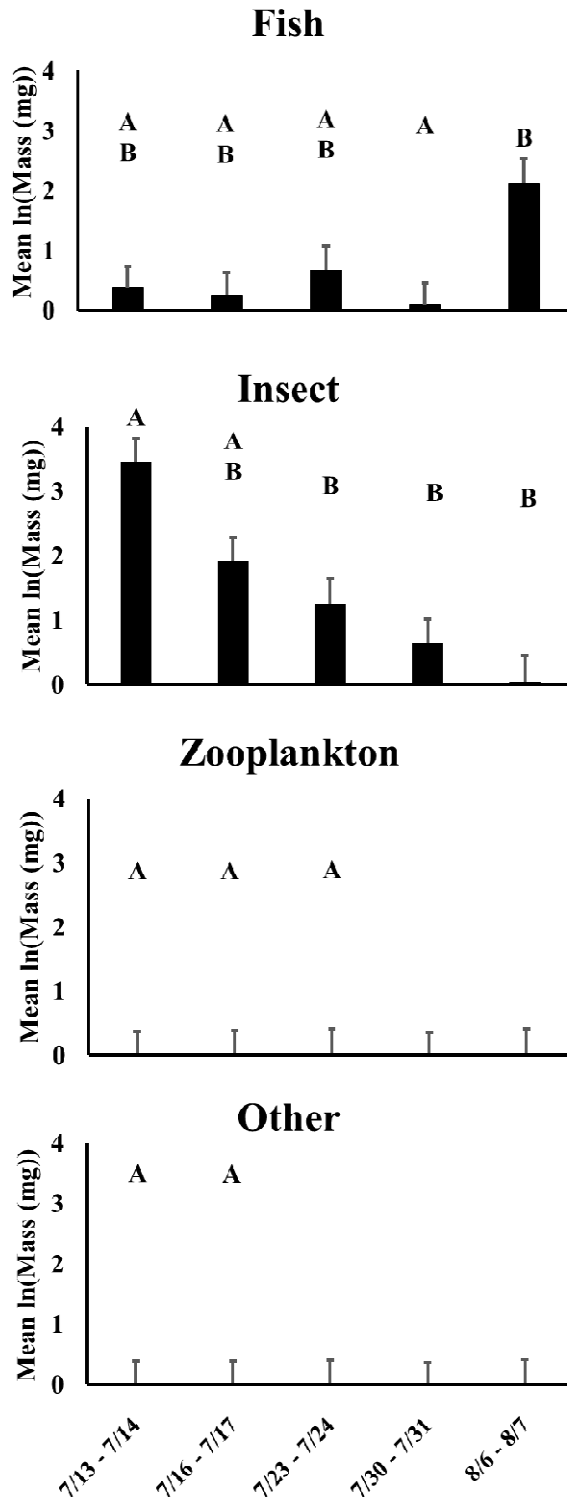
Figure 3. Mean pre-digested mass (mg) of four taxonomic groups consumed by Largemouth Bass across five dates. Graphs are grouped by taxa. Letters represent Tukey-Kramer groupings within each graph but not across graphs. Treatments with the same letter are not significantly different.
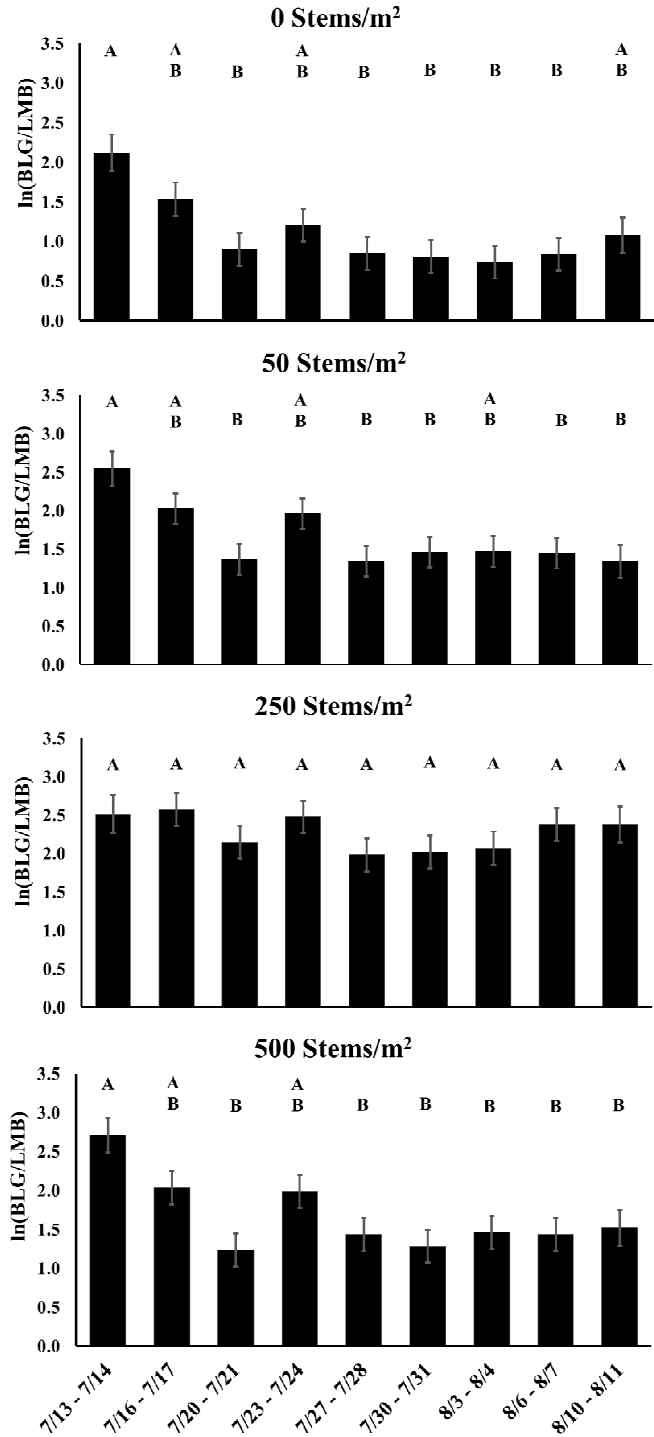
Figure 4. Mean ratio of uneaten Bluegill sampled / Largemouth Bass across nine sampling dates during an experiment testing the effects of vegetation stem density on piscivory by