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A Multi-Scale Approach To Evaluate The Effect Of The Invasive Aquatic Plant Hydrilla (Hydrilla Verticillata) On Littoral Zone Habitat Of Juvenile Largemouth Bass (Micropterus Salmoides)

Alexander James Perret

A MULTI-SCALE APPROACH TO EVALUATE THE EFFECT OF THE INVASIVE AQUATIC PLANT HYDRILLA (*HYDRILLA VERTICILLATA*) ON LITTORAL ZONE HABITAT OF JUVENILE LARGEMOUTH BASS (*MICROPTERUS SALMOIDES*)

By

Alexander James Perret

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Two experiments were conducted to investigate the hypothesis that exotic macrophytes alter littoral zone habitat and impact fish that inhabit these areas. The pond experiment was conducted to explore impacts of exotic invasive plants on growth and condition of juvenile largemouth bass (*Micropterus salmoides*). The second experiment was conducted at a smaller scale in aquaria to simulate an invasion of hydrilla (*Hydrilla verticillata*) and its influence on juvenile bass foraging. Fish experienced slower growth in the hydrilla treatment than in the diverse, and the ability of bass to capture prey fish was impeded in hydrilla. Juvenile bass growth decreased in habitats containing hydrilla and is likely a result of increased difficulty in capturing quality prey items such as small fish. Results from the two experiments collectively supported my hypothesis that hydrilla growth altered the littoral zone habitat such that foraging was hindered and resulted in slower growth.

DEDICATION

I would like to dedicate this thesis to my family, especially my wife Jessica, and my parents David and Mary Perret. They have always supported me in pursuing a career that I truly enjoy and take great pride in. I am blessed to have such a strong support system and source of motivation for being a success at everything I do.

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I also would like to thank all of the individuals who assisted with field and laboratory work throughout the course of my project. Heather Theel worked closely with me from start to finish and provided needed support and knowledge as well as assistance with data collection. Colin Cooper devoted many hours of plant collection, planting, and propagation to prepare the ponds for fish stocking. I also must thank Mike Habrat and Amy Shaw who assisted with fish collection, and Beth LaValley who helped with the stomach contents analysis in the laboratory. They were all a pleasure to work with. Also, this research would not have been possible without the funding provided by the U.S. Geological Survey.

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CHAPTER I

INTRODUCTION

Non-native macrophyte infestations in lakes and waterways of the United States have become a cause for concern in recent years. Aquatic plants provide substrate for macroinvertebrate populations which in turn provide food for juvenile fish that attract larger piscivorous fish, thus contributing to the importance of vegetation in aquatic habitats (Keast 1984, Schramm et al. 1987, Dibble et al. 1996). These macrophytes provide habitat for many of the forage fish that are important to the recruitment of largemouth bass (*Micropterus salmoides)* to adult size (Barnett and Schneider 1974, Gutreuter and Anderson 1985), while at the same time reducing predation on forage fish (Aggus and Elliot 1975, Crowder and Cooper 1979, Strange et al. 1975). The density and species composition of aquatic plant growth can impact abundance, growth, and foraging efficiency of fishes that inhabit these areas (Savino and Stein 1982, Anderson 1984, Bettoli et al. 1992).

Exotic macrophytes such as hydrilla (*Hydrilla verticillata*) and Eurasian watermilfoil (*Myriophyllum spicatum*), usually grow quickly and form a dense surface canopy that displaces native vegetation typically found in littoral zone habitats important to fish (Colle and Shireman 1980, Keast 1984, Nichols 1994, Boylen et al. 1999). The structural complexity of invasive plants is typically quite

high due to a high frequency of small gaps in the vegetation (Lillie and Budd 1992) making it difficult for fish to maneuver (Engel 1995). Exotic invasive growth can alter temperature, light, oxygen, and pH (Titus and Adams 1979, Carpenter and Lodge 1986, Madsen et al. 1991) in the water column below the canopy, thus restricting fish to the canopy (Valley and Bremigan 2002) where increased structural complexity can reduce the ability to capture prey (Crowder and Cooper 1979). As a result this may increase the difficulty of capturing forage fish and the amount of energy required to capture prey, and reduce growth and condition (Colle and Shireman 1980, Dibble et al. 1996). Variations in plant density, complexity, and architecture also can affect foraging efficiency and diet composition of fishes inhabiting these areas (Crowder and Cooper 1982, Savino and Stein 1989, Dionne and Folt 1991, Dibble and Harrel 1997). Others have hypothesized that energy gained by juvenile centrarchids may be greater in native rather than exotic invasive plant beds (Pedlow 2003) and it may be linked to increased foraging efficiency in these sites due to a decrease in habitat complexity (Bettoli et al. 1992, Engel 1995, Harrell and Dibble 2001).

In contrast, most native macrophyte beds provide open areas because of the variability in architecture due to size, number, and orientation of stems and leaves (Valley and Bremigan 2002). This increases largemouth bass foraging success (Colle and Shireman 1980, Killgore et al. 1989, Olson et al. 1998). Bass can move more freely in these habitats, allowing them better access to forage species. This results in greater predator-induced mortality of small fishes which restricts the population density of these species and reduces competitive

interactions (Savino and Stein 1982, Mittelbach 1988, Gotceitas and Colgan 1989).

The increased occurrence of exotic plant infestations in the past 30 years has provided the impetus for conducting many field and laboratory experiments that investigate the impacts of this invasive growth on fish (Colle and Shireman 1980, Anderson 1984, Lillie and Budd 1992, Dibble et al. 1996, Valley and Bremigan 2002). Most of this field research has been conducted in large water bodies and was intended to determine if presence of invasive plants affects fish abundance, size, and condition. Previous laboratory experiments have investigated fish responses to increased levels of stem density and coverage, including patch selection and foraging efficiency. However, few field experiments have been conducted to determine if fish growth is affected by exotic plant invasion that shifts habitat from a diverse native plant bed to a single species monoculture. I am aware of no laboratory research that has incorporated live plants in a simulated invasion of an exotic species in an effort to identify mechanisms that affect fish growth. A shift of research experiments in this direction may lead to a better understanding of the impacts invasive macrophytes have on fish.

Approach

A multi-scale experiment was designed to evaluate the influence of a non-native macrophyte invasion on littoral zone habitat and how it may impact juvenile largemouth bass. I investigated these effects by conducting a pond

experiment to compare growth and condition in different vegetated habitats and an aquarium experiment to research foraging ability during exotic plant invasion. The objectives of this research were to evaluate the level at which the invasive homogeneous plant growth of the exotic hydrilla alters native plant coverage and stem density, and the impact it may have on the growth, condition, and foraging ability of young largemouth bass.

Chapter 2 describes the pond experiment conducted at the Mississippi Agricultural and Forestry Experiment Station (MAFES) in Starkville, MS from June to November 2005. This experiment evaluated the null hypothesis that juvenile largemouth bass growth would not differ between a diverse native vegetated habitat and a hydrilla-dominated one. Based on previous research (Colle and Shireman 1980, Killgore et al. 1989, Olson et al. 1998), I expected bass in the diverse treatment to have greater gains in total length and weight than those in the hydrilla ponds (Crowder and Cooper 1979, Colle and Shireman 1980, Dibble et al. 1996). Increased structural complexity of some invasive macrophytes (Lillie and Budd 1992) decreases the maneuverability of fish (Engel 1995) and reduces their ability to capture prey (Crowder and Cooper 1979). This may cause reduced growth and condition (Colle and Shireman 1980, Dibble et al. 1996) of fish inhabiting these monotypic areas. Ponds containing either a mix of native plants or hydrilla were stocked with juvenile largemouth bass and redear sunfish (*Lepomis microlophus*) as forage. After approximately 5 months, bass were harvested and measurements of total length and weight were used to compare growth and condition (relative weight) among treatments.

The aquarium experiment described in Chapter 3 was designed to address the issue of decreased foraging ability as the mechanism that causes lesser juvenile largemouth bass growth in habitats taken over by an invasive macrophyte. It was conducted in an aquarium laboratory at Mississippi State University from December 2005 to March 2006. This procedure was intended to mimic what happens in natural systems when hydrilla is introduced, outcompetes native macrophytes, and forms a dense monoculture. Based on previous experiments conducted with artificial plants (Savino and Stein 1982, Anderson 1984, Gotceitas and Colgan 1987, Valley and Bremigan 2002) and knowledge that increases in complexity decrease predator maneuverability (Engel 1995), I predicted that the ability of juvenile largemouth bass to capture forage fish would decrease as the percentage of hydrilla increased and tested the null hypothesis that no difference among foraging behavior would be observed across different treatments of hydrilla concentration. It is my goal and intent that this work will lead to a better understanding of how exotic plant infestation affects littoral zone habitat, and how a shift in habitat may alter mechanisms responsible for mediating growth in juvenile largemouth bass.

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CHAPTER II

EVALUATION OF TWO DIFFERENT VEGETATED HABITATS ON JUVENILE LARGEMOUTH BASS GROWTH AND CONDITION IN A POND EXPERIMENT

Introduction

Non-native plant invasion has recently become a popular research topic in the areas of fisheries science and aquatic ecology, brought on by the increased occurrences of these infestations in the aquatic systems of the United States. Much of this research has focused on determining fish abundance and condition for various species associated with different exotic plant beds in large systems (Colle and Shireman 1980, Hoyer and Canfield, Jr. 1996, Brown and Maceina 2002, Tate et al. 2003), as well as the impacts of invasive plant removal on littoral zone fish species in large lakes (Serafy et al. 1994, Olson et al. 1998, Pothoven et al. 1999, Unmuth et al. 1999, Hunt and Annett 2002). A less common level of investigation has sought an understanding of how the varying growth forms of different plants affect the behavior of the fish that inhabit them. It is at this level that we may better quantify how invasive macrophytes alter habitat important to fish.

