Effects of a Large-scale Habitat Enhancement Project on Largemouth Bass Behavior, Feeding, and Growth in Grand Lake, Texas

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EFFECTS OF A LARGE-SCALE HABITAT ENHANCEMENT PROJECT ON
LARGEMOUTH BASS BEHAVIOR, FEEDING, AND GROWTH IN GRAND LAKE,
TEXAS

BY

CHANCE KIRKEENG

A thesis submitted in partial fulfillment of the requirements for the
Master of Science
Major in Wildlife and Fisheries Sciences
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EFFECTS OF A LARGE-SCALE HABITAT ENHANCEMENT PROJECT ON
LARGEMOUTH BASS BEHAVIOR, FEEDING, AND GROWTH IN GRAND LAKE,
TEXAS

CHANCE KIRKEENG

This thesis is approved as a creditable and independent investigation by a candidate for
the Master of Science in Wildlife and Fisheries Science degree and is acceptable for
meeting the thesis requirements for this degree. Acceptance of this thesis does not imply
that the conclusions reached by the candidate are necessarily the conclusions of the
Department of Natural Resource Management.

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I dedicate this thesis to my wife, Kirstie Kirkeeng, and other family members who were so supportive during my studies.
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The quality of habitat, or the environment suitable for an organism to survive and reproduce, is often described by the type of features present and the quantity and condition of such features. Habitats in many ecosystems are declining and the loss of important habitats likely affects the success of organisms reliant upon those features. Habitats in reservoir ecosystems are especially at risk because of aging processes that are degrading reservoir habitats at faster rates than habitats in other ecosystems. Habitat enhancement projects are one tool used to combat the effects of aging reservoirs but the benefits of these management actions to sportfish populations are poorly understood. We evaluated the effects of a large-scale habitat enhancement project on Largemouth Bass movement behavior, feeding, and growth in an aging reservoir in eastern Texas. To understand behavioral responses, we compared adult Largemouth Bass habitat selectivity, daily movement rates, and seasonal use area sizes before and after the habitat enhancement project. Adult Largemouth Bass behavior changed following the large-scale habitat enhancement project. Although Largemouth Bass selected areas with structural features during both study periods, they selected strongly for areas with newly added habitat. Largemouth Bass daily movement rates and seasonal use area sizes remained similar to those observed before the addition of habitat. We also compared growth rates
and diets of Largemouth Bass following the habitat enhancement project. Largemouth Bass growth increased following the addition of structural habitat, which resulted in a predicted increase in growth of 120 mm (TL) at age 5. Largemouth Bass diets (calculated as mean percent composition by wet weight) did not change following the addition of structural habitat, and often included large amounts of fish. Changes in Largemouth Bass habitat selectivity and growth in response to the addition of structural habitat may be the result of an improved foraging environment that facilitates increased consumption rates by Largemouth Bass. Habitat enhancement projects, such as adding structural features, may increase production of top predator sportfish populations by providing environmental conditions favorable for foraging that facilitates increases in growth.
INTRODUCTION

Habitat is defined as the area where the environment is suitable for an organism to survive, and reproduce (e.g. Fisher et al. 2012; Breeggemann 2016). Declines in habitat quality and quantity may reduce an organism’s survival, health, growth, recruitment, and/or reproduction (e.g. Fahrig 2001; Munday 2004; Hinam and St. Clair 2008). The quality of an organism’s habitat is often based on the type of features present (biologically, chemically, and structurally), the quantity and condition of such features, and the connectivity of these features to other important areas (e.g. Sylvester and Seabloom 1965; Fahrig 2003; Daugherty et al. 2014). Organisms living in poorer quality habitats may expand their ranges to include needed habitat features. Thus, studies on many classes of organisms show increased home range size and/or movements in response to decreased habitat quality (e.g. Tufto et al. 1996; Barraquand and Benhamou 2008; Santangeli et al. 2012). For example, Siffczyk et al. (2003) found that wintering willow tits increased their territory size in forested areas that either contained unsuitable vegetative habitat or that did not contain preferred mature coniferous forest habitats.

Food availability is a feature of habitat that is important to the quality of an area to an organism, so animals often have larger home ranges, movement patterns, or both in areas without abundant food. Vedder (1984) found Mountain Gorillas ranging patterns to be influenced more strongly by the abundance and distribution of the high quality foods rather than by the abundance and distribution of all possible food items. Moreover, animals foraging in areas with lower quality habitat are often less efficient at foraging. Northern saw-whet owls, for example, spent more time perched during foraging in habitats that had low forest cover and were highly fragmented (Hinam and St. Clair
The increased time spent perching resulted in decreased predatory success and this resulted in correspondingly lower provisioning rates by male owls to young (Hinam and St. Clair 2008). In addition, elk in Yellowstone shifted diets to poorer quality feed because of a predator mediated habitat shift forcing elk to spend more time near forest edges, which have less nutritious food compared to the open meadow habitats that they prefer (Hernández and Laundré 2005). Poor quality habitat can have drastic negative effects on populations, and so it is important to maintain areas with high quality habitat.

Unfortunately, habitat loss threatens success of living organisms in most biomes across the world (Saunders et al. 1991; Brooks et al. 2002; Hoekstra et al. 2005; Niebuhr et al. 2015). It increases extinction risk of species (Rahel et al. 1996; Brooks et al. 2002; Fahrig 2003; Munday 2004), and decreases ecosystem function (Saunders et al. 1991; Dobson et al. 2006). Reservoirs are aquatic ecosystems especially susceptible to habitat loss because processes like sedimentation (Patton and Lyday 2008; Graeb et al. 2009; Juracek 2015), decomposition of woody habitat, and erosion of shoreline (Agostinho et al. 1999), occur at quicker rates than those in natural lake systems (Kimmel and Groeger 1986; Krogman and Miranda 2016). This senescence of reservoir habitats, or ageing process, is likely to occur at different rates dependent on reservoir characteristics, like morphology, depth, and nutrient inputs (Miranda and Krogman 2015), but is expected to decrease the usefulness of small reservoirs (i.e. those with a volume less than 123,348 m³) in only 30 years (Kimmel and Groeger 1986). In addition, most reservoirs were constructed to serve human needs (i.e. supply water, generate power, control flooding) and thus had limited design lives of 50 to 100 years (Juracek 2015). Most U.S. reservoirs are approaching or surpassing these intended lifespans, creating vulnerable systems that
do not meet the initially intended needs and/or have structurally weakened dams (Juracek 2015; Krogman and Miranda 2016). One of the reasons this is problematic is because many of these reservoirs now provide important recreational fishing opportunities (Kimmel and Groeger 1986; Dauwalter and Jackson 2005). Thus, understanding how to slow the aging processes in reservoirs and retain these important fisheries has moved to the forefront of aquatic research focus and direction (AFWA 2012; Miranda and Krogman 2015; Pegg et al. 2015). Habitat enhancements, including planting native aquatic plants, stabilizing shorelines, dredging sediment, and installing artificial structure, have been used to slow the reservoir aging process using bottom-up mechanisms to varying degrees of success (Pegg et al. 2015). Although habitat enhancement projects are commonly implemented, their effectiveness is not commonly evaluated.

Installation of artificial structure, which acts as important cover to fishes, is one of the oldest used fishery improvement techniques (Brown 1986), and continues to remain commonly recommended for future research and use in improving aging reservoirs. The first evaluation of large-scale additions of artificial structure occurred on Table Rock Lake, Missouri, which was chosen for the first habitat enhancement pilot study under the National Fish Habitat Action Plan (NFHAP) and received $4 million to improve fish habitat and recreational opportunities (Allen et al. 2014). Over 2000 different artificial habitat structures, ranging from different tree types to rock and concrete structures, were deployed between 2007 and 2013 to improve habitat in Table Rock Lake. After completing the project, the fishery response and angler satisfaction were monitored to determine the value of large-scale habitat enhancement projects in improving aging reservoirs. Largemouth Bass (*Micropterus salmoides*) and Crappie (*Pomoxis spp.*) were
attracted to all structure types and anglers were more satisfied with their fishing trips (Allen et al. 2014). The results were positive and supported using artificial habitat to replace structural habitat being lost in aging systems. These findings were similar to other studies that focused on small-scale artificial habitat additions, which found artificial structure successfully concentrates fishes and increases angler harvest (e.g. Paxton and Stevenson 1979; Prince and Maughan 1979; Wege and Anderson 1979; Brown 1986; Bolding et al. 2004). For example, Helfman 1979 found higher fish densities under artificial floating structures than in either the adjacent areas or control plots. Attracting fishes to a centralized location is great for anglers, but adding artificial habitat to aging reservoirs may also increase production of these important sportfish populations through improving growth.

The mechanisms by which artificial habitat benefits fishes may be better understood by focusing on acquired and needed energy. Fish energy budgets are often represented by the equation:

\[ G = C - (R_{SA} + R_{SDA} + F + U) \]

where: \( G \) = growth, \( C \) = consumption, \( R_{SA} \) = standard metabolism plus metabolism due to activity, \( R_{SDA} \) = specific dynamic action, \( F \) = egestion, and \( U \) = waste (Rice et al. 1983; Hartman and Hayward 2007). In other words, the energy leftover from maintenance and diet processing from consumed prey are available for use in growth and activity. If fishes benefit energetically from the installation of artificial structure, then it is assumed that they will show improved somatic or gonadal growth. Habitat can potentially benefit fishes energetically through two primary mechanisms: by decreasing metabolic costs,
specifically activity costs; or by increasing energetic gain through increasing consumption rate or energetic value of prey consumed (i.e. habitat-facilitated diet shift).

Grand Lake is an aging reservoir experiencing decreased Largemouth Bass production and previous research highlighted the need for habitat improvements to benefit the Largemouth Bass population (Breeggemann 2016). In response to this need, a large-scale habitat enhancement project was completed between September and November 2014. Beyond concentrating fishes, the benefits of adding artificial structure to aging reservoirs are poorly understood. Through the work outlined in this thesis, I examined the immediate response of a Largemouth Bass fishery to added artificial habitat. I focused on understanding the mechanisms by which habitat may affect a Largemouth Bass population. Activity costs and diet habits were explored as possible mechanisms influencing changes in growth following the habitat enhancement.

Hypotheses

1. Largemouth Bass in Grand Lake will select positively for areas with the newly added structural habitat because the reservoir is experiencing “aging” processes that limit the availability and/or quality of other structural features in Grand Lake.

2. Largemouth Bass in Grand Lake will decrease the size of seasonal use areas and move shorter distances daily following the addition of structural habitat, due to an increase in habitat quantity and quality.

3. Largemouth Bass in Grand Lake will shift to foraging on more energetic prey sources following the addition of structural habitat because the structural features will attract prey fish (Prince and Maughan 1979; Wege and Anderson
1979; Brown 1986; Bolding et al. 2004) to areas where Largemouth Bass will be attracted (Allen et al. 2014).

4. Largemouth Bass growth will increase substantially following the addition of structural habitat features because more energy will be ingested and less energy will be spent on foraging.
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and water uses for impounded river systems. American Fisheries Society, Symposium 62, Bethesda, Maryland.


FEEDING AND GROWTH OF LARGEMOUTH BASS IN AN AGING RESERVOIR BEFORE AND AFTER A LARGE-SCALE HABITAT ENHANCEMENT PROJECT

ABSTRACT

Aging reservoir processes can reduce the quantity and quality of available habitat. Habitat enhancement projects, such as adding structural features, provide innovative solutions to combat reservoir aging, but the benefits to sportfish populations are unknown. Newly added structural habitat may improve growth of fish by providing feeding habitat and reducing energy required for foraging. We compared growth and diets of Largemouth Bass in an aging reservoir in eastern Texas before and after a large-scale habitat enhancement project. Before the addition of structural habitat Largemouth Bass growth slowed during a period following a stocking event. Largemouth Bass growth then increased during the period following the addition of structural habitat and was predicted to result in an increase of 120 mm (TL) at age 5. All in all, Largemouth Bass growth was greater than the pre-habitat period but similar to the pre-stocking period. Largemouth Bass diets (calculated as mean percent composition by wet weight) did not change following the addition of structural habitat, and often included large amounts of fish (>40% fish in all seasons except summer 2015). The observed increases in Largemouth Bass growth may be the result of increases in consumption rates because of improved foraging conditions provided by the structural habitat. Largemouth Bass consumption rates may be improved by structural habitat through one of the following pathways: 1) increased encounters with prey attracted to habitat sites, or 2) increased capture rates because of cover that facilitates ambush foraging. Adding structural habitat to aquatic systems may improve growth of top-level sportfish.