juvenile Largemouth Bass. Letters represent Tukey-Kramer groupings within each graph but not across graphs. Treatments with the same letter are not significantly different.
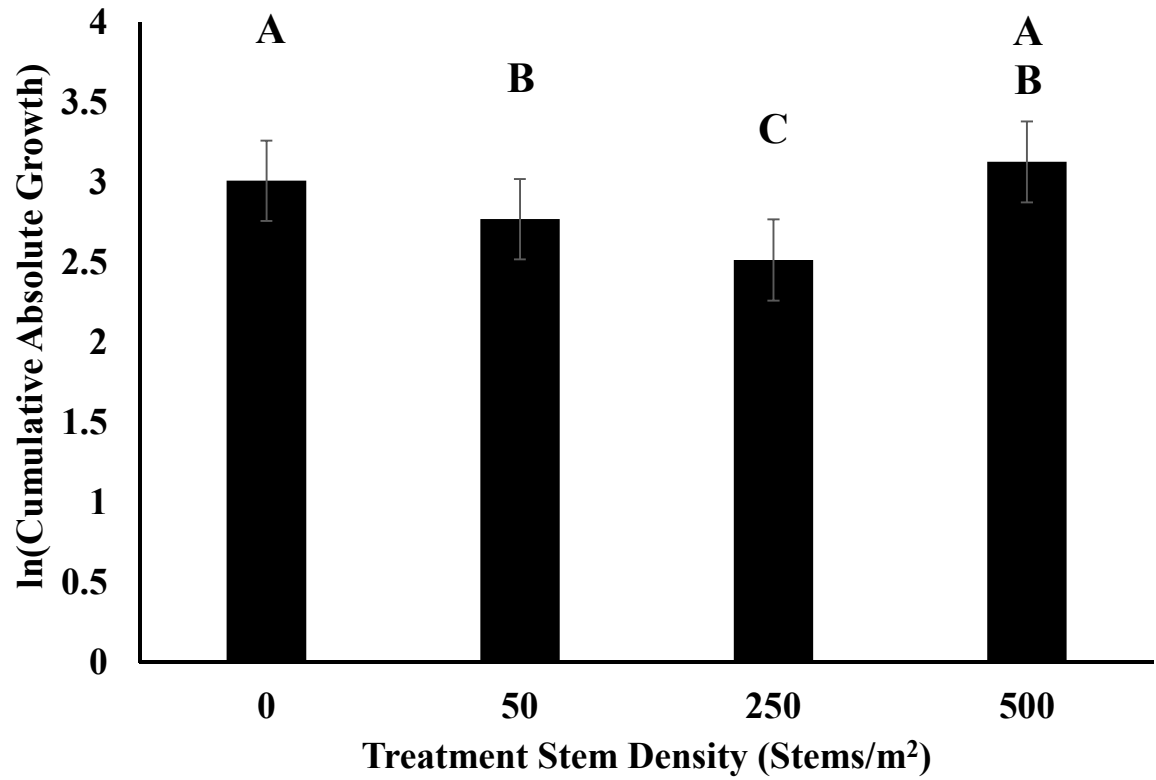
Figure 5. Mean cumulative absolute growth of individual Largemouth Bass in four vegetation
stem density treatments. Letters represent Tukey-Kramer Groupings. Treatments with the same
letter are not significantly different.

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VITA

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