Aquatic plants provide substrate for macroinvertebrate populations that in turn provide food for small and juvenile fishes that comprise the forage base for

predatory species (Keast 1984, Schramm et al. 1987, Dibble et al. 1996). These forage fish are important to the recruitment of largemouth bass (*Micropterus salmoides*) to adult size (Barnett and Schneider 1974, Gutreuter and Anderson 1985). At intermediate densities, aquatic macrophytes can increase foraging efficiency and increase prey availability, resulting in greater predator feeding rates (Crowder and Cooper 1979). The density and diversity of aquatic plant growth can impact the density, growth, and foraging efficiency of the fishes that inhabit these areas (Savino and Stein 1982, Anderson 1984, Bettoli et al. 1992, Savino et al. 1992).

Most native macrophyte beds contain multiple species and provide open areas because of the variability in size, number, and orientation of stems and leaves (Valley and Bremigan 2002). This increases largemouth bass foraging success (Killgore et al. 1989, Olson et al. 1998). Bass can move more freely in these habitats, allowing them better access to forage species while still providing ambush opportunities. This results in greater predator-induced mortality of small fishes that reduces the population density of these species and reduces competitive interactions (Savino and Stein 1982, Gotceitas and Colgan 1989).

Invasive macrophytes, such as the exotic hydrilla, typically grow rapidly and form dense surface canopies that displace native vegetation (Colle and Shireman 1980, Keast 1984, Nichols 1994, Boylen et al. 1999). The structural complexity of invasive macrophytes is usually high due to a high frequency of small gaps (Lillie and Budd 1992) which makes it difficult for fish to maneuver (Engel 1995). These plants can alter temperature, light, oxygen, and pH (Titus

and Adams 1979, Carpenter and Lodge 1986) below the canopy, thus decreasing the habitable areas of the water column. Fish become restricted to the canopy (Valley and Bremigan 2002) where increased structural complexity reduces their ability to capture prey (Crowder and Cooper 1979).

It has been hypothesized that the increased difficulty of capturing forage fish and amount of energy required to feed may result in reduced growth and condition (Colle and Shireman 1980, Dibble et al. 1996). However, few studies have investigated this hypothesis by comparing these plant-induced habitats under controlled conditions. I hypothesize and predict that fish feeding in a diverse plant assemblage, because of its increased structural heterogeneity and available foraging habitat, will exhibit better condition and growth than fish feeding in a habitat heavily dominated by a single species. I conducted a pond experiment to test the null hypothesis that condition, growth, and diet of juvenile largemouth bass would not differ between a diverse native plant habitat and an invasive monotypic one dominated by hydrilla.

Methods

Pond design

The pond experiment was conducted in six, 0.04 ha ponds at the Mississippi Agricultural and Forestry Experiment Station (MAFES) at Mississippi State University. The experimental treatment consisted of two different vegetated habitats: 1) diverse, native plant assemblage, and 2) monotypic, single-species plant culture. The diverse, native assemblage consisted of

fragrant water lily *Nymphaea odorata*, water-shield *Brasenia schreberi*, coontail *Ceratophyllum demersum*, large leaf pondweed *Potamogeton nodosus*, and arrowhead *Sagittaria latifolia*. The monotypic treatment was dominated by the exotic hydrilla, and represented a typical invasion condition (Tate et al. 2003). In addition to the two plant treatments, two ponds were left unplanted contatining a predominantly open-water environment. All treatments were replicated twice.

All plants used in the pond experiment were collected from Noxubee National Wildlife Refuge and the Tennessee-Tombigbee Waterway. After collection, plants were propagated and grown in large pools in a greenhouse until they had a large enough root base to survive being transplanted into the ponds. Water lilies were planted in large and small plastic pots, pondweed and coontail were planted in 7.5 mm peat pots, and watershield was grown in small plastic pots.

Preparation of the ponds began in June 2004. Destruction of the introduced diverse plants by herbivores persisted throughout the summer and rendered the 2004 planting efforts generally unsuccessful. In the spring of 2005, fences were erected around each of the diverse ponds to lessen effects of herbivory. At this time water levels in all ponds were drawn down until they were near empty and treated with a 25% permethrin solution to dampen the effects of crayfish on the new plant growth. After three days, the ponds were filled to 25% capacity and planting began.

Ten large plastic containers (2 m diameter) and twelve small plastic containers (1 m diameter) were placed in each of the diverse ponds and filled

with a combination of potting soil and hydrated soil from the site from which the plants were collected. One large pot and two small pots of the rooted water lilies, three peat pots each of the rooted pondweed and coontail, and three rooted watershield plants were placed in each of the small containers. The large containers contained two large and three small pots of the water lilies, four peat pots each of pondweed and coontail, and five rooted watershield plants. Three of the arrowhead plants were planted in different areas in each of the diverse ponds. Water levels in the ponds were raised as the plants grew until the pond reached and was maintained at full capacity.

Introduction of the hydrilla in June and July 2004 resulted in a large monotypic plant bed filling each of the designated ponds. However, it did not grow back as expected in spring 2005. It was introduced into these ponds again at the same time the diverse ponds were being prepared, with forty rooted bunches being planted throughout each of the ponds while the water level was at approximately 25% of pond capacity. Water levels were raised gradually as the hydrilla growth spread. The control ponds were drained and treated for crayfish with the 25% permethrin solution along with the other four. Sparse growth of emergents was present along the fringes of the ponds, but no submersed species were present.

Fish community

Juvenile largemouth bass (45-65mm) were stocked in mid-June 2005 at a density of 50 fish per pond to resemble population densities found in coves of

reservoirs in Mississippi (Meals and Miranda 1991) and to account for stocking mortality. Vegetation in the ponds had been established and growing for approximately 1month at the time of all fish introductions. The forage base consisted of recently hatched redear sunfish (*Lepomis microlophus*) 1-3 weeks old and fathead minnows (*Pimephales promelas*) 25.4mm-50.8mm stocked at densities of 300 and 100 fish per pond respectively in June 2005. These fish were introduced solely as a source of food for the bass as they grew throughout the experiment.

Juvenile largemouth bass were measured and weighed prior to their introduction into the ponds. Twenty bass in each pond were marked with VI Alpha fluorescent subcutaneous tags prior to stocking to obtain individual growth data. Pre-stock measurements represented original total length (TL) of the fish, with the final TL being obtained six months later at the beginning of November 2005 when the fish were collected. At this point all ponds were drained, requiring approximately 6 hours each. Approximately 12 inches of water was left in the control ponds which were then seined repeatedly until no more fish were collected. Then ponds were drained completely and fish were picked out by hand. All fish collected were preserved whole in a 10% formalin solution and transferred to the laboratory for stomach removal and diet assessment.

Growth and condition

All length and weight measurements obtained were used to compare average fish growth between treatments. Individual gains in length and weight

obtained from tagged fish were used to determine if a significant difference in individual growth occurred between treatments and to compare the distribution of growth among the fish. Condition factors were calculated using the final length and weight measurements of all fish collected at the conclusion of the experiment. Condition was expressed as relative weight (W_r) and calculated as follows: $W_r = (W/W_s) \times 100$ (Anderson and Neumann 1996).

Diet composition

Once in the laboratory, stomachs were removed from all bass, placed in a 70% ethanol solution, and stored until each was dissected and the contents removed for identification. A dissecting microscope was used to identify each item present in the stomachs. Items were classified into two prey types and referred to as either fish or invertebrates. To accurately compare the food items consumed in each treatment contents from each individual stomach were placed in a drying oven at 100 °C for 24 hours, and each prey type was weighed and expressed as dry weight (Bowen 1996). The dry weight method was used to remove variation in water weight that may have resulted during fixation and because it may be the most appropriate approach for analyzing stomach contents for piscivorous fish (Hyslop 1980).

Habitat measurements

To monitor changes in habitat structure, presence-absence of plants and stem densities were measured bimonthly among the two treatments of aquatic vegetation during July 2005 through the end of October 2005. These vegetation

measurements were modified after Madsen et al. (1991) and Canfield (1941). A grid was applied to each pond and each intersection was numbered for random selection of sampling points and to ensure that presence-absence was recorded consistently at the same spots. Presence-absence was determined at each point using a 0.33 m^2 quadrat, and all species present at each point were identified. For each sample, the number of points containing vegetation was expressed as a percentage of the total number of points sampled, or percent coverage. Stem density was measured at 10 randomly selected points in each pond during each sampling session. At each selected point a 0.33 m^2 quadrat was placed 0.6 m below the surface to count submergent as well as emergent forms of vegetation. The species of plants present were identified and total number of stems counted.

Water quality was monitored bimonthly using YSI 55 (dissolved oxygen) and YSI 63 (pH, conductivity, and temperature) meters deployed at five randomly selected points in each pond. Data from all ponds were combined to follow changes in water quality throughout the experiment. Light transmission to a depth of 0.6 m was measured by using a LiCore LI-1400 lightmeter at each of the ten randomly chosen stem density points in each pond. These data allowed comparisons of plant structure and architecture present in the two treatments by analyzing amount of light allowed through the water column by each type.

Statistical analyses

Differences between treatments for all habitat and fish growth measurements were tested for in SAS using an analysis of variance (ANOVA) in

which ponds were nested within treatment. Treatment affect will be explained by significant differences between ponds which indicate a Tukey-Kramer adjusted $p<0.05$. A log-linear regression was run on a distribution of gains in individual total length from each treatment to determine if significant differences existed (Littell et al. 2006). Data were grouped by treatment for distribution analysis due to varying numbers of tagged fish harvested from each pond. Analyses of the diet data included the numbers and dry weights of fish and invertebrates that were removed from stomachs of the bass. Differences in stomach contents among treatments were tested for using a multivariate analysis of variance (MANOVA) in SAS. These tests were conducted at a 95% confidence level.