Keywords: aging reservoir, habitat, Largemouth Bass, diet, growth, stocking
INTRODUCTION

Habitat is defined as the physical, chemical, and biological components of the area where an organism lives (Hudson et al. 1992; Hayes 1999, Fisher et al. 2012). Habitat quantity and quality are important because both can impact animal survival, health, and reproduction (e.g. Fahrig 2001; Munday 2004; Hinam and St. Clair 2008). Habitats in many systems are declining in quantity and/or quality (Saunders et al. 1991; Brooks et al. 2002; Hoekstra et al. 2005; Niebuhr et al. 2015). Reservoir systems deserve special attention because these habitats are lost at quicker rates than natural lake systems (Kimmel and Groeger 1986; Krogman and Miranda 2016) and do not have disturbance regimes that replace lost habitat features. Habitat features in reservoirs are lost primarily to “aging” processes like sedimentation (Patton and Lyday 2008; Juracek 2015), decomposition of woody structure, and erosion of shoreline (Agostinho et al. 1999). The loss of reservoir habitats is important to many state and federal management agencies (AFWA 2012; Miranda and Krogman 2015; Pegg et al. 2015; Miranda 2017). Planting aquatic plants, stabilizing shorelines, dredging sediments, and installing artificial reefs and structures are common strategies used by these agencies to try to provide or improve reservoir habitats (Pegg et al. 2015; Miranda 2017), but “improvements” following such management actions are difficult to quantify.

Increased fish production (i.e., amount of fish biomass produced per unit time) is often the goal for habitat enhancement projects (Miranda 2017). Fish biomass is the mass of fish present in an area or volume and is equal to the abundance of fish multiplied by the average fish weight. If abundances are unaltered following habitat enhancements, then changes in growth over a given time may be used to understand changes in
production. This is important because previous research indicates that growth of fishes changes following changes in habitat. For example, Pardue (1973) found that Bluegill *Lepomis machrochirus* biomass increased linearly with available habitat as such structure promoted macroinvertebrate production. Many age classes of Bluegill and Largemouth Bass experienced increased growth following large-scale macrophyte manipulations (Olson et al. 1998). Finally, Sass et al. (2006) found Largemouth Bass growth rates decreased following the removal of coarse woody habitat. Growth responses by fish following additions of structural habitat may indicate improved production in these aquatic systems.

Growth of fishes is often discussed based on an energetic budget, which is represented by the equation:

\[
G = C - (R_{S+A} + R_{SDA} + F + U)
\]

where: \(G\) = growth, \(C\) = consumption, \(R_{S+A}\) = standard metabolism plus metabolism due to activity, \(R_{SDA}\) = specific dynamic action, \(F\) = egestion, and \(U\) = waste (Rice et al. 1983; Hartman and Hayward 2007). Based on this equation, changes in growth following habitat manipulations are likely the result of the effects of habitat on consumption or activity of fishes. Given that growth often changes following habitat manipulations, it is important to evaluate the influence of habitat on these parameters. Rice et al. (1983) noted that Largemouth Bass growth and condition are affected primarily by feeding behavior. It is likely that changes in Largemouth Bass growth following the addition of habitat are the result of effects on consumption and so this parameter should be of primary focus and concern.
Habitat characteristics can influence fish foraging through two mechanisms. First, habitat influences predator foraging success and consumption rates. Fishes are attracted to quality structural habitat and prey fish abundances are often higher near structure, providing for greater localized food availability to predators (Prince and Maughan 1979). Wege and Anderson (1979) found Largemouth Bass growth to be significantly greater for fish using newly added structures because of higher prey abundances and favorable capture conditions provided by the structures. However, not all structural habitat is of equal quality, and so density, morphology, and configuration of structural features are important to how habitat impacts predator success (e.g. Savino and Stein 1982; Warfe and Barmuta 2004; Daugherty et al. 2014). Although encounter rates often increase in areas with structural habitat present, too much structure may limit capture success (Crowder and Cooper 1979; Savino and Stein 1982; Janssen et al. 2007). For example, Gotceitas and Colgan (1989) found a cover density threshold of 276 stems/ m² to be the point where Largemouth Bass foraging success on Bluegill significantly decreased. Savino and Stein (1989) found that heterogeneous habitats, which include both structure in densities higher than the 276 stems/ m² threshold and open-water features, provide ideal spatial configurations of structural habitat features for predators and capture success remains high. They concluded that both Largemouth Bass and Northern Pike were most successful at capturing prey in environments with 50% cover (i.e. evenly sized areas of high density structures and open-water). In addition, Warfe and Barmuta (2004) found the morphology of macrophytes to have significant effects on the success of aquatic predators to find and capture prey. They found that capture success decreases with increasingly complex structural morphologies as density remains constant. Fishes can
also shift foraging strategies in response to habitat features (Savino and Stein 1982; Savino and Stein 1989; Warfe and Barmuta 2004). Largemouth Bass, for example, can shift from roving to ambush predators when dense vegetation is present. This shift allows Largemouth Bass to focus efforts on areas with higher prey densities and favorable capture conditions (Savino and Stein 1989).

The second way that habitat can improve energy gained through foraging is by facilitating predators to shift diets to higher quality prey. Habitat can concentrate fishes providing direct access to a previously underutilized resource. For example, Largemouth Bass have been documented to shift their diets in response to structural habitat availability (Schramm and Zale 1985; Sass et al. 2006). Sass et al. (2006) studied the response of a Largemouth Bass population to a large-scale removal of coarse woody habitat. Results from the study showed that Largemouth Bass in the treatment basin quickly depleted the Yellow Perch prey population and then shifted to a diet subsidized heavily by terrestrial sources. Prior to the habitat manipulation, terrestrial inputs only composed around 10% of the diets but they composed about 50% of the diets post-habitat removal. These terrestrial prey sources have lower energy densities and value than the fishes primarily eaten before the removal of woody habitat, which caused Largemouth Bass growth to slow. These results suggest that Largemouth Bass may increase diet breadth to include lower quality prey when structural habitat is lacking.

Small private impoundments provide an opportunity to study improvements to fisheries that may result from habitat improvement efforts. The goal of this study is to measure changes in Largemouth Bass growth and feeding in response to a habitat improvement project in eastern Texas. Grand Lake is a 45ha private impoundment in
eastern Texas managed as trophy Largemouth Bass system. The ecology of the Grand Lake fishery was studied between 2012 and 2014, during which Largemouth Bass growth was deemed not ideal for a trophy fishery. Habitats in Grand Lake are depleted because of “aging” processes and were hypothesized to be limiting Largemouth Bass growth. In response, a large-scale habitat enhancement project was completed on Grand Lake in the fall of 2014. The habitat enhancement project consisted of adding 21 “fish cities” around the shoreline area, providing areas with high density structures adjacent to open water areas. The objectives of this study are to: 1) quantify growth of Largemouth Bass following the addition of artificial structure and compare growth to the pre-habitat period; and 2) describe Largemouth Bass diets following the addition of habitat and compare to the pre-treatment period to understand if diet shifted.

METHODS

Study Site

Grand Lake is located in eastern TX, USA and was built in the 1950’s (Figure 2.1). The 45 hectare private impoundment (mean depth = 3.2 m, maximum depth = 7.9 m) is managed for trophy Largemouth Bass. Florida Largemouth Bass alleles, which promote superior growth, dominate the genetics of the population (Breeggemann et al. 2016). Prey is intensively managed to maintain abundant available feed for Largemouth Bass, including stockings of Coppernose Bluegill (*Lepomis macrochirus purpureascens*), Gizzard Shad (*Dorosoma cepedianum*), Threadfin Shad (*Dorosoma petenense*), Mozambique Tilapia (*Oreochromis mossambicus*), and red swamp crayfish (*Procambarus clarkii*). Grand Lake has a diverse fish community in addition to stocked prey, including Bluegill (*Lepomis macrochirus*), Redear Sunfish (*Lepomis microlophus*),...
Redbreast Sunfish (*Lepomis auritus*), Brook Silverside (*Labidesthes sicculus*),
Blackstripe Topminnow (*Fundulus notatus*), Silverside Shiner (*Notropis candidus*),
Black Crappie (*Pomoxis nigromaculatus*), White Crappie (*Pomoxis annularis*), Channel
Catfish (*Ictalurus punctatus*), Black Bullhead (*Ameiurus melas*), Flathead Catfish
(*Pylodictis olivaris*), Common Carp (*Cyprinus carpio*), and Grass Carp
(*Ctenopharyngodon idella*). Grass Carp were stocked to manage aquatic vegetation but
numbers are declining as the population reaches old age. Submersed aquatic vegetation
became more prevalent throughout the duration of this study in response to this decline
(Figure 2.2) A diverse community of emergent aquatic plants were abundant in the
littoral zone. Water lotus (*Nelumbo lutea*) are prevalent in depths >1m but are chemically
treated to control range expansion.

*Habitat Treatment*

A total of 21 Mossback Fish Habitat© (MFH) “fish cities” were placed around the
boundary of Grand Lake between September and November 2014 (Figures 2.3 and 2.4).
Two Mossback SH-5832 horizontal Safe Haven units were placed perpendicular to the
shoreline to connect the shallow littoral zone to deep water habitat. At the ends of the
horizontal Safe Havens, three vertical Safe Haven Kits were placed to provide additional
high density structural habitat. Three Trophy Tree Kits were placed on each side of the
high density habitat, and Four Trophy Tree XL Kits were placed in deep water at the end
of all pre-mentioned features. This spatial arrangement resulted in the high density
features being surrounded by structural features with larger interstitial spacing. The final
habitat addition covered nearly 13% of Grand Lake shoreline in artificial habitat.

*Field Methods*
Fish Collection

Largemouth Bass and prey fish were collected using pulsed DC (amps ≈ 12; volts ≈ 400) boat electrofishing. Sampling occurred seasonally during early May, late June/early July, and early November in 2015 and 2016 and middle January in 2016 during daylight hours. All Largemouth Bass collected during electrofishing were measured (Total Length (TL); mm), and weighed (g). Prey fishes were also collected using pulsed DC electricity. The lake was split into three sections and a stratified random design was used to select three littoral shoreline transects to sample prey fish. Sampling occurred for ten minutes per transect during summer 2015, fall 2015, spring 2016, summer 2016, and fall 2016. All prey fishes collected during electrofishing were measured (Total Length (TL); mm), and weighed (g).

PIT Tagging

Breeggeemann et al. (2016) inserted Passive Integrated Transponder (PIT) tags into all Largemouth Bass collected with TL measuring ≥ 250mm from May 2012 through October 2014, so marked fish were still present in the population at the beginning of this study. All Largemouth Bass collected with TL measuring ≥ 250mm were checked for a PIT tag. If the fish contained a PIT tag, then the corresponding PIT Tag number was recorded. If the fish did not contain a PIT tag, then a Biomark GPT-12 PIT tag was inserted into dorsal muscle via a bevel-down implantation technique with a 12-gauge needle (CBFWA 1999; Cook et al. 2014).

Largemouth Bass (n = 121) were collected during November 2016 and sagittal otoliths were removed for estimating growth following the addition of habitat. The goal was to compare Largemouth Bass growth to the pre-habitat period that was estimated by
Breeggemann et al. (2016). Otoliths were prepared following the same protocol as Breeggemann et al. (2016). One sagittal otolith from each Largemouth Bass was embedded in epoxy, which was a mixture of five parts Buehler© Epoxicure® Epoxy and one part Buehler© Epoxicure® Epoxy Hardener. Then a Buehler© IsoMet™ Low Speed Saw was used to cut transverse cross sections through the focus. The cross sections were glued to microscope slides using cyanoacrylate adhesive and polished with 3 micron lapping film. Immersion oil was placed on the otolith cross sections while they were viewed through an Olympus© SZH10® dissecting microscope with transmitted light. Ages were estimated double-blind by two experienced readers. If age estimates for an otolith did not agree between the two readers, then a consensus age was determined by both readers simultaneously looking at the otolith. The edge was considered an annuli since the otoliths were collected in November 2016 and Breeggemann et al. (2016) counted the edge annuli for otoliths collected in December 2011.

Diet Collection and Processing

Diet sampling occurred once per season between spring 2015 and fall 2016. Diets were collected from all Largemouth Bass ≥ 250 mm TL using pulsed gastric lavage (Kamler and Pope 2001; Breeggemann et al. 2016). We used a stratified random sampling design based on fish size to get a representative sample of diets for the population. The size categories were 250-380 mm, 381-508 mm, and >508 mm TL. The goal was to collect 20 diets from each size class during each sampling event. Diet samples were preserved in a 10% formalin solution. Before processing, diet samples were transferred into water for one week and then into a 70% ethanol solution for long-term
storage. Diets were identified to species for fish and other vertebrates or family for invertebrates when possible. All diet items were weighed to the nearest 0.01g.