Results

Habitat

Each treatment provided a different level of stem density and plant coverage as was intended to expose the fish to various habitat complexities (Figure 2.1 and Table 2.1). Hydrilla, in its respective ponds, increased in density throughout the sample season (Figure 2.1). Mean percent plant coverages were 81.70% and 90.54% for hydrilla, and 70.73% and 85.96% for diverse ponds and significant differences were detected between several ponds (Figure 2.2). Mean stem densities were 151 stems/m^2 and 113 stems/m^2 for hydrilla ponds, and 45 stems/m^2 and 53 stems/m^2 for diverse ponds. Significant differences existed between several ponds (Figure 2.3). Mean values for monitored water quality

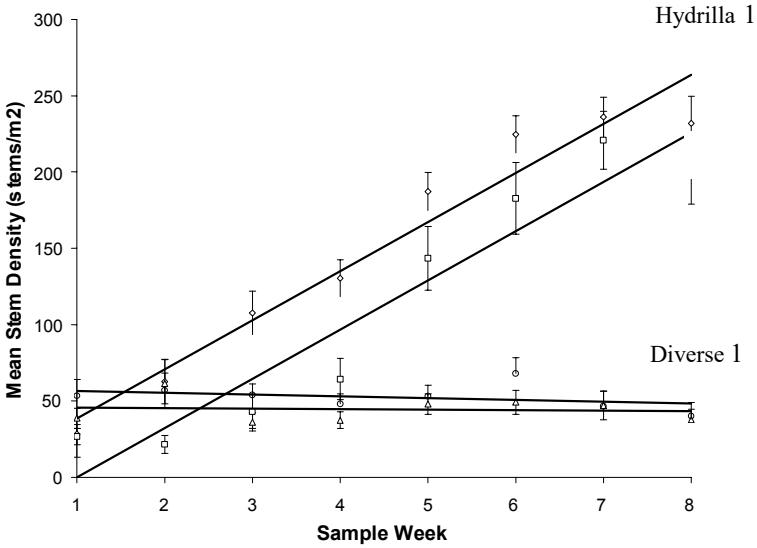

Figure 2.1. Mean weekly stem density measured at 10 different random points across treatments in the pond experiment at Mississippi State University from July to October 2005 (bars represent standard error).

Table 2.1. Percent plant coverage measured at 41 different points across treatments in the pond experiment at Mississippi State University from July to October 2005.

	Percent Plant Coverage			
Sample Week	Hydrilla 1	Hydrilla 2	Diverse 1	Diverse 2
1	68.3	70.7	75.6	70.7
2	95.1	80.5	70.7	73.2
3	100.0	78.1	70.7	82.9
4	100.0	95.0	75.6	90.2
5	100.0	100.0	70.7	95.1
6	100.0	100.0	68.3	92.7
7	100.0	100.0	68.3	92.7
8	100.0	100.0	65.9	90.2

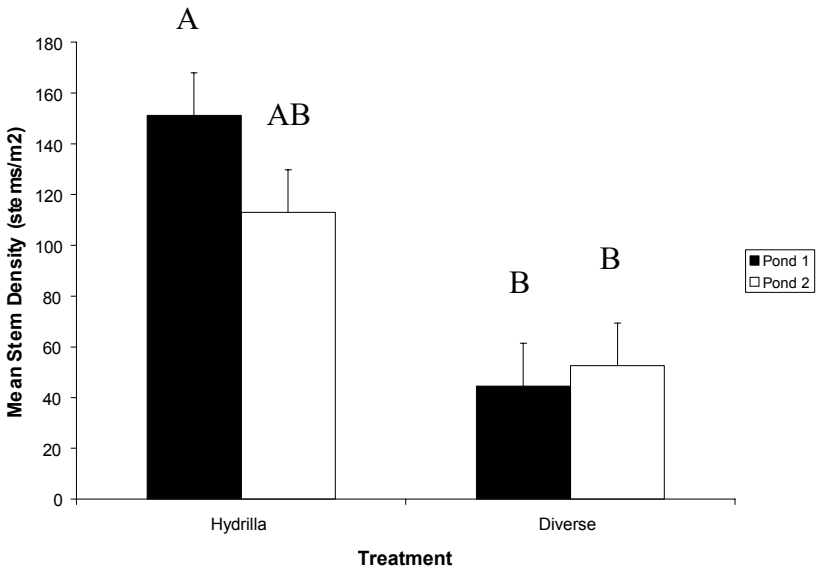

Figure 2.2. Mean stem density measured at 10 different random points across treatments in the pond experiment at Mississippi State University from July to October 2005 (different letters indicate a significant difference and bars represent standard error).

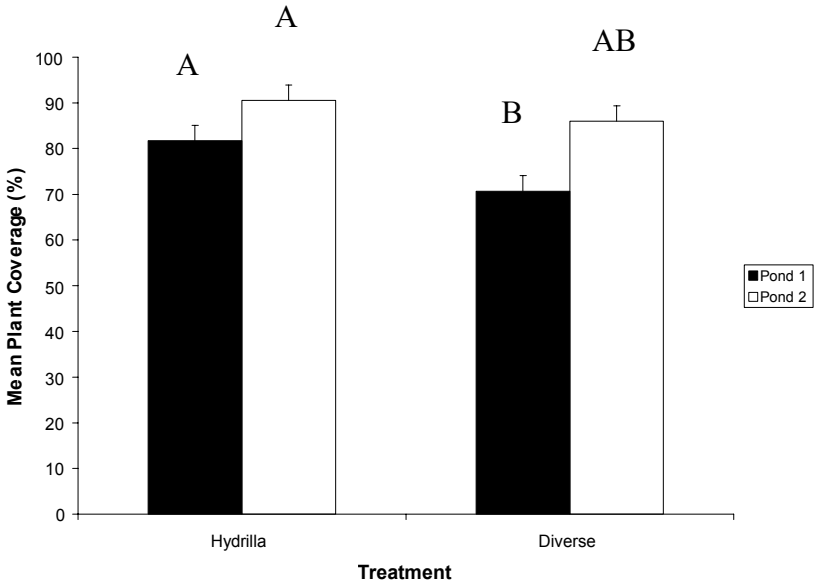

Figure 2.3. Mean percent plant coverage measured at 41 different points across treatments in the pond experiment at Mississippi State University from July to October 2005 (different letters indicate a significant difference and bars represent standard error).

parameters throughout the experiment were 24.93 °C, 8.59, 178.27 mS/cm, and 5.62 g/mL for temperature, pH, specific conductivity, and dissolved oxygen, respectively. The average percentage of light transmitted through the water column was 6.78 % and 8.15 % for hydrilla ponds, and 8.31 % and 8.74 % for diverse ponds. Ponds did not differ significantly for light transmission.

Growth and condition of fish

Mean largemouth bass sizes just prior to stocking for hydrilla ponds were 54 mm and 53 mm for total length, and 1.47 g and 1.36 g for weight. Mean pre-stock largemouth bass measurements for the diverse ponds were 52 mm and 53 mm total length and 1.34 g and 1.46 g for weight. There were no significant differences in pre-stock total length or weight between ponds. Post-harvest means for bass total length were 174 mm and 183 mm for hydrilla ponds, and 213 mm and 188 mm for diverse ponds. Nested ANOVA detected significant differences in total length between several ponds (Figure 2.4). Mean post-harvest weights were 64.17 g and 71.31 g for hydrilla ponds, and 119.82 g and 76.73g for diverse ponds. Significant differences in post-harvest weight existed between ponds (Figure 2.5).

Individual largemouth bass averaged gains in total length of 119 mm and 129 mm in hydrilla ponds, and 154 mm and 136 mm in diverse ponds during the experiment. Mean individual gains in weight for bass in hydrilla ponds were 59.02 g and 67.91 g, and mean gains for those in diverse ponds were 105.14 g and 75.97 g during the growth trial. Several ponds differed significantly for

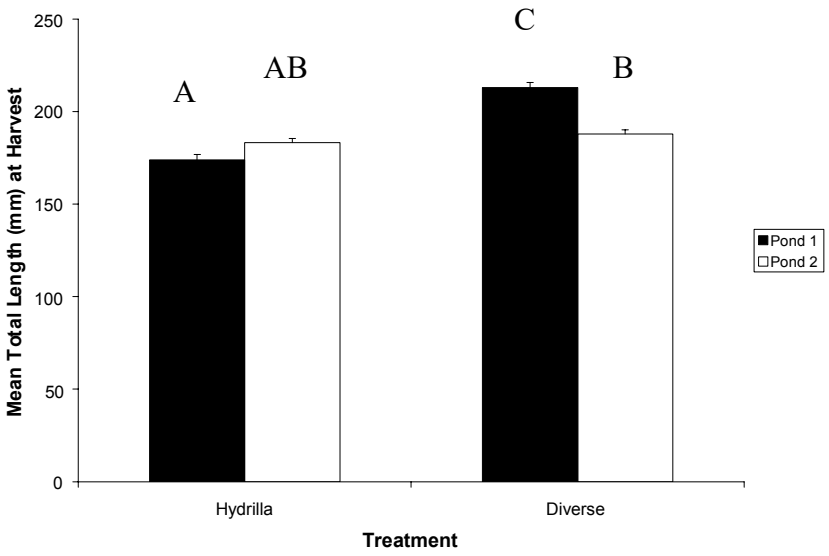

Figure 2.4. Mean total length at harvest of juvenile largemouth bass measured across treatments in the pond experiment at Mississippi State University from June to November 2005 (different letters indicate a significant difference and bars represent standard error).

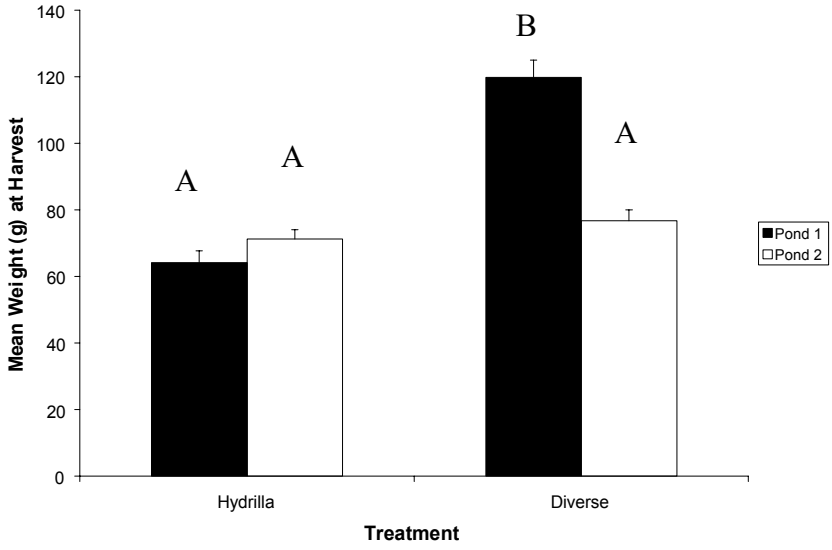

Figure 2.5. Mean weight at harvest of juvenile largemouth bass measured across treatments in the pond experiment at Mississippi State University from June to November 2005 (different letters indicate a significant difference and bars represent standard error).