**Data Analysis**

**Growth**

To assess changes in growth of Largemouth Bass, data were analyzed for the following three time periods: 1) prior to December 2011 (Pre-habitat period 1); 2) May 2012-September 2014 (Pre-habitat period 2); and 3) October 2014-November 2016 (Post-habitat period). The pre-habitat period was split into two different growth periods because a large stocking event occurred on Grand Lake between December 2011 and March 2012. During this stocking event, 646 adult Largemouth Bass (sizes ranging between 240mm TL and 258 mm TL) were introduced to the Grand Lake system. Growth of Largemouth Bass was analyzed using two methods, which both estimate parameters of the von Bertalanffy model. To estimate parameters, von Bertalanffy growth models were fit to length at age data during the first analysis, and Fabens models were fit to tag-recapture data during the second analysis. The von Bertalanffy model is represented by the equation:

\[
  l_t = L_\infty (1 - e^{-K(t-t_0)})
\]

where \( l_t \) = length at time \( t \), \( L_\infty \) = asymptotic length, \( K \) = growth coefficient, and \( t_0 \) = time coefficient where length theoretically equals 0 (von Bertalanffy 1938; Isely and Grabowski 2007). Data collected by Breeggemann et al. (2016) were used to estimate growth during the pre-habitat periods (i.e., period 1 (growth prior to December 2011) and period 2 (May 2012-September 2014). Breeggemann et al. (2016) assigned ages to otoliths collected in December 2011. These data were used to estimate growth of
Largemouth Bass for the first pre-habitat period (i.e., growth prior to December 2011). Length at age data collected during this study were used to estimate growth of Largemouth Bass during the post-habitat period (i.e., October 2014-November 2016). A series of von Bertalanffy growth curves were fit to these data to assess changes in growth between the two periods. Model selection using second order Akaike Information Criterion (AICc) was then used to select the model(s) that most likely explained growth of the Largemouth Bass population. All analyses were completed in Program R using packages FSA, AICcmodavg, nlstools, and nlsMicrobio (Baty and Delignette-Muller 2013; Baty et al. 2015; Mazerolle 2016; Ogle 2016; R Core Team 2016). The models that were tested included the following:

1) General Model: All parameters of the von Bertalanffy growth curves are different between pre-habitat period 1 and the post-habitat period.

2) Common: All parameters of the von Bertalanffy growth curves are similar for the pre-habitat period 1 and the post-habitat period.

3) K Same: The growth coefficient (K) parameters are similar for the von Bertalanffy growth curves for the two periods, but all other parameters are different.

4) Linf Same: The asymptotic length \((L_\infty)\) parameters are similar for the von Bertalanffy growth curves for the two periods, but all other parameters are different.

5) \(t_0\) Same: The time coefficient parameters where length theoretically equals 0 \((t_0)\) are similar for the von Bertalanffy growth curves for the two periods, but all other parameters are different.
6) Linf and K Same: The growth coefficient (K) and asymptotic length ($L_\infty$) parameters are similar for the von Bertalanffy growth curves for the two periods, but the time coefficient parameters where length theoretically equals 0 ($t_0$) are different.

7) Linf and $t_0$ Same: The time coefficient where length theoretically equals 0 ($t_0$) and the asymptotic length ($L_\infty$) parameters are similar for the von Bertalanffy growth curves for the two periods, but the growth coefficient (K) parameters are different.

8) K and $t_0$ Same: The time coefficient where length theoretically equals 0 ($t_0$) and the growth coefficient (K) parameters are similar for the von Bertalanffy growth curves for the two periods, but the asymptotic length ($L_\infty$) parameters are different.

In addition, Fabens models were fit to size at tag and size at recapture data collected during PIT Tag studies to estimate Largemouth Bass growth. Breeggemann et al. (2016) collected tag-recapture data between May 2012 and September 2014, which was used to estimate growth for the second pre-habitat period (i.e., May 2012-September 2014). Tag-recapture data was also collected during this study and was used as a second means of estimating growth during the post-habitat period. Data collected during this study and for the 2012-2014 period (Breeggemann et al. 2016) were analyzed independently to compare Largemouth Bass growth during the two periods. We included only individuals that were tagged and recaptured at least four growing season months (May-October) in advance. This was the majority of a full growing season, which allowed for observable changes in growth and minimized model error related to
measurement error. Fabens models are used to estimate parameters of the von Bertalanffy model (except $t_0$) using tag-recapture data (Isely and Grabowski 2007). Fabens models have also been modified to account for individual heterogeneity when estimating parameters (Wang 1998). Fabens models and modified Fabens models were fit to the tag-recapture data from each of the two time periods using Program R (packages FSA, AICcmodavg, nlstools, and nlsMicrobio; Baty and Delignette-Muller 2013; Baty et al. 2015; Mazerolle 2016; Ogle 2016; R Core Team 2016). Growth curves were observed graphically to assess differences in growth between the two periods.

Food Habits

Diet items and their associated weights were summarized into seven larger prey categories (i.e., fish, vertebrates other than fish [frogs, salamanders, turtles, and snakes], Cambaridae, invertebrates other than Cambaridae, pellets [fish feed], vegetation and other). Vegetation was included in analysis but assumed to be consumed unintentionally Breeggemann et al. (2016). The relative importance of these different diet categories were calculated per season for each size class described previously (i.e., 250-381 mm TL, 382-508 mm TL, and >508 mm TL), as well as for the entire population as a whole. The mean percent composition by wet weight index (Bowen 1996; Chipps and Garvey 2007; Garvey and Chipps 2012) was used to quantify relative importance. Results were compared to those found by Breeggemann et al. (2016) via graphical comparison to assess whether relative importance of these seven diet categories shifted during the period following the addition of habitat. Graphical comparisons focused on small and medium size classes due to low sample sizes of large size classes.

RESULTS
Growth

Ages were assigned to all 121 Largemouth Bass that otoliths were collected from during sampling in November, 2016. Four of the fish were removed from the analysis because they were recaptured individuals that were stocked as adults during the large stocking event and growth prior to stocking was unknown. Of the remaining 117 Largemouth Bass, the maximum assigned age was 7 and the maximum size was 565 mm TL (age 6). Model selection using AICc strongly supported the general model for explaining growth of Largemouth Bass (Table 2.2; Figure 2.5), indicating that all three parameters of the von Bertalanffy growth curves (i.e., \( L_\infty \), \( t_0 \), and \( K \)) for the first pre-habitat period and post-habitat period were different. The general model predicted that growth during the post-habitat period was slower to age-1 but more rapid from age-1 till age-3 (Table 2.1; Figure 2.5). Additionally, growth for Large adults (age- >5) was slower during the post-habitat period (Figure 2.5).

Fifty-four and forty-two tagged Largemouth Bass were recaptured at least four growing months in advance during the second pre-habitat period (May 2012-August 2014) and post-habitat period (October 2014-November 2016), respectively. Initial capture sizes ranged between 263 mm TL and 549 mm TL for the first pre-habitat period and between 260 mm TL and 521 mm TL for the post-habitat period (Figure 2.6). The Fabens and modified Fabens models both predicted faster growth for Largemouth Bass during the post-habitat period than during the second pre-habitat period (Figure 2.7). The modified Fabens model, which accounts for individual variability in growth, predicted faster growth for Largemouth Bass during the post-habitat period than did the Fabens model (Table 2.1; Figure 2.7). Conversely, the modified Fabens model predicted slower
growth than did the Fabens model during the second pre-habitat period (Table 2.1; Figure 2.7).

All three models predicted similar growth for Largemouth Bass during the post-habitat period for the first three ages (Table 2.3; Figure 2.8). The modified Fabens model predicted larger growth after age 3 than did either the Fabens method or the von Bertalanffy method (Table 2.3; Figure 2.8). The von Bertalanffy model and Fabens model predict similar growth up to age seven, which is the last age with length-at-age data, for the post-habitat period (Table 2.3; Figure 2.8). The von Bertalanffy and Fabens models predicted Largemouth Bass growth to be between the 50th and 75th percentiles for Ecoregion 8 for ages 1-5 (Table 2.3). Growth was predicted to be less than the 50th percentile following age 5 (Table 2.3). However, the modified Fabens method predicts growth to be greater than the 95th percentile for ages 5-7 in Ecoregion 8 (Table 2.3). Predicted growth for the older age classes (>5 years) provided the largest discrepancy in predicted growth for the post-habitat period.

Largemouth Bass growth for the pre-habitat period was different between the first and second pre-habitat periods. The von-Bertalanffy model predicted growth for the first pre-habitat period to be greater than the Ecoregion 8 75th percentile for the first 4 ages (Table 2.3). Then growth was predicted to slow and be between the 50th and 75th percentiles for ages 5-7 (Table 2.3). Growth during the second pre-habitat period was much slower. Both the Fabens and modified Fabens models predicted growth to be less than the Ecoregion 8 5th percentile for ages 1-8 (Table 2.3). Largemouth Bass growth during the first pre-habitat period was similar to growth during the period following the addition of habitat. Whereas growth during the second pre-habitat period, which occurred
following the stocking event, was much slower than these other two evaluation periods (Table 2.3; Figure 2.8).

Prey Abundance and Food Habits

Total prey abundances across all species increased following the addition of habitat and relative abundances of *Lepomis spp.* increased the most. Before the large-scale habitat addition, total prey abundances averaged between 55 and 315 fish/h electrofishing (Figure 2.9). After the habitat addition, total prey abundances averaged between 400 and 600 fish/h electrofishing. Abundance of *Dorosoma spp.* was highly variable between seasons and years (Figure 2.9). Conversely, the abundances of *Lepomis spp.* were consistent and averaged between 19 and 87 fish/h electrofishing prior to the summer 2015. After the summer 2015, abundances of *Lepomis* averaged between 204-471 fish/h electrofishing (Figure 2.9).

Fish and crayfish (Cambaridae) were important Largemouth Bass diet items in the spring seasons before and after the addition of habitat. The Largemouth Bass population (i.e., size classes pooled) in Grand Lake consumed primarily fish and crayfish in early May 2015 (Figure 2.10). Fish (56.8%) and crayfish (32.8%) accounted for 89.6% of the mean percent composition by wet weight of collected diets (Figure 2.10). A large proportion of the fishes observed in stomachs were unidentifiable fish parts, but Gizzard Shad and Largemouth Bass were the two identifiable species. Invertebrates accounted for nearly 7% of the mean percent composition by wet weight of collected diets and identifiable invertebrates included Odonata, Diptera, and Coleoptera (Figure 2.10). Crayfish composed the most of diets by wet weight (67%) and fish composed the second largest amount of diets by weight (33%) for the largest size class (i.e., >508 mm).
Crayfish were observed in two of the three large size class diets and a 271g Gizzard Shad was collected from the other. Similarly to diets collected in 2015, fish (55.7%) and crayfish (28.9%) accounted for 84.6% of the mean percent composition by wet weight of diets collected in spring 2016 (Figure 2.11). In addition to Gizzard Shad and Largemouth Bass, *Lepomis spp.* were present in many diets collected in spring 2016 (frequency of occurrence = 24.4%). The mean percent composition by wet weight of fish for the small and medium size classes were 68.9% and 41.1%, respectively (Figure 2.11). Crayfish (41.3%) and vertebrates (i.e., Squamata and Ranidae) (10.6%) composed more of the medium size class diets by weight in the spring 2016 (Figure 2.11). One diet was collected from the large size class and was composed entirely of crayfish (Figure 2.11).

Spring diet compositions by wet weight for small and medium size classes observed by Breeggemann et al. (2016) during the pre-habitat period were similar to spring diets observed during the post-habitat period. Relative importance of fish varied between about 25% and 65% depending on year and size class.