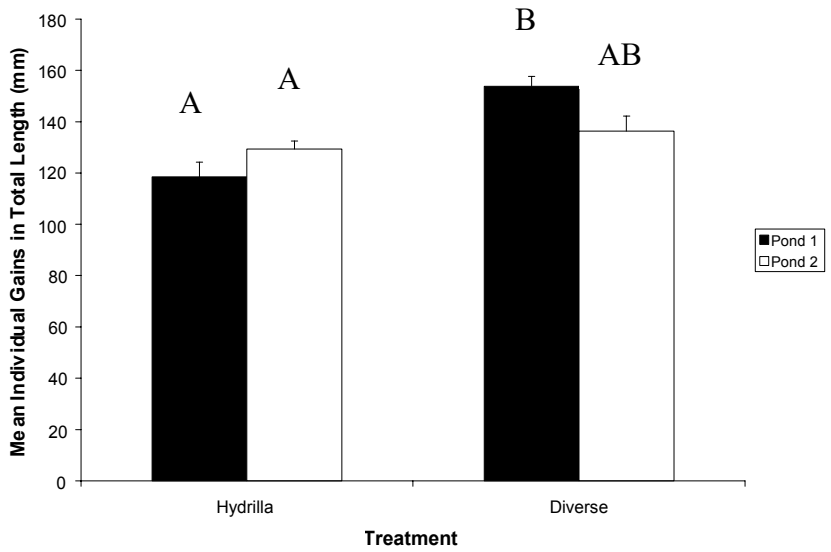

Figure 2.6. Mean individual gains in total length of juvenile largemouth bass measured across treatments in the pond experiment at Mississippi State University from June to November 2005 (different letters indicate a significant difference and bars represent standard error).

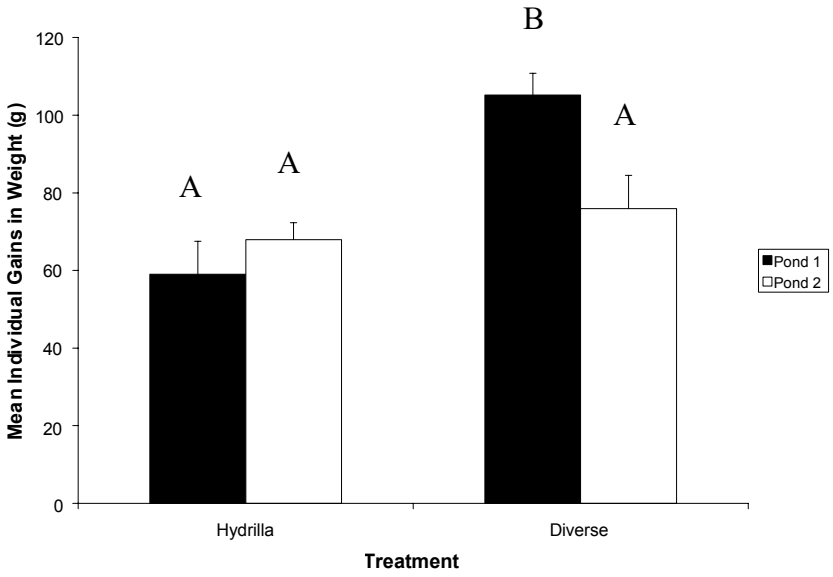

Figure 2.7. Mean individual gains in weight of juvenile largemouth bass measured across treatments in the pond experiment at Mississippi State University from June to November 2005 (different letters indicate a significant differences and bars represent standard error).

individual gains in total length and weight (Figures 2.6 and 2.7). Mean relative weight calculations for condition of all largemouth bass were 93.02 and 87.32 for hydrilla ponds, and 90.14 and 86.64 for diverse ponds. A significant difference in relative weight was detected among experimental ponds (Figure 2.8).

The distribution of gains in length details the growth of the individually tagged fish from each treatment throughout the experiment (Figure 2.9). Seventy-nine percent of the fish in the hydrilla treatment gained less than 140 mm whereas 43 % and 33 % from the diverse and control ponds, respectively, experienced that level of growth. The median growth class, 140 mm – 149.9 mm, contained 16 %, 19 %, and 53 % of the bass from the monoculture, diverse, and control treatments, respectively. The diverse assemblage of plants resulted in the greatest percentage (38 %) of fish that grew more than 150 mm. Only one bass (5 %) from the hydrilla treatment and two (13 %) from the control grew more than 150 mm. Log-linear regression performed on the frequency of distributions revealed significant differences between the hydrilla and diverse treatments (F = 20.46, $P \leq 0.001$) and the hydrilla and control (F = 19.14, $P \leq 0.001$). There was no significant difference in the frequency of distributions of largemouth bass growth between the diverse treatment and the control (F=0.04, P=0.834).

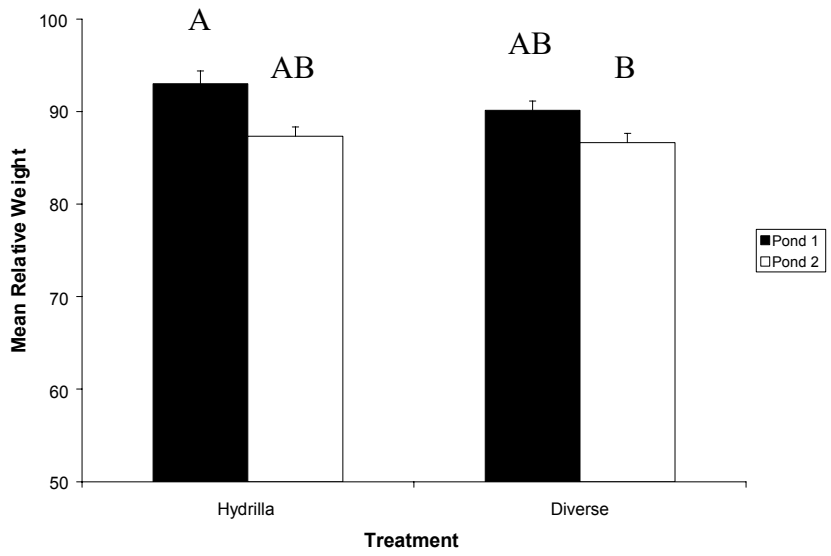

Figure 2.8. Mean relative weight of juvenile largemouth bass measured across treatments in the pond experiment at Mississippi State University from June to November 2005 (different letters indicate a significant difference and bars represent standard error).

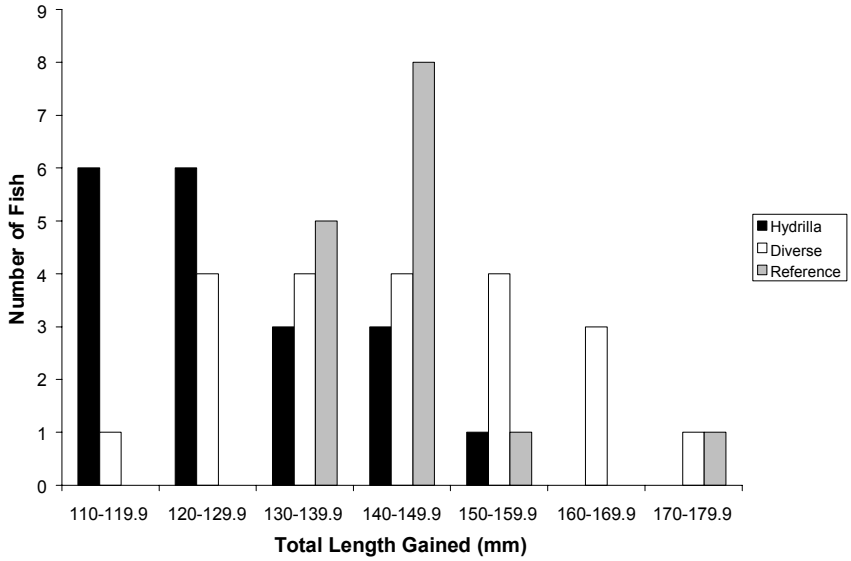

Figure 2.9. Frequency distribution of mean gains in individual total length of juvenile largemouth bass measured across treatments in the pond experiment at Mississippi State University from June to November 2005.