Although Largemouth Bass diets during the summer seasons were variable among years, fish and crayfish were important Largemouth Bass diet items before and after the addition of habitat. Unlike the spring diets, summer diet samples were much different between 2015 and 2016. The summer Largemouth Bass diets (collected in early July, 2015) for the population were composed primarily of crayfish (46.2%) and fish (32.9%) by weight (Figure 2.10). Identifiable fishes included Largemouth Bass, *Dorosoma spp.*, and *Pomoxis spp.*, and invertebrates included Odonata, and Arachnida. The mean percent composition by wet weight of medium size class diets was similar to the composition of population diets (i.e., 46.3% crayfish and 39.8% fish) (Figure 2.10). The small size class
was also composed of similar amounts of crayfish (49.2%), but fish composed less of diets (17.8%) while vegetation composed more of small size class diets (22.8%) by weight (Figure 2.10). 9 of 10 small size class diets with vegetation included either fish or crayfish prey, but vegetation had a high percent composition by weight (>50%) in two of three diets because only small pieces of fish (< 0.2g) remained undigested. The one large size class diet was composed entirely of unidentifiable fish remains. In summer 2016, fish accounted for more of the mean percent composition by wet weight than did crayfish for both size classes observed (Figure 2.11). Fish composed 86.7% and 54.3% of diets by weight for the small and medium size classes respectively (Figure 2.11). Crayfish still composed 26.8% of diets by weight for the medium size class in 2016 (Figure 2.11). Invertebrates were relatively unimportant (< 2% mean percent composition by wet weight) in summer 2016 diets but included Odonata, Chironomidae, Coleoptera, and Belostoma (Figure 2.11). The other prey category also composed 1.4% of medium diets by weight, which was driven by one diet sample that included a 23.2g plastic worm, 64.5g Bluegill, and 0.3g Coleoptera. Summer diet compositions by wet weight for small and medium size classes observed by Breeggemann et al. (2016) during the pre-habitat period were similar to those observed in 2016. Relative importance of fish for the two smaller size classes varied between about 50 and 85% depending on year and size class. Fish were relatively unimportant to small (17.8%) and medium-sized (39.8%) bass diets in summer 2015 as compared to summer seasons pre-habitat or summer 2016.

Fish were the most important Largemouth Bass diet item in the fall seasons before and after the addition of habitat. Fall diets were composed primarily of fish during 2015 and 2016. At the population level Largemouth Bass consumed primarily fish (64.1%) and
crayfish (25.0%) by weight in the fall 2015 (diets collected in early November) (Figure 2.10). Largemouth Bass, *Dorosoma spp.*, and *Lepomis spp.* were fishes identified from fall diet samples. Vegetation composed nearly 8% of fall diets, but was only observed in samples with fish or crayfish also present. Diet composition by size class showed slightly different patterns than at the population level. Fish composed a higher percentage of small size class diets (80.0%) while crayfish composed a smaller percentage (5.6%) by weight (Figure 2.10). Conversely, medium size class diets were composed of less fish (50%) and more crayfish (43.7%) by weight (Figure 2.10). Only one diet was collected from the large size class, which was composed of crayfish (93.9%) and vegetation (6.1%) by weight (Figure 2.10). Fall 2016 diets were similar to fall 2015 diets. The biggest difference was that fish composed a larger amount of the medium size class diets by weight in 2016 than in 2015 (Figure 2.10; Figure 2.11). Fish accounted for 85.3%, 77.9%, and 100% of mean percent composition by wet weights for small, medium, and large size class diets respectively (Figure 2.11). Crayfish composed less of small (3.8%), and medium (9.3%) diets in 2016 (Figure 2.11). *Lepomis spp.*, *Dorosoma spp.*, *Ameiurus spp.*, Largemouth Bass, and Mozambique Tilapia were fishes identified in fall 2016 diets with *Lepomis spp.* occurring the most frequently (frequency of occurrence = 32.7%). Fall diet compositions by wet weight for small and medium size classes observed by Breeggemann et al. (2016) during the pre-habitat period were highly variable amongst years. In general, relative fish importance varied between 40% and 95% contribution by weight. Similar variability was observed for the post-habitat period. The variability in relative importance of diet categories amongst years was higher than amongst periods (pre-habitat period vs. post-habitat period).
In the winter season fish remained an important Largemouth Bass diet item while crayfish became relatively unimportant, which was similar to the pre-habitat period. The winter diet samples were collected in January, 2016 and showed that the Largemouth Bass population consumed primarily fish (64.3% mean percent composition by wet weight) (Figure 2.11). Vegetation (15%) and invertebrates (14.3%) were the other two prey categories that composed large amounts of diets by weight (Figure 2.11). Crayfish composed very little (4.2%) of Largemouth Bass diets by weight in the winter 2016 (Figure 2.11). *Lepomis spp.*, *Ameiurus spp.*, and Mozambique Tilapia were all fishes observed in winter 2016 diet samples, while Coleoptera, Nematoda, and Odonata were observed invertebrates. The small and medium size classes showed similar patterns of diet composition as the overall population (Figure 2.11). Notable differences included less fish consumed by the small size class (55%) and more fish consumed by the medium size class (74.3%) by weight (Figure 2.11). The largest diet sample collected in January 2016 was composed of a 219.3g Tilapia which was collected from a 465 mm TL Largemouth Bass. One diet was collected from the large size class and was composed entirely of fish remains (Figure 2.11). Winter diet compositions by wet weight for small and medium size classes were observed during only one year by Breeggemann et al. (2016) and for the post-habitat period.

**DISCUSSION**

Stocking fish inevitably affects population density and density-dependent responses by the environment or fish are expected (Einum and Fleming 2001). Changes in levels of food availability and growth of conspecifics are two numerical responses to density dependence that are supported by the results from our study. Although the
availability of prey fishes in Grand Lake, TX prior to stocking was unknown, the lowest observed availability during a three-year evaluation period occurred in the initial period following stocking. The immediate depression response in fish prey abundance is expected since Largemouth Bass undergo an ontogenetic diet shift to fish prey within their first year and then select for available fish prey (Olson 2006; Shoup and Wahl 2009). These results agree with other studies that have found altered prey community structures by direct consumptive effects of fish predators (e.g., Mittelbach et al. 1995; Batzer et al. 2000). Since food is limiting in aquatic habitats (Walters and Post 1993), depleted resources during periods of increased predator densities may also result in decreased resource acquisition. Amundsen et al. (2007) demonstrated that density-dependent resource acquisition can affect growth. Arctic Charr (Salvelinus alpinus) per capita feeding rates decreased with Arctic Char abundance because of density-dependent resource limitation, which resulted in slowed growth rates in a dimictic lake in northern Norway (Amundsen et al. 2007). Stocking Largemouth Bass in Grand Lake, TX may have depleted food resources that resulted in decreased resource acquisition and slowed growth rates. Regardless of mechanism growth responses are expected following periods of increased predator densities.

Growth of Largemouth Bass in Grand Lake slowed during the period following the stocking of 646 adult Largemouth Bass (i.e., after December 2011), which increased densities by about 14.4 Largemouth Bass per hectare. These results were in agreement with previous research that supports stocking and density dependence as depressing growth (e.g., Vincent 1987; Lorenzen and Enberg 2001; Sass et al. 2004; Amundsen et al. 2007). For example, Vincent (1987) found stocking of catchable size Rainbow Trout
(Oncorhynchus mykiss) to have a significant negative effect on biomass of wild trout in both the Madison River, MT and O’Dell Creek, MT. Similarly, lakes in the ceded territory of Northern Wisconsin with densities averaging about 8.3 Walleye (Sander vitreus) per hectare had significantly lower asymptotic lengths because of density-dependent growth (Sass et al. 2004). Finally, Guy and Willis (1990) found Largemouth Bass abundance (indexed as catch-per-unit-effort (CPUE)) to be correlated with size structure in 13 small impoundments in central South Dakota.

After a two-year period of slowed growth, growth of Largemouth Bass in Grand Lake improved during the period following the large-scale habitat addition. This was partially expected since compensatory growth is often described as a period of accelerated growth following a period of depressed growth and often occurs when a decrease in predator abundance allows for increases in food (i.e., mesopredator release hypothesis; Ali et al. 2003). For example, Ferreri and Taylor (1996) found a compensatory growth response of Lake Trout (Salvelinus namaycush) following depressed abundances by sea lampreys in Lake Superior, MI that allowed for increases in Lake Trout prey. Following the addition of structural habitat to Grand Lake, individual growth of Largemouth Bass improved while abundances remained at levels similar to those following the large stocking event (i.e., post-stock: 18-45 Largemouth Bass/h; post-habitat: 33-50 Largemouth Bass/h). Furthermore, Largemouth Bass prey abundances increased during this period. Contrary to the mesopredator release hypothesis, the abundance of the apex predator (i.e., Largemouth Bass) did not decrease before the abundance of the mesopredators (prey fishes) increased. Since compensatory growth
following mesopredator release is not supported, adding structural habitat may have increased production of Largemouth Bass through bottom-up effects.

The newly added structural habitat may have improved Largemouth Bass foraging, which improved individual growth. Structural habitat can improve Largemouth Bass resource acquisition by either facilitating a diet shift to better resources or increasing consumption of resources. Largemouth Bass in Grand Lake did not appear to shift diets following the addition of structural habitat. The relative contribution of prey fish to Largemouth Bass diets remained variable among years and seasons, which was similar to the pre-habitat period (Breeggemann 2016). Furthermore the highest contributions of fish to diets occurred in the fall seasons (around 80% of diets by wet weight), which was also consistent with results from the pre-habitat period (Breeggemann 2016). These results are different than other studies which did find diet shifts in response to adding structural habitat (Schramm and Zale 1985; Sass et al. 2006). For example, Largemouth Bass switched from selecting for Bluegill to selecting for Blue Tilapia (*Oreochromis aureus*) in experimental tanks when vegetative cover was present (Schramm and Zale 1985). In addition, Largemouth Bass shifted diets to include more terrestrial prey sources, causing individual growth to slow, following a reduction in coarse woody habitat in a northern Wisconsin lake (Sass et al. 2006). Grand Lake has a highly managed prey community (i.e., through stocking of prey fish) that maintains relatively high abundances of fish prey (> 100 fish/h electrofishing) at all times. Prey management may limit detecting a diet shift during periods of improved conditions. For example, during periods when conditions are poor (i.e., pre-habitat period) fish prey still contribute highly (>40% proportion by wet weight) to Largemouth Bass diets. In the
northern Wisconsin lake, terrestrial sources switched from contributing between 9 and 12% of total Largemouth Bass diets to between 51 and 55% of the total diets after coarse woody habitat was removed (Sass et al. 2006). The switch to something other than fish prey was inevitable once Yellow Perch (*Perca flavescens*) were depleted by Largemouth Bass. However, fish prey is highly abundant and readily available in Grand Lake even when natural reproduction is limited, which may prevent significant shifts in diet and energy acquisition.

Newly added structural habitat also may increase growth of top predators by facilitating increased consumption rates. Structural habitat attracts predator fishes and prey fishes and may increase encounter rates between the two (Pardue 1973; Prince and Maughan 1979; Wege and Anderson 1979; Daugherty et al. 2014). In a Texas reservoir, 90% of fishes collected from areas with Christmas tree structures were centrarchid species, and a majority (57% of total catch) were Bluegill and Largemouth Bass (Daugherty et al. 2014). Spatiotemporal arrangement of structural features influenced use by these species. For example, cluster-shaped structures had larger sizes of Largemouth Bass during the day as well as greater abundances of smaller sized Bluegill (Daugherty et al. 2014). These results suggest that a clustered arrangement of features may promote the greatest encounters between centrarchids. The habitat treatment sites in Grand Lake were clustered in shape which may provide ideal conditions for Largemouth Bass capture success and increase consumption rates of fishes attracted to habitat sites. Interestingly, *Lepomis spp.* were identified more frequently in Largemouth Bass stomach samples collected in 2016 (i.e., averaged 25% frequency of occurrence per season) as compared to those collected in 2015 (i.e., averaged 4% frequency of occurrence per season). Increased
frequency of occurrence may be related to increased consumption facilitated by structural features, increased Lepomis spp. abundances, or both.

In addition to attracting prey, structural habitat can also improve foraging rates by providing ambush cover (Savino and Stein 1982; Sass et al. 2006). Too small of interstitial spaces within structures may limit capture success (Crowder and Cooper 1979; Savino and Stein 1982; Janssen et al. 2007). For example, cover densities greater than 276 stems/m² is suggested to decrease Largemouth Bass foraging success on Bluegills by limiting the ability of Largemouth Bass to maneuver (Gotceitas and Colgan 1989). However, Savino and Stein (1989) discovered that habitats with areas of high density cover (>276 stems/m²) adjacent to open waters areas provide optimal conditions for Largemouth Bass to forage. Specifically, they discovered that both Largemouth Bass and Northern Pike were most successful at capturing Bluegills and Fathead Minnows (Pimephales promelas) in experimental pools with 50% cover and 50% open water because of covered ambush points (Savino and Stein 1989). In northern Wisconsin lakes Largemouth Bass moved less and consumed more prey in lakes with more abundant coarse woody habitat because of a shift to a sit-and-wait ambush foraging strategy (Ahrenstorff et al. 2013). The habitat treatment sites in Grand Lake were composed of structures with both small and large interstitial spacing surrounded by areas of open water, which likely provides ambush foraging areas where Largemouth Bass capture success and consumption rates increased. Structural features that provide ambush cover may increase Largemouth Bass consumption rates of species that may not be attracted to the features, which is important in systems with complex prey communities with different behaviors and morphologies. Deboom and Wahl (2013) discovered that Largemouth Bass
capture efficiency was highest in experimental tanks with high levels of coarse woody habitat structural complexity. They also found Largemouth Bass capture efficiency was higher regardless of prey behavioral strategy (i.e., Bluegills that are adapted to maneuvering in structural features vs. open-water adapted Golden Shiners). Capture efficiency was higher for Largemouth Bass predating on Golden Shiners because of increased capture rates, and capture efficiency was higher when predating on Bluegills because of a combination of increased capture rates and decreased activity rates (Deboom and Wahl 2013). This study demonstrated that structural habitat consistently improves Largemouth Bass capture rates, but that it can also influence Largemouth Bass foraging behavior and energetic gains differently depending on prey behavior. Grand Lake is a complex system with a prey community composed of many open-water adapted fishes, so these results may explain why Largemouth Bass activity rates remained similar to pre-habitat levels (Chapter 3) while changes in consumption rates may have increased growth rates.