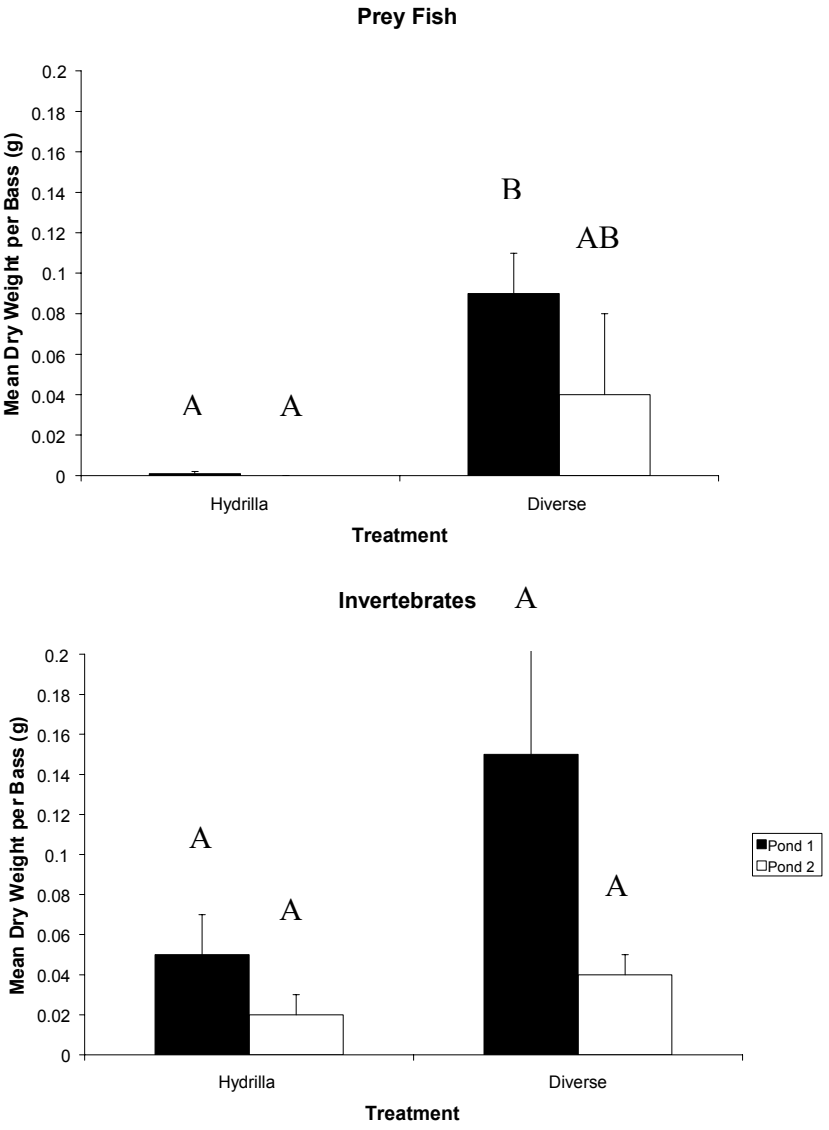

Figure 2.10. Mean dry weights of two types of food items found in each stomach of juvenile largemouth bass measured across treatments in the pond experiment at Mississippi State University from June to November 2005 (different letters indicate a significant difference and bars represent standard error).

Diets

Mean dry weight of prey fish found in each stomach was 0.001 g and 0.000 g for hydrilla ponds, and 0.085 g and 0.061 g for diverse ponds. Prey fish dry weight was significantly higher in diverse pond 1 than both hydrilla pond 1 ($P=0.013$) and hydrilla pond 2 ($P<0.002$) (Figure 2.10). Mean dry weights of the invertebrates found in each bass stomach were 0.048 g and 0.021 g for hydrilla ponds, and 0.149 g and 0.092 g for diverse ponds. Mean invertebrate dry weights in the hydrilla ponds did not differ significantly from those in the diverse treatment (Figure 2.10).

Discussion

The nested analyses of data by pond revealed that the hydrilla ponds generally resulted in higher vegetation density, lower bass growth, and less prey fish eaten. Results also showed that Diverse Pond 2 exhibited plant coverage and density levels that fell somewhere between a monotypic hydrilla bed and a true diverse plant habitat growing in patches with large open spaces. This may explain some results of the fish growth analyses which showed that this pond was not significantly different from ponds in either treatment. However, results do show that largemouth bass living in hydrilla-dominated ponds generally experienced less growth and foraged on less fish.

A possible explanation for greater juvenile largemouth bass growth in the diverse treatment may be that their movement was unrestricted and they were able to forage freely and successfully. The increased habitat complexity of the

hydrilla resulted in an increase of individual bass experiencing less growth. Although I did not measure for this, suppressed growth was likely caused by reduced access to prey items. Similar effects and alterations of exotic plants on largemouth bass diets and growth have been suggested (Savino and Stein 1982, Wiley et al. 1984, Dibble and Harrel 1997). It is suggested that the dense nature and complexity of invasive plants inhibits the ability of largemouth bass to move freely and thus forage successfully (Lillie and Budd 1992, Engel 1995). The impeded ability to capture quality prey items such as small fish, as well as the increased energy requirement to do so, may result in less growth and poorer condition (Colle and Shireman 1980, Dibble et al. 1996, Harrel and Dibble 2001).

Relative weight calculations for largemouth bass from both treatments revealed that there was no overall difference in the condition of the fish. Colle and Shireman (1980) reported that levels of hydrilla coverage greater than 50 % resulted in a decrease in the condition of small largemouth bass in hydrilla-infested lakes. Reasons for poorer condition may be the increased refugia for prey fish and reduced predator foraging efficiency which resulted in greater abundance of small fishes and stronger competition for food such as invertebrates (Mittelbach 1988, Olson et al. 1998). Numbers of stocked forage fish were identical throughout the experimental ponds and new fish were not able to inhabit favorable vegetated areas as in a natural system. The lack of differences in condition of juvenile largemouth bass among treatments may have been a result of the controlled nature of the experiment and the missing mechanism of more small fish populating the dense vegetation to avoid predators

and feeding on invertebrates. Juvenile largemouth bass in the hydrilla ponds may not have had to compete for food as they would have had the plant bed existed in a large system where other small fishes could inhabit the vegetation.

Stomach contents analysis showed that dry weight of prey fish found in bass stomachs was greater in the diverse plant habitat than in the dense hydrilla ponds. This supports the hypothesis that predators in dense vegetation are restricted in their ability to capture prey fish inhabiting these areas. Dibble and Harrel (1997) suggested that largemouth bass may experience differences in foraging success depending on the architecture of the vegetation they inhabit. They showed that juvenile bass diets were comprised of more prey fish than invertebrates (67 % and 33 %, respectively) in Eurasian watermilfoil, but greater amounts of invertebrates than fish (71 % and 29 %, respectively) in common pondweed. Although they are both invasive exotic plants, differences in architecture may explain why bass are able to forage predominantly on fish in the milfoil but not the hydrilla. Differences in growth forms were apparent in my experiment where both types of plant habitats had high coverage levels on the surface (Table 2.1), yet subsurface environments were different as evidenced by the different stem densities (Figure 2.1).

It is possible that the elevated growth level of the bass in the true diverse vegetation pond was a result of the plant patchiness and habitat heterogeneity which provides more edge and better foraging conditions (Trebitz et al. 1997, Unmuth et al. 1999). Bass in the dense hydrilla beds may have been restricted in movement and not able to actively search for food or ambush prey due to the

lack of edge present (Engel 1995). Vegetated habitats provide small prey fish the opportunity to feed on small invertebrates while avoiding larger predators (Schramm and Jirka 1989). Due to the density of the hydrilla, invertebrates were abundant yet not readily available (Theel 2007). This may explain why invertebrates were the predominant forage item for bass in the hydrilla treatment.

Less growth of the fish in the monotypic hydrilla ponds may have been due to delayed onset of piscivory in largemouth bass as a result of highly complex habitats which others have noted in reservoirs containing dense exotic invasive plant beds (Bettoli et al. 1992). This study in Lake Conroe, Texas investigated piscivory in young-of-the-year largemouth bass when the lake was heavily and sparsely vegetated. Although it was concluded that piscivory was indeed delayed at high levels of vegetation, plant growth and complexity may not be the sole cause. It was suggested that changes in the prey fish community brought about by changes in plant abundance may explain the disparity in largemouth bass size at the onset of piscivory.

Bettoli et al. (1992) expressed the need for manipulated experiments varying vegetation complexity without altering the available prey base. In my experiment, identical numbers and species of fish comprising the forage base were stocked into each pond, regardless of treatment, and similar to the Lake Conroe experiment, I found significantly greater amounts of prey fish in bass from the treatments containing lower levels of vegetation. This suggests that the initiation of piscivory in young largemouth bass may be delayed in heavily vegetated habitats. It is possible that less encounters with forage fish reduce the

opportunity to feed on quality items, forcing bass to settle for a diet largely comprised of invertebrates. However, effects of invasive plant growth on predator foraging must be further investigated at a smaller scale to better understand the mechanisms that may affect first year growth.

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CHAPTER III

AN EXPERIMENTAL SIMULATION OF A NON-NATIVE MACROPHYTE INVASION ON JUVENILE LARGEMOUTH BASS FORAGING HABITAT

Introduction

Increased occurrences of exotic aquatic plant infestations have provided a need for field and laboratory experiments investigating their impacts on fish. The structural components of vegetated habitats differ with plant type and morphology (Dibble et al. 1996). This variation in growth form results in different levels of complexity which affects fish foraging behavior and ultimately growth (Savino and Stein 1982, Anderson 1984, Bettoli et al. 1992).

Most of the field research in this area has been conducted in large water bodies and intended to determine if presence of invasive plants affects fish abundance, size, or condition (Colle and Shireman 1980, Hoyer and Canfield 1996, Brown and Maceina 2002, Tate et al. 2003). Some laboratory experiments have investigated behavioral responses of fish to increased levels of stem density and coverage, including patch selection and foraging efficiency (Savino and Stein 1982, Anderson 1984, Gotceitas and Colgan 1987, Gotceitas and Colgan 1989, Savino and Stein 1989, Gotceitas 1990, Hayse and Wissing 1996, Valley and Bremigan 2002). These procedures used either string or plastic plants to simulate varying levels of habitat complexity. Excluding the experiment

that used artificial plants (Anderson 1984), this research does not address the impact of dense exotic plant growth on fish behavior.

I am aware of no previous laboratory research that has incorporated live plants in a simulated invasion of an exotic species in an effort to determine the actual mechanisms that result in suppressed juvenile largemouth bass growth. Such research experiments could lead to a better understanding of why invasive macrophytes, such as hydrilla, have negative effects on fish. I designed an aquarium experiment to simulate the invasion of hydrilla (*Hydrilla verticillata*) in a habitat previously occupied by a mix of vegetation and to quantify the effects on largemouth bass foraging. I hypothesized that a shift in plants from a diverse assemblage to a dense hydrilla monoculture would decrease the ability of largemouth bass to feed on small fish.

Methods

Aquarium design

This experiment was conducted in an aquarium laboratory at Mississippi State University using a 130 gallon aquarium (180cm X 75cm X 24.5cm). The experimental arena in this aquarium was 50.8cm X 75cm X 24.5cm. The process was designed to mimic what happens in aquatic systems when hydrilla is introduced and becomes established. This procedure consisted of a treatment of different species compositions of vegetated habitat that simulated hydrilla invasion: (1) 0% hydrilla / 100% diverse vegetation, (2) 25% hydrilla / 75% diverse vegetation, (3) 50% hydrilla / 50% diverse vegetation, (4) 75% hydrilla /

25% diverse vegetation, (5) 100% hydrilla, (6) 300% hydrilla, and (7) control (no vegetation). The composition of the 100% diverse vegetation treatment was based on Teels et al. (1976) and stem density resembled what I had measured in the ponds planted with the diverse assemblage of vegetation in the previous experiment (Chapter II). The treatment of diverse vegetation consisted of fragrant water lily (*Nymphaea odorata*), large leaf pondweed (*Potamogeton nodosus*), and coontail (*Ceratophyllum demersum*), all native plant species common to aquatic systems of the southeastern United States. For the purposes of this experiment, 22 stems were present in the experimental arena. Stem density was defined as a basal unit and stems were connected at the bottom of the plant near the root. The 100% hydrilla treatment remained at the same stem density as the 100% diverse treatment, only all stems present were hydrilla. In the 300% hydrilla treatment the stem density was tripled and thus resembled the dense, monotypic growth that is usually associated with hydrilla (Tate et al. 2003).

All vegetation used in this experiment was collected from the Noxubee National Wildlife Refuge and the Tennessee-Tombigbee Waterway in Mississippi. Plants were propagated and grown in large pools in a greenhouse prior to being placed in the aquarium. To avoid using soil or gravel, a grid was fitted on the bottom and contained 66 different points. Points were randomly selected and a stem was attached to each point. Points selected more than once were given multiple stems.

Predators and prey

Juvenile largemouth bass (range = 81-99 mm total length) were obtained from a local hatchery to serve as the predator in this foraging experiment. Mosquitofish *Gambusia affinis* (range = 29-40 mm total length) were obtained from local ponds and creeks to serve as the prey fish for this procedure. The bass were held in a 100 gallon aquarium containing the three plant species present in the diverse treatment to resemble a natural surrounding. The mosquitofish were kept in two 20 gallon aquaria prior to introducing them into the experimental arena.

Foraging ability

The six treatments and the control were replicated 15 times each during the experiment. Valley and Bremigan (2002) conducted a power analysis and determined that 13 replicates were necessary to achieve significant results for a similar experiment. The experiment was divided into three trials, each composed of the same six treatments and a control, to avoid changes in architecture due to plants dying and deteriorating. Fresh plants and a separate randomization of stems were used for each trial to maintain density and species composition, and also to assure that the bass would not become conditioned to the environment. Five replicates of each treatment and control were performed in each trial. Predators were used only once per treatment in each trial so that they would not learn the layout of the vegetation and thus have a predatory advantage.

For each replicate three largemouth bass, starved for 24 hours (Savino and Stein 1989), and three mosquitofish were placed into separate sides of the prepared experimental arena 20 minutes prior to the start of videography (Anderson 1984). These areas were separated by a divider, allowed the fish equal amounts of time to acclimate to the surroundings, and prevented them from seeing each other before the divider was raised. When the acclimation period was over, the divider was removed and videography began. Each replicate was allowed to run until all prey fish were captured or 30 minutes had elapsed (Gotceitas and Colgan 1989).

For this experiment, foraging ability of largemouth bass was quantified by number of mosquitofish captured per bout, number of attempts per capture, number of feeding attempts that did not result in a capture, and amount of time required to capture each prey fish (Savino and Stein 1982, Gotceitas and Colgan 1989). This time included such behaviors (as described by Savino and Stein 1982) as: (1) following: moving and orienting to prey; (2) pursuit: following prey at burst speed; (3) attack: making contact with prey; and (4) capture: engulfing and handling prey. To record accurate measurements, videography was used in a manner similar to the methods used by Anderson (1984) to classify observations and measure time elapsed. A black curtain was used to enclose the aquarium and video unit in an effort to reduce distractions that may excite or stress the fish.

Statistical analyses

Data were organized and analyzed by treatment (% hydrilla). Significant differences between treatments were tested using a one-way analysis of variance in SAS. Measurements analyzed included number of prey captured, non-capture attempts, time required for each capture, and attempts per capture. All tests were conducted at a 95% confidence level.

Results

The mean number of captures per replicate ranged from 1.73 to 2.87 (Table 3.1). Significant differences between several treatments were detected, in particular that between the 100 % and 300 % hydrilla habitats ($F=21.29$, $P \leq 0.001$) (Figure 3.1 and Table 3.2). Mean attempts per capture ranged from 1.33 to 2.67 (Table 3.1), and significant differences were noted between some treatments, most notably the 0 % (diverse) and 100 % hydrilla treatments ($F=4.45$, $P=0.038$) (Figure 3.2 and Table 3.2).

Table 3.1. Mean values for juvenile largemouth bass foraging parameters measured across six treatment levels of hydrilla composition and a control during the aquarium foraging experiment conducted at Mississippi State University December 2005 to March 2006.

Treatment	Forage Parameters			
(% Hydrilla)	Captures / Bout	Attempts / Capture	Time (s) / Capture	Non-capture Attempts
0	2.00	1.50	4.17	2.13
25	2.00	1.39	3.81	1.80
50	1.87	2.07	6.18	4.54
75	2.20	2.35	6.03	4.07
100	2.87	2.09	5.30	3.73
300	1.73	2.67	7.89	5.53
Control	2.80	1.33	2.71	0.53

Table 3.2. Analysis of variance results for juvenile largemouth bass foraging parameters measured across six treatment levels of hydrilla composition and a control during the aquarium foraging experiment conducted at Mississippi State University from December 2005 to March 2006.

Treatment Comparison (% Hydrilla)	Captures / Bout F value	p-value	Attempts/Capture F value	p-value	Non-Capture Attempts F value	p-value	Time/Capture F value	p-value
0 x 25	0.00	1.000	0.37	0.545	0.20	0.655	0.74	0.392
0 x 50	0.19	0.667	4.32	*0.042	3.99	0.056	11.31	*0.001
0 x 75	0.46	0.505	9.30	*0.003	4.25	*<0.049	10.17	*0.002
0 x 100	16.21	*<0.001	4.45	*0.038	1.86	0.183	4.77	*0.032
0 x 300	0.79	0.382	9.63	*0.003	9.89	*<0.004	15.41	*<0.001
0 x no plants	12.92	*<0.002	0.74	0.393	6.29	*0.018	13.64	*<0.001
25 x 50	0.17	0.682	6.86	*0.011	7.17	*0.012	15.18	*<0.001
25 x 75	0.41	0.526	13.03	*<0.001	7.32	*<0.012	14.11	*<0.001
25 x 100	13.44	*0.001	6.80	*0.011	3.12	0.088	8.06	*0.006
25 x 300	0.71	0.406	7.52	*0.008	14.06	*<0.001	18.62	*<0.001
25 x no plants	10.84	*<0.003	0.07	0.792	7.00	*0.013	7.20	*0.009
50 x 75	1.05	0.313	0.70	0.405	0.02	0.893	0.04	0.839
50 x 100	15.59	*<0.001	0.00	0.948	0.03	0.870	1.82	0.182
50 x 300	0.16	0.688	1.54	0.22	2.03	0.165	2.49	0.121
50 x no plants	12.94	*<0.002	8.86	*0.004	23.19	*<0.001	39.44	*<0.001
75 x 100	7.69	*<0.010	0.68	0.412	0.07	0.790	1.39	0.242
75 x 300	2.14	0.154	0.48	0.493	1.62	0.213	3.40	0.070
75 x no plants	5.91	*<0.022	16.73	*<0.001	22.09	*<0.001	38.65	*<0.001
100 x 300	21.29	*<0.001	1.80	0.184	1.78	0.193	8.33	**0.005
100 x no plants	0.23	0.638	9.27	*0.003	9.66	*0.004	29.75	*<0.001
300 x no plants	17.92	*<0.001	12.82	*<0.001	29.25	*<0.001	38.3	*<0.001

* denotes significant difference at $\alpha = 0.05$

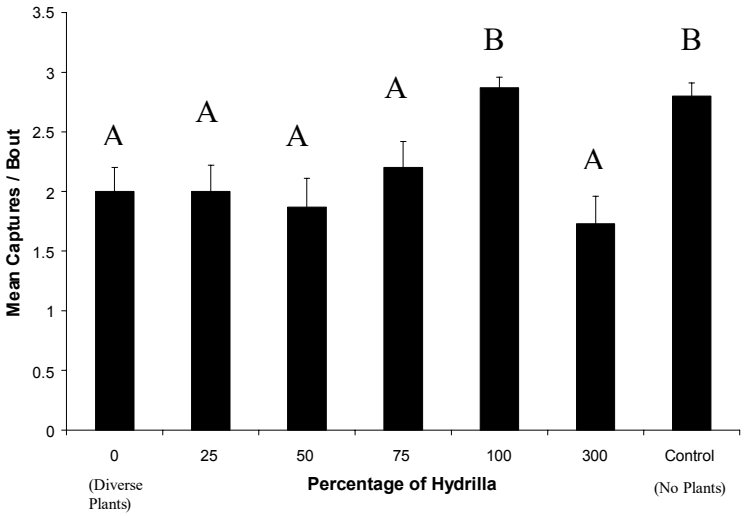

Figure 3.1. Mean numbers of mosquitofish captured by juvenile largemouth bass measured across six treatment levels of hydrilla composition and a control during the aquarium foraging experiment conducted at Mississippi State University December 2005 to March 2006 (different letters indicate a significant difference and bars represent standard error).