There is a chance that the findings in this study were an anomaly or influenced by environmental variability. First of all, the amount of precipitation differed between the pre-habitat and habitat evaluation study periods within this region of eastern Texas. For example, stream gauges in the Trinity River at Trinidad, Texas recorded lower mean daily discharge for the pre-habitat period (2013- 1,450 cubic feet per second (cfs); 2014-1,386 cfs) than for the post-habitat period (2015- 8,794 cfs; 2016- 14,000 cfs) (NWIS 2017). Increased precipitation is important because precipitation is often correlated with fish growth (Guyette and Rabeni 1995; Rypel 2009; Richard and Rypel 2013). Largemouth Bass collected from six rivers and five reservoirs from the southeastern
United States (i.e., Georgia, Alabama, and Mississippi) had negatively correlated growth with annual precipitation, which resulted in Largemouth Bass growth being the highest in the warmest, driest years (Rypel 2009). Similarly, Largemouth Bass collected from Ouachita River, Arkansas experienced slower growth during high-flow years (Hecke et al. 2016). Results consistently support improved Largemouth Bass growth in the southern United States during years with lower precipitation. If precipitation had a large effect on growth during this study, then growth would be predicted to be accelerated during the pre-habitat period. Precipitation may not have had a large effect on growth of Largemouth Bass in Grand Lake during this study, however. Climactic effects on fish growth may be buffered in small impoundments because of strong biotic effects, such as food availability. Rypel (2009) sampled two small impoundments located in areas with high levels of nutrients, which did not show the same pattern of decreasing Largemouth Bass growth in response to increased precipitation. Grand Lake is a eutrophic (secchi depth ≤ 0.75m) small impoundment where growth of top predators may be influenced more by biotic interactions.

Submersed aquatic vegetation is beginning to reestablish in Grand Lake as the Grass Carp population declines. Abundance of submersed aquatic vegetation is another environmental factor that affects fish growth (e.g., Bettoli et al. 1993, Pothoven et al. 1999; Sammons et al. 2005). Largemouth Bass often grow more quickly in environments with intermediate levels of submersed aquatic vegetation. Brown and Maceina (2002) observed faster growth and better conditions for Largemouth Bass collected from Lake Seminole, Georgia in areas of the reservoir with lower levels (26-32%) of submersed aquatic vegetation compared to Largemouth Bass collected from areas with high levels
(76%). Additionally, Texas reservoirs with less than 20% submersed aquatic vegetation coverage had lower Largemouth Bass standing crops (Durocher et al. 1984). Grand Lake, Texas has been free of aquatic macrophytes since the introduction of Grass Carp and although coverage may be increasing, coverage levels do not approach the optimal 20%-40% coverage reported in other studies. The effect of aquatic macrophytes on Largemouth Bass growth is also not consistent. Largemouth Bass populations in Florida lakes <300 ha in size did not show a relationship between macrophyte abundance and abundances of sub-adult or adult Largemouth Bass (Hoyer and Canfield, Jr. 1996). With the low levels of submersed aquatic vegetation throughout the study and the inconsistent effects of macrophyte coverage on Largemouth Bass growth it may be unlikely that increasing levels of macrophyte coverage had a large effect on growth of Largemouth Bass during the following study.

In summary, growth of Largemouth Bass in Grand Lake, TX increased following the addition of structural habitat. A habitat facilitated diet shift that increased the energy Largemouth Bass gained through consumption is not supported as the mechanism that explains the increases in Largemouth Bass growth. Fish were a relatively important diet item to Largemouth Bass during most seasons and years, and Largemouth Bass diets remained similar among the pre-habitat and post-habitat periods. Changes in consumption rate may be a likely path through which Largemouth Bass growth increased. Structural habitat may facilitate top predators to increase consumption rates by providing areas that increase encounters with prey attracted to similar areas as well as environments with features, such as ambush cover, that promote improved capture rates. Large-scale
habitat enhancement projects may increase production of important sportfish populations and may be useful for fisheries managers trying to combat the effects of reservoir-aging.
REFERENCES


Fisheries Society, North Central Division, Special Publication 6, Bethesda, Maryland.

Table 2.1. Summary table of the von Bertalanffy growth parameters estimated by different growth models and data from Largemouth Bass in Grand Lake, TX during the first pre-habitat period (prior to December 2011), second pre-habitat period (May 2012-September 2014), and post-habitat period (October 2014-November 2016). The von Bertalanffy model was fit to length-at-age data and the Fabens and modified Fabens models were fit to tag-recapture data.

<table>
<thead>
<tr>
<th>Evaluation Period</th>
<th>Model</th>
<th>$L_\infty$</th>
<th>$K$</th>
<th>$T_0$</th>
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<tr>
<td><strong>Pre- Habitat Period 1</strong></td>
<td>von Bertalanffy</td>
<td>513.56</td>
<td>0.2946</td>
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<td></td>
<td>Fabens</td>
<td>478.64</td>
<td>0.1666</td>
<td></td>
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<tr>
<td></td>
<td>Modified Fabens</td>
<td>305.90</td>
<td>0.2794</td>
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<tr>
<td><strong>Pre- Habitat Period 2</strong></td>
<td>von Bertalanffy</td>
<td>425.06</td>
<td>0.5753</td>
<td>0.5227</td>
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<td></td>
<td>Fabens</td>
<td>508.09</td>
<td>0.2963</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Modified Fabens</td>
<td>886.22</td>
<td>0.1593</td>
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Table 2.2. Model comparisons testing support of different von Bertalanffy growth models at explaining Largemouth Bass growth during the first pre-habitat period (prior to December 2011) and post-habitat period (October 2014-November 2016) within Grand Lake, TX. The general model assumes all parameters of the von Bertallanffy growth curves are different between the two periods.

<table>
<thead>
<tr>
<th>Model</th>
<th>K</th>
<th>Log-Likelihood</th>
<th>$\text{AIC}_c$</th>
<th>$\Delta\text{AIC}_c$</th>
<th>$\text{AIC}_c$ Weight</th>
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<td>General</td>
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<td>1996.04</td>
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<td>0.98</td>
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<td>K- Same</td>
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<td>-996.42</td>
<td>2005.3</td>
<td>9.26</td>
<td>0.01</td>
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<td>L$_\infty$ and K- Same</td>
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<td>-997.97</td>
<td>2006.26</td>
<td>10.22</td>
<td>0.01</td>
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<tr>
<td>L$_\infty$- Same</td>
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<td>-997.97</td>
<td>2008.38</td>
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<tr>
<td>L$_\infty$ and T$_0$- Same</td>
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<td>2021.04</td>
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<tr>
<td>T$_0$ and K- Same</td>
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<tr>
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<td>2050.86</td>
<td>54.82</td>
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Table 2.3. Predicted lengths-at-ages for Largemouth Bass in Grand Lake, TX during the first pre-habitat period (prior to December 2011), second pre-habitat period (May 2012-September 2014), and post-habitat period (October 2014-November 2016) based on a von Bertalanffy growth model. Parameters for the von Bertalanffy growth model were estimated by either fitting a von Bertalanffy curve to length-at-age data or by fitting Fabens and modified Fabens models to tag-recapture data. Lengths-at-ages for different percentiles of growth for Ecoregion 8 were copied from Bonar (2009).

<table>
<thead>
<tr>
<th>Age</th>
<th>Pre- Habitat Period 1 (von-Bertalanffy)</th>
<th>Pre- Habitat Period 1 (Fabens)</th>
<th>Pre- Habitat Period 1 (Modified Fabens)</th>
<th>Pre- Habitat Period 2 (von-Bertalanffy)</th>
<th>Pre- Habitat Period 2 (Fabens)</th>
<th>Pre- Habitat Period 2 (Modified Fabens)</th>
<th>Habitat Evaluation Period (von-Bertalanffy)</th>
<th>Habitat Evaluation Period (Fabens)</th>
<th>Habitat Evaluation Period (Modified Fabens)</th>
<th>50th Percentile</th>
<th>75th Percentile</th>
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<td>74.6</td>
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<td>130.3</td>
<td>130.5</td>
<td>123.8</td>
<td>130.3</td>
<td>130.5</td>
<td>231.0</td>
<td>268.0</td>
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<td>135.6</td>
<td>131.0</td>
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<td>227.2</td>
<td>241.8</td>
<td>231.0</td>
<td>241.8</td>
<td>231.0</td>
<td>290.0</td>
<td>330.0</td>
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<tr>
<td>3</td>
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<td>188.3</td>
<td>173.6</td>
<td>322.8</td>
<td>299.2</td>
<td>336.7</td>
<td>290.0</td>
<td>299.2</td>
<td>336.7</td>
<td>335.3</td>
<td>383.0</td>
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<tr>
<td>4</td>
<td>384.4</td>
<td>232.8</td>
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<td>352.8</td>
<td>417.6</td>
<td>335.3</td>
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<td>248.7</td>
<td>406.9</td>
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<td>545.5</td>
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<td>545.5</td>
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<td>7</td>
<td>460.2</td>
<td>329.5</td>
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<td>8</td>
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<td>480.1</td>
<td>520.0</td>
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</table>
Figure 2.1. Bathymetric map and location of Grand Lake in eastern Texas.
Figure 2.2. Maps of Grand Lake, Texas showing availability of aquatic vegetation during the pre-habitat period (left; 2012-2014) and post-habitat period (right; 2015-2016).
Figure 2.3. Map of Grand Lake, Texas showing the locations of “fish cities” that were added during the large-scale habitat enhancement project completed between September and November of 2014.
Figure 2.4. Graphical design of each “fish city” placed around the shoreline of Grand Lake, Texas during the large-scale habitat enhancement project completed between September and November of 2014.
Figure 2.5. Graph of the best supported von Bertalanffy growth model with predicted curves fit to Largemouth Bass length-at-age data for the post-habitat period (October 2014-November 2016; black line and black asterisks;) and first pre-habitat period (prior to December 2011; grey line and grey circles).
Figure 2.6. Size-dependent growth for PIT Tagged Largemouth Bass that were captured and subsequently recaptured at least four growing season months in advance. Black asterisks indicate Largemouth Bass observed during the post-habitat period (October 2014- November 2016) and grey circles indicate Largemouth Bass observed during the second pre-habitat period (May 2012-September 2014).
Figure 2.7. Predicted growth for Largemouth Bass during the post-habitat period (October 2014-November 2016; black lines) and the second pre-habitat period (May 2012-September 2014; grey lines) based on Fabens (dashed lines) and modified Fabens (dotted lines) growth models and tag-recapture data.
Figure 2.8. Predicted Largemouth Bass growth for the post-habitat period (October 2014-November 2016; black lines), first pre-habitat period (prior to December 2011; solid grey line), and the second pre-habitat period (May 2012-September 2014; dashed and dotted grey lines). Von Bertalanffy models and length-at-age data were used to predict growth during the first pre-habitat period (solid grey line). Fabens and modified Fabens models and tag-recapture data were used to predict growth during the second pre-habitat period (dashed and dotted grey lines). Both methods were used to predict Largemouth Bass growth during the post-habitat period.
Figure 2.9. Mean catch per unit effort of prey fishes sampled in Grand Lake, TX per one hour of electrofishing. The colored bars correspond to different fish categories sampled within each season and the error bars represent 1 standard error.
Figure 2.10. Mean percent composition by wet weight of major diet categories from Largemouth Bass sampled in Grand Lake, TX in spring (A), summer (B), and fall (C) 2015. The bars correspond to different size classes of Largemouth Bass within each season and the numbers in parentheses represent the sample size per size class.
Figure 2.11. Mean percent composition by wet weight of major diet categories from Largemouth Bass sampled in Grand Lake, TX in winter (A), spring (B), summer (C), and fall (D) 2016. The bars correspond to different size classes of Largemouth Bass within each season and the numbers in parentheses represent the sample size per size class.
MOVEMENT AND HABITAT SELECTION OF LARGEMOUTH BASS IN AN AGING RESERVOIR BEFORE AND AFTER A LARGE-SCALE HABITAT ENHANCEMENT PROJECT

ABSTRACT

Structural habitats in reservoirs are declining in quality and quantity because of aging processes. Largemouth Bass are an important sport fish that often select for structural habitat features, such as coarse woody habitat. Adding structural features to aging reservoirs may enhance structural habitats and affect movement behaviors of Largemouth Bass. We compared adult Largemouth Bass habitat selectivity, daily movement rates, and the size of seasonal use areas before and after the completion of a large-scale habitat enhancement project in an aging reservoir in eastern Texas. Largemouth Bass moved at similar rates but switched the pattern of movement and focused around areas with newly added structural habitat following the habitat enhancement project, indicating that movement behaviors changed. Largemouth Bass selected for areas with structural features pre and post-habitat enhancement, and selected strongly for using areas with newly added habitat following the habitat enhancement project. Largemouth Bass daily movement rates (7.77 m/hr to 20.24 m/hr depending on season) and seasonal use area sizes (1.82 ha to 3.65 ha depending on season) remained similar to those observed before the addition of habitat. Diverse prey fish assemblages (pelagic species and littoral species) may limit changes in Largemouth Bass movement rates by providing conditions that favor multiple behavioral strategies even after habitat enhancement projects. For example, sedentary Largemouth Bass may benefit from increased capture rates facilitated by ambush points located near features that also attract prey fishes, whereas active Largemouth Bass may benefit from increased encounters with
prey fishes when moving amongst pelagic and littoral areas with structural features. Largemouth Bass may select for structural habitat because foraging conditions may be improved. Adding structural features to reservoirs may promote improved energy acquisition for top-level predators by providing features to focus foraging efforts around. Keywords: aging reservoir, habitat, Largemouth Bass, behavior, habitat selectivity, movement, seasonal use area
INTRODUCTION

Habitat is defined as the area where an organism lives, which includes the physical, chemical, and biological components of the environment (Hudson et al. 1992; Hayes 1999, Fisher et al. 2012). The quality of habitats required by an organism may impact survival, health, and reproduction (e.g. Fahrig 2001; Munday 2004; Hinam and St. Clair 2008). Many habitats are threatened and declining in quantity and/or quality, affecting the success of organisms that rely upon critical features (Saunders et al. 1991; Brooks et al. 2002; Hoekstra et al. 2005; Niebuhr et al. 2015). Reservoir habitats are no exception. The loss of reservoir habitats occurs at quicker rates than those in natural lake systems because of reservoir aging processes (Kimmel and Groeger 1986; Krogman and Miranda 2016), including sedimentation (Patton and Lyday 2008; Juracek 2015), decomposition of woody structures, and erosion of shorelines (Agostinho et al. 1999). Unlike natural systems, which are maintained as heterogeneous environments by disturbance (Sousa 1979), reservoirs do not experience self-maintenance of habitats because they are managed as relatively stable environments. Thus, there are two issues affecting reservoir habitats: aging and “replacement” of habitats. The loss of reservoir habitats affects many fishes, including important sport fish species.

Aquatic scientists are rapidly increasing attention toward managing habitats in aquatic systems, including lakes and reservoirs (AFWA 2012; Norris 2016; Miranda 2017; Sass et al. 2017). Habitat enhancement management activities include planting native aquatic plants, stabilizing shorelines, dredging sediment, and installing artificial structures (Pegg et al. 2015). Installation of artificial structures is one of the oldest used fishery improvement techniques (Brown 1986) and continues to remain commonly
recommended for future research and use in improving aging reservoirs. Artificial structures are commonly added to reservoirs as a habitat enhancement strategy to replace degraded or lost woody structures. Artificial structures may attract prey fishes, increasing abundances in localized areas (e.g. Helfman 1979; Paxton and Stevenson 1979; Prince and Maughan 1979; Bolding et al. 2004). More recent work indicates that predators are also attracted to these structural habitat sites (Allen et al. 2014), which is not surprising since these areas are forage “hotspots”. In addition to providing greater food availability, artificial structures can provide predators an environment conducive to an “ambush foraging” strategy by providing necessary cover (Wege and Anderson 1979). Although artificial structures likely attract fishes and may influence predator-prey dynamics (Sass et al. 2006), the role artificial structures play in increasing fish production (i.e., amount of fish biomass produced per unit time) is still lacking (Miranda 2017).

One way to understand the role of artificial structures at improving fish production is to assess the influence of such structures on the different factors affecting fish growth (Miranda 2017). Fish growth is often conceptualized with an energetic budget (Rice et al. 1983; Hartman and Hayward 2007). The parameters that can be influenced by adding artificial structure are consumption and metabolism due to activity (Chapter 1). Rice et al. (1983) noted that Largemouth Bass growth and condition can be explained primarily by feeding rates but mentioned the need for better understanding activity patterns. Boisclair and Leggett (1989) found activity patterns to be an important parameter affecting growth in Yellow Perch. They concluded that the activity parameter is important for explaining variance in growth of actively foraging fishes and also inter-population differences in growth (Boisclair and Leggett 1989). Activity can be an
important parameter influencing growth in fishes and should be considered as a pathway through which management activities impact fish populations and system production.

Increased movements increase activity costs, so studying fish movements may allow for understanding possible changes in activity costs for fish populations. This is important because many animals, including fishes, decrease home range size and/or movement patterns in response to improved habitat quality (Tufto et al. 1996; Barraquand and Benhamou 2008; Santangeli et al. 2012). For example, Siffczyk et al. (2003) found that wintering willow tits in areas of poorer quality habitats increased their territory size. These were forested areas that either contained unsuitable vegetative habitat or did not contain preferred mature coniferous forest habitats. Similarly, Mountain Gorilla ranging patterns are influenced most by the abundance and distribution of high quality foods (Vedder 1984).

One fish species that is likely affected by aging reservoir processes is the Largemouth Bass. Largemouth Bass select for important structural habitat features when available (Colle et al. 1989; Sammons et al. 2003). Sammons et al. (2003) documented high usage of hydrilla by Largemouth Bass before a removal project, and a consequent shift to using large woody debris afterwards. Both of these are important structural habitats vulnerable to reservoir aging. Previous research documented Largemouth Bass decreasing movements in response to improved habitat quality and quantity. Ahrenstorff et al. (2009) found Largemouth Bass increase movements and home ranges when habitat quality decreases. Largemouth Bass home range sizes and movement rates were smaller in lake basins with increased abundance of coarse woody habitat, which was considered an important habitat feature for Largemouth Bass success. And Rogers and Bergersen
found increased home range size and movements of Largemouth Bass in a reservoir during a drawdown event, which causes Largemouth Bass to be displaced from quality littoral habitat and associated vegetative structure. The loss of reservoir habitats is cause for concern to fisheries managers because these relatively quick, permanent changes to reservoir systems may affect the growth of top-level predators.

Small private impoundments provide an opportunity to study improvements to fisheries that may result from habitat improvement efforts. The goal of this study is to measure changes in Largemouth Bass movement behavior in response to a habitat improvement project in eastern Texas. Grand Lake is managed as a trophy Largemouth Bass system with the goal of consistently producing 6.8kg Largemouth Bass. The ecology of the system was intensively studied from 2012 till 2014 and reservoir aging was determined to be a factor limiting Largemouth Bass production. Management recommendations from that study were to complete a large-scale habitat enhancement project. Previous research highlighted the importance of structural features to Largemouth Bass (Colle et al. 1989; Sammons et al. 2003; Allen et al. 2014), so a total of 315 artificial structures were added around the impoundment. The objectives of this study were to: 1) Quantify the sizes of seasonal use areas (SUA) following the habitat enhancement project and compare sizes to the pre-habitat period, 2) Quantify daily movement rates and distances following the habitat enhancement period and compare to the pre-habitat period, and 3) Evaluate and compare Largemouth Bass habitat selection during the pre-habitat (2013-2014) and post-habitat period (2015-2016).

METHODS

Study site
Grand Lake is located in eastern TX, USA and was built in the 1950’s (Figure 3.1). The 45 ha private impoundment is eutrophic (secchi depth $\leq 0.75$ m) with a mean depth of 3.2 m and maximum depth of 7.9 m. Grand Lake is an aging reservoir experiencing declines in physical habitat quality and quantity (Breeggemann 2016). A diverse community of emergent vegetation occurs in most of the littoral area. Additionally, submersed aquatic vegetation was present during the last two years of the study and appears to be recovering with the decline in Grass Carp (*Ctenopharyngodon idella*) (Figure 3.3). The fish community is diverse (see Chapter 2). The fishery is managed as a trophy catch-and-release Largemouth Bass (*Micropterus salmoides*) fishery. A large-scale artificial habitat addition was completed in Grand Lake from September through November 2014 to increase the availability of structural habitat in the lake. A total of 21 Mossback Fish Habitat™ (MFH) “fish cities” were placed around the lake boundary (Figure 3.2). Each fish city contained two SH-5832 horizontal Safe Haven units (MFH) were placed perpendicular to the shoreline to connect the shallow littoral zone to deep water habitat. At the ends of the horizontal safe havens, three vertical Safe Haven Kits (MFH) were placed to provide additional high density structural habitat. Then, three Trophy Tree Kits (MFH) were placed on each side of the high density habitat features, and Four Trophy Tree XL Kits (MFH) were placed in deep water at the end of all features described above (Figure 3.4). The final habitat addition covered nearly 13% of Grand Lake shoreline in artificial habitat.

*Field Methods*

Radio-Tagging
Sixteen radio-telemetry tags inserted into Largemouth Bass by Breeggemann (2016) were still transmitting at the start of tracking in June 2015. Thus, we continued to track and use the marked locations from these individuals for seasonal use area (SUA) and daily movement analyses until either the tags quit transmitting or the fish died. In addition, Advanced Telemetry Systems © (ATS) F1235 fish body implant tags (dimensions = 18 x 78 mm; weight = 30 g) were surgically implanted into the abdominal cavity of 27 Largemouth Bass between May 2015 and May 2016. Largemouth Bass radio-tagged during this study ranged in size from 472-641mm total length (TL), and weighed between 1770 and 4695g. Thus, behavior and growth of Largemouth Bass were not expected to be negatively affected by tagging because all individuals were large enough to meet the 2% rule (Winter 1983, 1996). Largemouth Bass that were selected for radio-tag implantation were collected during food habits sampling (Chapter 2). Only Largemouth Bass that survived for at least two weeks following surgery were included as a part of this study.

Surgical procedure and protocol were similar to those used by Cooke et al. (2003) and Breeggemann (2016). All non-disposable surgical tools and radio tags were disinfected with an ethanol solution and rinsed with purified water before each surgery (Winter 1996; Cooke et al. 2012). Largemouth Bass were placed in a cooler with diluted clove oil that was administered at a concentration of 60 parts per million (ppm) for 2 to 4 minutes (Wagner and Cooke 2005; Hamackova et al. 2006; Bowker et al. 2017). After Largemouth Bass were immobilized, they were measured, weighed, and transferred to a surgery trough that supported fish during surgery (Cooke et al. 2012). An incision (20-30 mm) was made on the right side of the ventral midline with a disposable #10 scalpel, and
the radio tag was then inserted into the abdominal cavity. Afterwards the incision was closed with four interrupted sutures using 3-0, 3/8 circle reverse cut needle and blue 19 mm polypropylene non-absorbable monofilament surgical sutures that often produce minimal inflammation (Wagner and Cooke 2005). Water was continually pumped in the mouth and over the gills throughout surgery (Cooke et al. 2012). After surgery was complete, the fish were moved to an aerated tank where they were monitored and allowed to recover for a half hour. Once the Largemouth Bass looked to be in good condition (i.e., upright and swimming normally), they were released back to Grand Lake (Cooke et al. 2012). They were released at the surgery site rather than the initial site of capture to reduce further handling and movement stress. Largemouth Bass were then given three weeks to recover and resume normal behavioral activities before any location or movement data was recorded Breeggemann (2016).