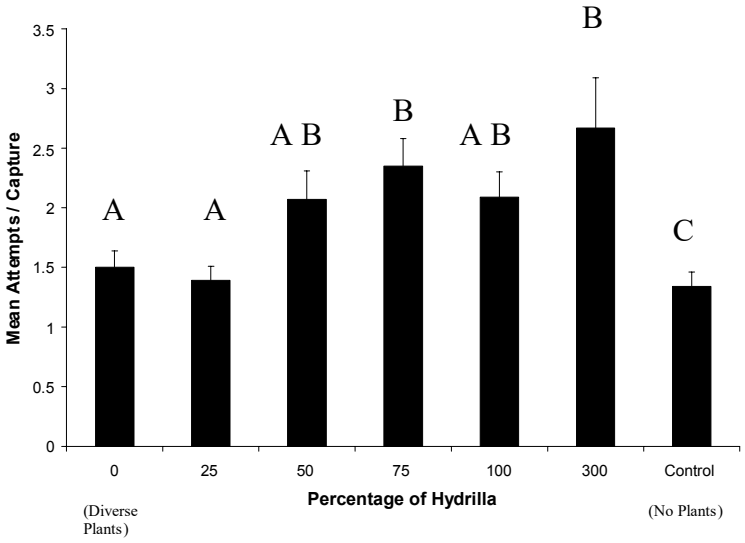

Figure 3.2. Mean numbers of attempts per capture of mosquitofish by juvenile largemouth bass measured across six treatment levels of hydrilla composition and a control during the aquarium foraging experiment conducted at Mississippi State University December 2005 to March 2006 (different letters indicate a significant difference and bars represent standard error).

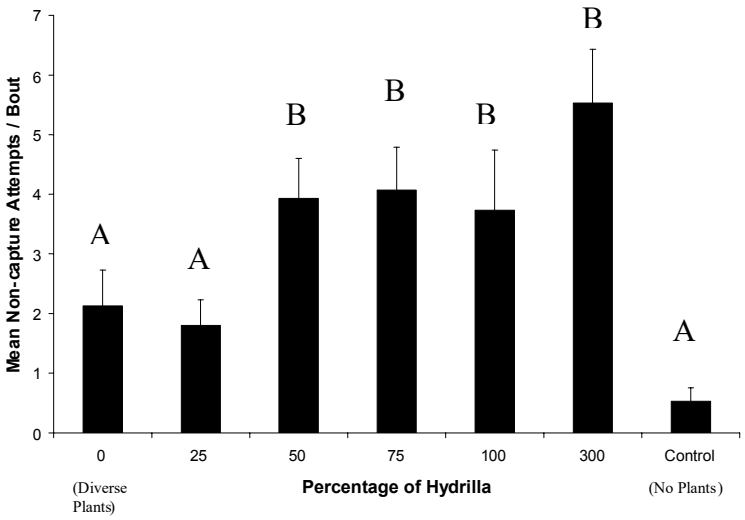

Figure 3.3. Mean numbers of attempts to capture mosquitofish by juvenile largemouth bass that never resulted in a catch measured across six treatment levels of hydrilla composition and a control during the aquarium foraging experiment conducted at Mississippi State University December 2005 to March 2006 (different letters indicate a significant difference and bars represent standard error).

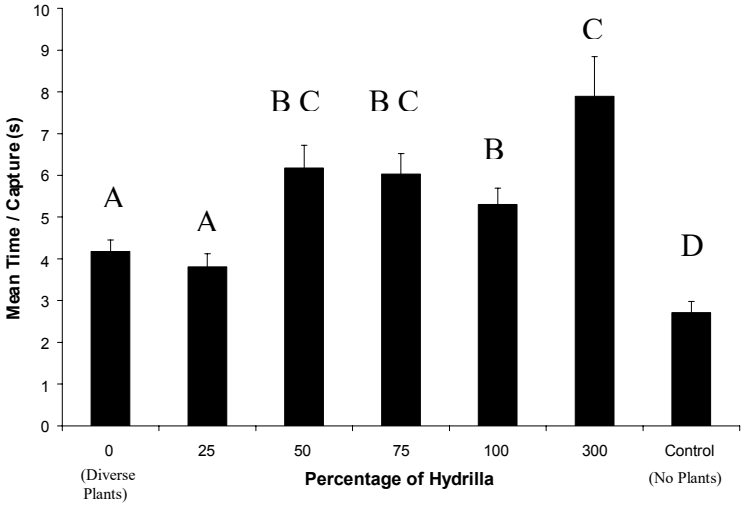

Figure 3.4. Mean time (s) required to capture a mosquitofish by juvenile largemouth bass measured across six treatment levels of hydrilla composition and a control during the aquarium foraging experiment conducted at Mississippi State University December 2005 to March 2006 (different letters indicate a significant difference and bars represent standard error).

Mean number of feeding attempts in a replicate that never resulted in a fish capture ranged from 0.53 to 5.53 (Table 3.1). Significant differences in non-capture attempts were detected, notably those between the 25 % and 300 % treatments ($F=14.06$, $P=0.008$) and the 0 % (diverse) and 300 % hydrilla ($F=9.89$, $P=0.0039$) (Figure 3.3 and Table 3.2). Mean capture times ranged from 2.71 s to 7.89 s (Table 3.1). Several treatments differed significantly, particularly the 0 % and 300 % treatments ($F=15.41$, $P<0.001$) and the 25 % and 300 % treatments ($F=18.62$, $P<0.001$) (Figure 3.4 and Table 3.2).

Discussion

When at the same stem density as a diverse plant bed, hydrilla did not provide adequate refuge for prey species and did not inhibit predator movement. The hydrilla at this level appeared to provide a favorable environment for predator foraging. On the other hand, the 300 % hydrilla treatment resulted in an average number of captures per bout that was 11 % less than in any other treatment. This stem density simulated a very structurally complex vegetated environment, similar to naturally occurring hydrilla beds (Colle and Shireman 1980, Nichols 1994) and appeared to provide a poor foraging habitat for the bass.

Number of feeding attempts required by the bass to capture a prey fish was approximately 31 % less in the diverse (0 %) and 25 % hydrilla treatments than in any other simulated habitat. These were the habitats containing the least amount of hydrilla. The complex architecture of this growth was either not

present or minimal. This suggests that this habitat provided less obstruction and more favorable area for the bass attempting to capture the mosquitofish which accounted for the greater capture rate. Others have suggested similar relationships between fish and vegetated habitats that affect chances for a successful outcome in foraging (Colle and Shireman 1980, Killgore et al. 1989, Olson et al. 1998). Largemouth bass required 11 % more attempts to capture a forage fish in the 300% hydrilla treatment than in any other habitat. The dense nature of this habitat made it difficult for the predator to accurately strike at its prey. The lack of open areas in the plant growth forced bass to chase the smaller *Gambusia* through the vegetation where stems and leaves prevented the opportunity for a clean strike, requiring repeated attempts to capture the prey.

Amount of time required for a largemouth bass to catch forage fish was 9 % less in the habitat containing slight hydrilla levels (25 %) than in the others, except for the control. It appeared that the fish were able to identify, pursue, and capture prey with ease due to the lack of obstructions from plant growth and no refuge for the *Gambusia* to escape to. On the other hand, habitat simulating the maximum infestation (300% hydrilla) resulted in a mean capture time 22 % greater than any other as could be expected (Crowder and Cooper 1979, Engel 1995). Increased habitat complexity appeared to decrease the maneuverability of the predator and probably contributed to an increased ratio of unsuccessful feeding attempts per capture which reflects an increased difficulty of capturing prey and thus would have required more time.

A diverse plant environment (0 % hydrilla) or one simulating a new or slight infestation (25 % hydrilla) resulted in mean numbers of non-capture attempts approximately 47 % less than any other except the control (no plants). Low levels of habitat complexity and absence of refugia may be the reason. The largemouth bass appeared to be less impeded in these simulated habitats and rarely failed in their attempts to capture prey. Conversely, average number of unsuccessful attempts in the 300% hydrilla habitat was 18 % greater than in the others. High plant density and small spaces did not provide clear striking opportunities for the bass, and their limited mobility allowed the mosquitofish to distance themselves and hide among the plant growth.

Number of non-capture attempts, or strikes that never result in a capture, may be a very important factor when trying to determine why invasive plant growth results in slower largemouth bass growth. Increases in time required and number of attempts needed to capture a prey fish increases the amount of energy used and can decrease the overall gain in energy from that food item (Diana 1995). Lesser gains result in less energy available for growth. However, this can be even more detrimental when the food item is never ingested. Energy-wise it is costly for a fish to expend energy chasing and attempting to capture prey that are never consumed. This decrease in foraging ability may explain the delay in the onset of piscivory in young-of-the-year largemouth bass inhabiting large beds of invasive vegetation (Bettoli et al. 1992).

By simulating changes in vegetated habitat I was able to experimentally evaluate how a hydrilla invasion impacted foraging ability of juvenile largemouth

bass. The plant-free habitat provided the most efficient foraging opportunities due to a lack of physical obstructions caused by stem complexity, and refuge for prey. Treatments containing a mix of native plants and the low levels of hydrilla provided moderate complexity with open areas which are conducive to pursuing and capturing forage fish (Colle and Shireman 1980, Killgore et al. 1989, Olson et al. 1998). The 100 % hydrilla environment provided these advantages as well, and did not include the broad leaves of the native plants that are a source of refuge for the mosquitofish. The diverse native plant habitat also provided moderate complexity with open areas in which the bass could feed. However, the prey species in this experiment is a top-dweller (Ross 2001) and tended to seek refuge in the upper part of the water column. Water lily and pondweed stems included floating leaves that provided refuge for the *Gambusia* during and after pursuit by a bass. The presence of hydrilla at naturally occurring levels severely impacted the ability of bass to capture forage fish. Habitat complexity hindered predator mobility resulting in less captures with more attempts that required more time.