Radio Tracking Methods

Fish were located using a small electrofishing boat equipped with a 24.9 kg thrust electric trolling motor (Ahrenstorff et al. 2009; Breeggemann 2016), a R4500S receiver (3-5m accuracy; ATS), and 3-element folding Yagi antenna (ATS). The zero-point tracking method was used to locate each Largemouth Bass (Nelson 1990; Cooke et al. 2012; Breeggemann 2016). When locating a fish, the individual tracking fish moved the boat in the direction the antenna faced that produced the highest signal strength. The gain on the receiver was reduced each time it became saturated until the signal was omnidirectional and a gain of near zero was achieved. Once the zero point location was found, the global positioning system (GPS) coordinates were recorded using the receiver. The Garmin© R4500 GPS antenna, which is attached to the receiver, was not functioning
during tracking events occurring between July 15, 2015 and July 22, 2015, so locations recorded during this time were recorded using a handheld Garmin© GPSMAP78 (3-5m accuracy) (Cooke et al. 2012).

Seasonal Radio-telemetry

Breaggemann (2016) located Largemouth Bass weekly during the pre-treatment evaluation period, recording 12 locations per fish per 3 month season. Since minimum convex polygon (mcp) area estimates are significantly affected by the number of points used (i.e., minimum convex polygon estimates decrease with decreasing number of locations used; Jennrich and Turner 1969; Rogers and White 2007), seasonal radio-tracking during the post-habitat period (June 2015 - November 2016) also occurred twelve times per three month season. Largemouth Bass were located during one of three randomly selected 8-h intervals (i.e., 0800-1559, 1600-2359, 0000-0759) to continue collecting data for different periods of activity (i.e, morning-midday, afternoon-evening, overnight) and to prevent biasing the results by finding fish during the same times of day (Lucas and Baras 2000). During the post-habitat period radio-tracking occurred during four intensive tracking sessions per season, which resulted in recording locations for each fish three times within a two-week period with a minimum 48-h wait required before a second tracking event started to prevent temporal autocorrelation. The four tracking sessions were spread out over the seasons to gain locational data representative of the entire-three month time period. The overall tracking schedule resulted in an average of one location per week with clusters of data points closer together in time because the tracking events were not evenly spaced through time (i.e. not one location recorded per fish per week). The minimum 48-h wait between tracking events combined with the
alternating start times for locating fish at different times of day were assumed to produce statistically independent locations descriptive of seasonal areas of Largemouth Bass use (Winter 1996; Cooke et al. 2012). The locations gathered during the seasonal radio-telemetry were used to understand Largemouth Bass seasonal areas of use as well as habitat selectivity.

24-hr Radio-telemetry

In addition to the seasonal radio-telemetry, 24-hour intensive tracking events occurred to provide information on Largemouth Bass fine scale movement patterns. The methods were similar to those described by Breeggemann (2016) and the tracking procedure was the same as that described above. Largemouth Bass (n=5) were randomly selected without replacement for tracking to maximize the number of individuals for which movement data was recorded and to account for individual heterogeneity in movement. In the summer of 2015 and 2016 all fish were located at least once and so random selection without replication started over. The number of randomly selected Largemouth Bass tracked during one 24-hour period varied within and between seasons. The most fish tracked during any one sampling event was 10 (summer 2015) and the least amount of fish tracked was 1 (summer 2015). Radio-tracking began at 0800 on the sampling date and the randomly selected individuals were located every four hours thereafter (i.e., 1200, 1600, 2000, etc.) until the final locations were recorded at 0800 the following day. This tracking schedule resulted in a total of seven GPS locations per fish per 24-hour period. All together we sampled 7 times during the summer 2015, 1 time during the winter 2016, 3 times during the spring 2016, 4 times during the summer 2016, and 3 times during the fall 2016.
Data Analysis

Seasonal Radio-telemetry

Seasonal radio-telemetry locations were used to calculate Largemouth Bass 95% mcp seasonal use area (SUA) sizes for the post-habitat period (Odum and Kuenzler 1955; and Rogers and White 2007; Breeggemann 2016). For ease of comparing SUA sizes with pre-treatment SUA sizes, seasons remained the same as those defined by Breeggemann (2016) (i.e., summer = June-August, fall = September-November, winter = December-February, and spring = March-May). The adehabitatHR, sp, and maptools packages in program R were used to calculate and build shapefiles of each Largemouth Bass 95% mcp SUA (Pebesma and Bivand 2005; Calange 2006; Bivand et al. 2013; Bivand and Lewin-Koh 2015; R Core Team 2016). The SUA shapefiles were then loaded into ArcGIS 10.2.2 where the polygons were then clipped by the lake border using the clip tool and the polygon areas were then recalculated using the editor tool to get the within lake 95% mcp SUA size for each Largemouth Bass. Results from Breeggemann (2016) were used as the pre-habitat Largemouth Bass SUA sizes and analyzed with the habitat evaluation SUA sizes that were calculated during this project. 95% SUA sizes were compared using repeated measures linear mixed effects models in Program R (packages lme4, pbkrtest, lsmeans, and multcompView; Halekoh and Højsgaard 2014; Bates et al. 2015; Graves et al. 2015; Lenth 2016). Two main effects models were tested for significance using an ANOVA. The first model included only the habitat treatment (i.e., pre-habitat (2013-2014) and post-habitat (2015-2016)) as the main effect and the second model included only season (i.e., Summer 2013, Fall 2013, etc.) as the main effect. Each model included individual fish as a random effect. A TukeysHSD multiple range test was
then used to assess differences in SUA size for the levels of the main effects found to be different at an alpha of 0.05. Seasonal use area sizes were natural log transformed prior to analysis to meet the assumptions of the model.

24-hr Radio-telemetry

Minimum distance (m) between consecutive fish locations were calculated for all randomly selected Largemouth Bass tracked during the 24-hr radio-telemetry sampling events. Since 24-hr tracking produced seven locations per fish per day (i.e., 1 every 4 hours), six minimum movement distances were calculated per fish per day. The distances corresponded to the minimum distance moved by each Largemouth Bass during six time intervals: 0800-1159, 1200-1559, 1600-1959, 2000-2359, 0000-0359, 0400-0759. All distance calculations were completed in program R using the raster, gdistance, and rgdal packages (van Etten 2015; Bivand et al. 2016; Hijmans 2016). Largemouth Bass minimum movements were calculated using a least cost path framework that constrained movements within the lake boundary. Not all Largemouth Bass locations were recorded exactly four hours after the previous location so the distances were then divided by the elapsed amount of time between locations to get a movement rate (m/h) (Breeggemann 2016). Repeated measures mixed effects models were tested to determine if either of the two main effects (i.e., Season, Time of Day) were significant during the post-habitat period. One model with only season (i.e., Summer 2015, Fall 2015, etc.) as the main effect and a second model including only time of day (i.e., Time of Day) as the main effect were tested using an ANOVA. All analyses were conducted in Program R using packages lme4, pbkrtest, lsmeans, and multcompView (Halekoh and Højsgaard 2014; Bates et al. 2015; Graves et al. 2015; Lenth 2016; R Core Team 2016). Movement rates
were natural log transformed to meet the assumptions of the models. To evaluate the potential impact of adding habitat to Grand Lake on Largemouth Bass daily movement rates, coefficient estimates for the levels of the two main effects (i.e., season and time of day) were compared between the two time periods (i.e., Pre-Habitat, Habitat Evaluation). Coefficient estimates that did not have confidence intervals overlapping zero were considered significant effects on daily movement rates and could be positive or negative.

Habitat Selectivity

Following the large-scale habitat addition, Grand Lake structural habitat was mapped using side-scan sonar techniques similar to the methods described by Kaeser and Litts (2008). We used the recording technique instead of the ‘snapshot’ technique (Pilgrim et al. 2015). A Hummingbird® 998c SI system was used to record and save sonar data, which included the sonar imagery and GPS locations for each track. Rudimentary analysis of sonar tracks was completed using SonarTRX software, and then sonar tracks were viewed in ArcGIS 10.2.2. Structural features present were digitized and individual polygon layers were created for six classes of features: laydown logs, stumps, upright trees, brush bundles, docks, and Mossback Fish Habitat©. These features were considered stable throughout the duration of this study and were only mapped once. Vegetation was considered dynamic and was mapped in the middle month of each three-month season (i.e., summer = July, fall = October, winter = January, spring = April) using a Garmin© GPSMAP78 (3-5m accuracy) by recording tracks along the edges of vegetation patches. The tracks were also loaded into ArcGIS 10.2.2 and a polygon of available vegetation was created for each season. A final “open water” layer was created for each season by using the erase tool to remove the structural features and seasonal vegetation from the
lake polygon. The end result was seven habitat layers for each season of the pre-habitat period and eight habitat layers for each season of the post-habitat period with the one extra map being the Mossback Fish Habitat© layer. Each polygon map was converted to raster format with 1 m² cells and then the aggregate tool was used to increase the raster cell size by a factor of 10 to get final habitat raster maps with 100 m² cells. The aggregate tool was used so that the larger output cells were assigned as a habitat feature if any part of the cell area had that habitat feature present. By assigning the raster cells with this method, it increased the area of each habitat feature. The increased area acts as a spatial buffer since the telemetry and mapping techniques have spatial error present. An Outlying Mean Index (OMI, Dolédec et al. 2000) analysis was used to compare habitat selection through all seasons before and after the addition of habitat (Calenge and Basille 2008; Kadye and Booth 2013; Pape and Löffler 2015a). The OMI is appropriate for analyzing presence-only data so the Largemouth Bass telemetry locations recorded during seasonal radio-telemetry were used (Pape and Löffler 2015b). The selectivity analysis was a design Type II and, therefore, conducted at the population level. The OMI analysis is based on the concept of the ecological niche (Hutchison 1957; Pape and Löffler 2015a), and the marginality values provided by the OMI indicate the difference in mean habitat conditions used by individuals versus the mean habitat conditions of the sampled area. All analyses were conducted in Program R using packages adehabitat, adehabitatHS, raster, and sp (Pabesma, and Bivand 2005; Calenge 2006; Hijams 2016).

RESULTS

Seasonal Radio-telemetry
Largemouth Bass seasonal use area (SUA) sizes were variable among individuals. The number of Largemouth Bass tracked during each season ranged between 28 (summer 2015) and 5 (fall 2016). The largest Largemouth Bass 95% SUA size during the post-habitat period was 19.8 ha (summer 2015) and the smallest SUA was 0.2 ha (winter 2016) (Figure 3.5).

The addition of habitat did not significantly affect the seasonal use area sizes of Largemouth Bass. Habitat treatment (i.e., Habitat) was not a significant main effect on 95% SUA size (Table 3.1; Figure 3.6). Although the results from the mixed effects model were not significant at an alpha of 0.05, they were approaching significance and indicate that SUA size may have increased following the addition of habitat. The average size of Largemouth Bass 95% SUA sizes averaged 1.96 ha (95% CI [1.33, 2.91]) during the pre-habitat period (2013-2014) and 2.93 ha (95% CI [1.87, 4.59]) during the post-habitat period (2015-2016) (Figure 3.6).

Largemouth Bass SUA sizes were smaller in the winter and spring seasons compared to summer and fall seasons. ANOVA results show a significant main effect of season (i.e., Season) on 95% SUA size (Table 3.1; Figure 3.7). Coefficients from the regression analysis indicate that Largemouth Bass SUA size was significantly negatively reduced during the spring 2014 season (Table 3.2). However, no other seasons had either significantly increased or decreased SUA sizes. In general, SUA size was lower in the winter season averaging 1.62 ha in 2014 and 1.82 ha in 2016 (Figure 3.7). SUA sizes in the summer and fall seasons remained higher and between 2.36 ha (fall 2013) and 3.65 ha (fall 2015). Unlike pre-habitat spring SUA sizes, Largemouth Bass SUA sizes were not
reduced during the spring 2016 (2.75 ha) and were similar to post-habitat summer and fall SUA sizes (Table 3.2; Figure 3.7).

24-hr Radio-telemetry

Largemouth Bass daily movement distances and rates were variable among individuals. The furthest distance traveled by an individual Largemouth Bass during a single tracking event was 3232 m (summer 2015), and occurred at a maximum rate of 336 m/h during the 0400-0800 time period (Figure 3.8). The shortest distance traveled by a Largemouth Bass during a daily tracking event was 77 m.

Following the addition of habitat, Largemouth Bass moved more during the overnight period and less during the spring season. ANOVA results indicate significant main effects of time of day (i.e., Time of Day) and season (i.e., Season) on Largemouth Bass movement rates during the post-habitat period (Table 3.3). Pairwise comparisons between movement rates for different time of day periods indicate that Largemouth Bass moved significantly more during the 0400-0800 period than either the 1200-1600 or 1600-2000 time periods (Figure 3.9). Pairwise comparisons of movement rates during different seasons of the post-habitat period indicate Largemouth Bass movement rates during the spring season were significantly lower than movement rates during the summer seasons (Figure 3.9).