Results from this experiment have shown that hydrilla-infested environments may decrease the overall ability of largemouth bass to capture mosquitofish. Future investigations conducted at this level of the fish-plant interaction could further explain the reasons for poor bass growth and why the increases in abundance of small-sized fish are frequently observed (Mittelbach 1988, Olson et al. 1998) in large beds of invasive aquatic vegetation such as hydrilla. Incorporating other types of forage fish common to the largemouth bass

diet could answer possible variations in results due to prey morphology and behavior. Different prey species are likely to be affected by the increased habitat complexity in different ways. This may enhance or detract from a bass' ability to forage, depending on what type of fish is being targeted.

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CHAPTER IV

CONCLUSIONS

I compared the effects of hydrilla growth and native macrophytes on littoral zone habitat as well as juvenile largemouth bass growth, condition, and ability to forage. These two experiments were conducted at different scales to test the hypothesis that shifts in plant beds from a diversity of natives to a monotypic stand of invasive growth would impact juvenile largemouth bass. My work explained these effects by using methods that have not previously been used, including use and manipulation of natural plants, not artificial ones, and individually tagging juvenile bass to track growth in an effort to learn how growth is distributed among individuals within the population rather than calculating a mean increase in growth.

Aquatic plant infestations have drawn much interest from the research community recently, especially in areas concerning fish abundance, behavior, and growth (Dibble et al. 1996, Brown and Maceina 2002, Valley and Bremigan 2002). Much of this previous work has occurred in plant beds found in large lakes, or in aquaria with plastic plants or other artificial habitats (Colle and Shireman 1980, Savino and Stein 1982, Anderson 1984, Gotceitas and Colgan 1987 and 1989, Savino and Stein 1989, Gotceitas 1990, Hayse and Wissing 1996, Hoyer and Canfield, Jr. 1996, Brown and Maceina 2002, Valley and

Bremigan 2002, Tate et al. 2003). Similar to my work, these efforts predominantly focused on whether invasive exotic plants affected fish communities, behavior, size, or condition. I analyzed stomach contents to investigate if differences in growth were a function of the forage items that bass were able to capture in each environment. I also simulated a hydrilla invasion in aquaria using natural plants to most accurately replicate littoral zone habitats found in natural systems. Aspects of juvenile bass foraging behavior were measured to explain how this plant growth affects their ability to capture small fish. Impacted ability to capture forage fish may explain fluctuations in growth and condition that exist in these two different habitats.

My pond experiment showed that dense hydrilla beds may affect bass growth and foraging when compared to littoral zone habitats containing a mix of native plant species. Juvenile bass growth was less in the hydrilla, experiencing less than those in the diverse habitat. The reduced size of bass in the hydrilla ponds is likely a result of increased difficulty in capturing small fish (Crowder and Cooper 1979). This is evident in the stomach contents analysis which showed that bass from the diverse treatment contained significantly more fish and greater dry weights of prey fish than those in the hydrilla treatment. These results support previous speculation that the onset of piscivory is delayed in bass inhabiting dense, complex vegetation (Bettoli et al. 1992). These findings suggested that this was probably a result of the predator being restricted in capturing prey. The effect of hydrilla on this mechanism may explain the reduced fish growth commonly detected in habitats dominated by this plant.

The condition of juvenile largemouth bass did not differ between treatments in the ponds and may have been a result of the controlled nature of the experiment. Ecological mechanisms may have been interrupted, such as the increase in abundance of small fish in dense plant beds which can decrease the amount of invertebrates available (Mittelbach 1988, Olson et al. 1998) and cause poorer condition (Colle and Shireman 1980). An influx of more fish into the dense hydrilla was not possible, thus competitive interactions were not as strong and juvenile bass condition not suppressed as it may have been in a large natural system.

My aquarium experiment was designed to explain why juvenile bass grew more slowly, and ate fewer forage fish in the hydrilla treatment. Four aspects of the foraging process were quantified using videography. Average number of prey fish captured, number of forage attempts per capture, amount of time required to capture prey, and number of strikes that never result in a capture were measured for seven different vegetation levels simulating a hydrilla invasion in a native, diverse plant bed. Each of these foraging parameters was significantly less in the treatment containing hydrilla at naturally occurring levels. A lack of open areas forced chases where high numbers of stems and leaves prevented clean strikes (Savino and Stein 1982, Engel 1995, Valley and Bremigan 2002), increasing number of strikes necessary for success, thus increasing amount of time spent on each prey item. More time required and numbers of strikes needed to capture prey results in a greater amount of energy

used which would decrease the overall gain in energy from a food item (Savino and Stein 1982, Anderson 1984).

A 100% hydrilla treatment provided a favorable foraging habitat as long as the stem density was consistent with that of native plant beds. Unfortunately, hydrilla does not remain at this level for very long, and quickly becomes an extremely dense and complex bed that impedes fish movement (Colle and Shireman 1980, Nichols 1994). To fully understand how largemouth bass growth and foraging is disrupted by aquatic weeds, we must continue to explore these mechanisms by incorporating various types of prey and vegetation into experiments such as those that I have conducted. Different fish species should behave differently in these vegetated habitats, and plant types will offer variations of habitat complexities which can alter how predators feed and how efficient it is. Similar work is warranted to further explain the effects of invasive macrophytes on fish and to explain how they are impacted.

My work has provided some insight to the mechanisms that govern fish growth in aquatic environments that are invaded by hydrilla. Complexity of the habitat increases and forage items are less available. Juvenile largemouth bass experienced poorer capture rates and longer chase times when feeding on forage fish. This results in diets composed mostly of invertebrates which leads to slower bass growth ultimately caused by the dense and complex architecture of the invasive exotic hydrilla.

Knowledge gained from my research is applicable in managing aquatic systems containing largemouth bass, and also those infested with hydrilla.

Water bodies with vegetated littoral zones, especially small ponds, should provide an optimal growing and foraging habitat for juvenile bass provided that the plants present consist of a variety of native growth. If areas containing large hydrilla beds can be altered in a manner that decreases density and complexity of the environment or increases amount of open areas and edge, foraging conditions for bass may improve, as should growth. Greater growth rates usually mean bigger bass and happier anglers or pond owners.

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APPENDIX A

STATISTICAL COMPARISONS OF DATA COLLECTED FROM THE POND EXPERIMENT

Table A.1. Analysis of variance results for aquatic plant coverage and stem density measured across treatments in the pond experiment at Mississippi State University from July to October 2005.

	Plant Coverage		Stem Density	
Treatment Comparison	F-value	p-value	F-value	p-value
Monoculture x Diverse	14.24	*<0.001	16.58	*<0.001
Monoculture x Control	363.42	*<0.001	39.03	*<0.001
Diverse x Control	256.28	*<0.001	304.18	*<0.001

* denotes significant difference at α = 0.05

Table A.2. Mean values for water quality parameters measured across treatments in the pond experiment at Mississippi State University from July to October 2005.

Treatment	Temp	pH	Specific Conductivity	Dissolved Oxygen
Monoculture	24.39	8.99	170.40	5.70
Control	25.30	8.48	192.88	5.84
Diverse	25.10	8.29	171.53	5.33

Table A.3. Analysis of variance results for water quality parameters measured across treatments in the pond experiment at Mississippi State University from July to October 2005.

	Temp		pH		Specific Conductivity		Dissolved Oxygen	
Treatment Comparison	F value	p-value	F value	p-value	F value	p-value	F value	p-value
Monoculture x Diverse	0.11	0.746	8.30	*0.007	0.02	0.892	0.18	0.675
Monoculture x Reference	0.17	0.682	6.89	*0.014	12.30	*0.002	0.04	0.848
Diverse x Reference	0.01	0.921	0.77	0.390	9.14	*0.005	0.32	0.573

* denotes significant difference at α = 0.05

Table A.4. Analysis of variance results for total length (mm) and weight (g) of juvenile largemouth bass measured across treatments in the pond experiment at Mississippi State University from June to November 2005.

	Total Length		Weight	
Treatment Comparison	F-value	p-value	F-value	p-value
Monoculture x Diverse	44.84	*<0.001	36.36	*<0.001
Monoculture x Control	29.51	*<0.001	18.19	*<0.001
Diverse x Control	3.35	0.070	6.84	*0.010

* denotes significant difference at $\alpha = 0.05$

Table A.5. Analysis of variance results for individual gains in total length (mm) and weight (g) of tagged largemouth bass measured across treatments in the pond experiment at Mississippi State University from June to November 2005.

	Total Length		Weight	
Treatment Comparison	F-value	p-value	F-value	p-value
Monoculture x Diverse	14.87	*<0.001	11.99	*0.001
Monoculture x Control	20.42	*<0.001	25.39	*<0.001
Diverse x Control	0.04	0.846	0.00	0.991

* denotes significant difference at $\alpha = 0.05$

Table A.6. Analysis of variance results for relative weights (W_r) of tagged largemouth bass measured across treatments in the pond experiment at Mississippi State University from June to November 2005.

	Relative Weight	
Treatment Comparison	F-value	p-value
Monoculture x Diverse	0.60	0.441
Monoculture x Control	9.45	*<0.003
Diverse x Control	6.35	*0.013

* denotes significant difference at $\alpha = 0.05$

Table A.7. Analysis of variance results for numbers of forage fish found in the stomachs of largemouth bass measured across treatments in the pond experiment at Mississippi State University from June to November 2005.

	Forage Fish	
Treatment Comparison	F-value	p-value
Monoculture x Diverse	25.42	*<0.001
Monoculture x Reference	14.40	*<0.001
Diverse x Reference	1.78	0.184

* denotes significant difference at $\alpha = 0.05$

Table A.8. Analysis of variance results for dry weights of forage fish and invertebrates found in the stomachs of largemouth bass measured across treatments in the pond experiment at Mississippi State University from June to November 2005.

	Forage Fish		Invertebrates	
Treatment Comparison	F-value	p-value	F-value	p-value
Monoculture x Diverse	10.52	*<0.002	17.89	*<0.001
Monoculture x Reference	12.96	*<0.001	1.54	0.217
Diverse x Reference	4.28	*<0.041	2.35	0.128

* denotes significant difference at $\alpha = 0.05$