Largemouth Bass daily movement patterns remained similar following the addition of habitat. Largemouth Bass movement rates were significantly increased during the 0400-0800 time period during the pre-habitat period (Table 3.4). This was a significant positive effect and remained a significant positive effect on Largemouth Bass movement rates during the post-habitat period (Table 3.4). There were no other
significant time period effects at an alpha of 0.05 for either evaluation period. In addition, two coefficients from the pre-habitat regression analysis were significant (Table 3.5). Largemouth Bass movement rates during the pre-habitat period were significantly increased during the summer 2014 and significantly decreased during the spring 2014 (Table 3.5). Largemouth Bass movement rates were only increased during one of the two summer seasons during the pre-habitat period, so the effects of summer on Largemouth Bass daily movement rate were not consistently significantly positive. During the post-habitat period a similar significant decrease in Largemouth Bass movement rates was observed during the spring season (Table 3.5). Unlike the pre-habitat period, however, no significant positive effect of either summer season was found during the post-habitat period (Table 3.5). In conclusion, Largemouth Bass daily movement rates increased during the 0400-0800 time period and decreased during the spring season before and after the addition of habitat.

Habitat Selectivity

Habitat selectivity analysis for the pre-treatment period revealed two patterns. First, Largemouth Bass associated with some type of structural habitat and concurrently avoided open water areas each season. Second, spring season behavior was different than the rest of the seasons during the pre-habitat period. The amount of marginality accounted for by the first two axis of the OMI ranged between 57.95 and 66.51, except during the spring 2014 where nearly 77% of marginality was accounted for by the first two axis (Table 3.6). In the summer 2013, most Largemouth Bass selected for areas with brush bundles, vegetation, or upright trees (axis 1), and selected against areas with open water (axis 2; Table 3.6; Figure 3.10). In the fall 2013, most individuals selected for
woody features, including stumps, laydown logs, brush bundles (1st axis) and upright trees (2nd axis). Largemouth Bass selected for areas with vegetation and brush bundle features in the winter, 2014 (Table 3.6; Figure 3.10). Axis 1 explained 60% of marginality in the spring 2014 and this axis was primarily an indicator of Largemouth Bass selecting for vegetative areas and to a lesser extent areas away from open water. Axis two was less important but showed Largemouth Bass selecting for woody features, especially brush bundles (Table 3.6; Figure 3.10). In the summer 2014, most individuals selected for docks, brush bundles (axis 1) and upright trees (axis 2) and avoided open water.

Habitat selectivity analysis for the post-habitat period revealed two general patterns. First, Largemouth Bass associated strongly with structural features, including Mossback Fish Habitat© (MFH). Second, the amount of marginality accounted for by the first two axes increased throughout the evaluation period (Table 3.7). In the summer 2015, most individuals selected for areas with MFH (axis 1) and vegetation (axis 2) (Table 3.7; Figure 3.11). Largemouth Bass selected for docks (axis 1) and MFH (axis 2) in the fall 2015 (Table 3.7; Figure 3.11). More than 72 percent of marginality was described by the first two axis of the OMI in every season following the fall, 2015 season. This included the winter 2016 when 72 percent of marginality was described solely by axis 1, which indicated that Largemouth Bass selected for areas with MFH and vegetation (Table 3.7; Figure 3.11). During the spring, 2016 most Largemouth Bass were selecting for MFH (axis 1) with a couple selecting for docks and brush bundles (axis 2). Largemouth Bass habitat selectivity during the summer and fall seasons of 2016 were similar with Largemouth Bass selecting strongly for MFH (axis 1) and vegetation (axis 2;
Table 3.7; Figure 3.11). During all seasons of the post-habitat period, Largemouth Bass tended to avoid open water area.

**DISCUSSION**

Largemouth Bass behavior changed following the large-scale habitat enhancement project. A majority of Largemouth Bass selected for using areas of the lake with the newly added habitat features. It was surprising that seasonal use area (SUA) sizes and daily movement rates remained similar to the pre-habitat period since other studies have indicated Largemouth Bass home range sizes and movements decrease with increasing amounts of structural habitat. For example, Rogers and Bergersen (1995) found Largemouth Bass movement rates increased during fall drawdown periods when Largemouth Bass were displaced from vegetative habitats in Lower Derby Lake, Colorado. Similarly, Largemouth Bass movement rates increased following large reductions of hydrilla in Lake Seminole, Georgia (Sammons et al. 2003). Largemouth Bass home range sizes also decreased significantly with increasing levels of coarse woody habitat in two lakes in Vilas County, Wisconsin (Ahrenstorff et al. 2009).

In addition to the average daily movement rates, there were no behavioral shifts in the times of day or seasons with increased or decreased levels of movement following the habitat enhancement project. The 0400-0800 time of day had significantly increased rates of Largemouth Bass movement and the spring season had significantly reduced rates of movement during both periods. This was also unexpected since other studies found the largest movement rates in May and smallest movement rates in August (Messing and Wicker 1986; and Colle et al. 1989). Messing and Wicker (1986) speculated that movement rates were depressed in August in two central Florida Lakes because water
temperatures exceeded 30°C, but Largemouth Bass in Grand Lake did not show depressed movements even though water temperatures exceeded 30°C for much of each summer. Additionally, the spring season included the month of May and the spring seasons had significantly reduced levels of Largemouth Bass movement likely due to spawning activity (Breeggemann 2016).

Within established use areas, Largemouth Bass selected for areas where artificial structure was added, supporting the utility of artificial structures as attractors. Previous studies have supported the use of artificial structures as fish attractors (e.g. Paxton and Stevenson 1979; Prince and Maughan 1979; Wege and Anderson 1979; Brown 1986; Allen et al. 2014), with most studies focused on responses of prey fishes. However, Allen et al. (2014) found artificial structures in Table Rock Lake, Missouri also attracted Largemouth Bass and Crappie. Before the large-scale habitat enhancement project, Largemouth Bass in Grand Lake preferred areas with woody structure and/or vegetative structure. Similarly, Sammons et al. (2003) documented high percent of Largemouth Bass occurrences (>50%) near hydrilla (pre) and large woody debris (post) structures during an evaluation of removing hydrilla from Lake Seminole, Georgia. Colle et al. (1989) found Largemouth Bass preferred areas near pier structures and vegetation in Lake Baldwin, Florida. Structural habitat features are important to Largemouth Bass and habitat enhancement projects can provide needed structure to aquatic systems.

We hypothesized that Largemouth Bass would show decreased movement rates and use smaller areas of the lake following the large-scale habitat enhancement project because essential resources would be available in smaller areas. They selected for these sites but did not decrease activity rates by decreasing movements. Two reasons why
Largemouth Bass continued to move are: 1. Selective pressures within Grand Lake may favor Largemouth Bass maintaining individual behaviors with different movement rates within the population and 2. Prey dynamics within Grand Lake may still require Largemouth Bass to continually search for food resources.

Recent research noted that many animals, including fishes, show individual differences in behavior (e.g. Koolhaas et al. 1999; Dall et al. 2004; Sih et al. 2004; Toms et al. 2010; Conrad et al. 2011), and that consistent differences in behavioral traits often exist within populations (Wilson et al. 1993; Wilson et al. 1994). This variation in behavioral traits is considered important because it provides different adaptive solutions to complex environments (Wilson et al. 1993; Wolf and McNamara 2012; and Mittlebach et al. 2014). For example, Largemouth Bass show consistent differences in movement behavior with individuals in open water areas moving relatively more and those in littoral areas moving less (Colle et al. 1989). Many studies on Largemouth Bass home range size also found a broad range of sizes (ranging between <0.1 ha and 50 ha; e.g. Messing and Wicker 1986; Colle et al. 1989; Sammons et al. 2003), which are similar to the range of SUA’s observed during this study. Fitness tradeoffs are often used to explain the benefits of maintaining individual differences in behaviors within populations (Mittlebach et al. 2014). For example, Stamps (2007) described a scenario where a bolder individual is more likely to move and experience higher predation risk but higher encounter rates with prey. Increased resource acquisition from being a bold individual comes at the cost of increased rates of mortality, and so less bold individuals would also be favored. Top-level predators often face minimal mortality regardless of behavioral strategy, so fitness tradeoffs do not describe a scenario that would support maintaining multiple behaviors in
these systems. Multiple behaviors in these systems may rather be maintained through tradeoffs between different foraging strategies.

Limited attention, which is a cognitive constraint, requires foraging strategy tradeoffs that may maintain a continuum of personalities in top predator populations and may explain the results from the Grand Lake study. Largemouth Bass can switch foraging strategies from an ambush strategy to an active foraging strategy when cover is limiting (Savino and Stein 1982; Savino and Stein 1989; Warfe and Barmuta 2004), so the large-scale habitat enhancement project was intended to provide cover needed for Largemouth Bass to move less and ambush prey. This is important because decreasing activity was assumed to increase energy available for growth if diet and feeding frequency remained constant. This assumption may not be valid, however, since recent work suggests that animals have limited attention that influences animal behaviors and activities, including foraging activity (Dukas and Kamil 2001; Dukas 2002; Dukas 2004). Attention is one of the four main components of animal cognition and refers to an individual’s ability to process information at any given moment. Attention is limited by the processing limits of the brain (Dukas and Kamil 2001; Dukas 2002; Dukas 2004) and require tradeoffs between processing speed and detail (Gendron and Staddon 1983). One of the most commonly discussed tradeoffs exists between search rate and detection probability of prey (Gendron and Staddon 1983; Dukas 2002). When predators search for cryptic prey, they focus on fine details to increase detection probabilities, which comes at the cost of slower search rates and smaller areas searched. When searching for conspicuous prey, predators experience lower detection rates because they focus on coarse details but can
increase encounter rates by searching larger areas at faster rates (Gendron and Staddon 1983; Dukas 2002).

The prey community for Largemouth Bass in Grand Lake is diverse (see Chapter 2: Study Site for complete description), and abundant. Some of these prey are cryptic, such as Bluegill that associate with aquatic vegetation, and some are conspicuous like crayfish and Dorosoma spp.. The complex prey community would support Largemouth Bass maintaining multiple foraging behaviors in Grand Lake to maximize use of available resources. Prior to the habitat enhancement project, Largemouth Bass behaviors were in agreement with the search rate- detection probability tradeoff hypothesis. Individual Largemouth Bass movements ranged between nearly sedentary (< 0.1 km/day) to large-distance movements (>3 km/day). This supports the idea that some individuals use little energy by focusing efforts on a small area, while others use a lot of energy to cover large areas to increase encounters with prey. Following the habitat project, abundance and diversity of Largemouth Bass food resources did not change (Chapter 2) and the same range in Largemouth Bass behaviors was observed. As long as the environment provides favorable conditions for multiple foraging behaviors, then the need to maximize use of resources in complex environments may drive the individual behaviors and prevent seeing a rapid shift in movement behaviors.

Regardless of the mechanism driving individual behaviors, selective pressures favoring one strategy will be needed to force a change in behaviors and a behavioral shift may not be observable for a few generations. Further support for this idea comes from the findings by Ahrenstorff et al. (2009). As mentioned previously, they found Largemouth Bass home range sizes decreased significantly with increasing levels of coarse woody
habitat in two lakes in Vilas County, Wisconsin (Ahrenstorff et al. 2009). Interestingly though, the only significant differences in Largemouth Bass home range sizes were between lakes with unaltered levels of coarse woody habitat. The “naturally” high (Little Rock Lake) and “naturally” low (Camp lake) systems where Largemouth Bass had multiple generations to adapt to the environments were significantly different. The significant differences between the unaltered lakes indicates these populations are adapted to their respective environments. Largemouth Bass home range sizes within each treatment basin had large amounts of variability and were not significantly different from their respective reference (or “natural”) basins in the same lake, however. The changes in home range sizes within each lake, albeit not significant, following the respective treatments would lend support for behavioral plasticity. Behavioral plasticity allows animals to respond to changes in the environment (Sol et al. 2002; Sutter and Kawecki 2009) and is considered one of the biggest challenges in assessing changes in animal personalities/behaviors (Mittlebach et al. 2014). Attempting to understand such behavioral plasticity may be the only way to assess treatment effects on animal behaviors in the short-term, however. In the case of the Grand Lake population Largemouth Bass use areas remained similar based on the ranges of observed sizes. Although Largemouth Bass movements did not change, Largemouth Bass did show behavioral plasticity by shifting to using the new habitat features within the established use areas. Animal behaviors may mask significant effects of management actions since evaluations do not often last long enough for selective pressures to influence the population of interest.

Changes in Largemouth Bass foraging behavior may provide a way to evaluate individual behaviors and effectiveness of management actions. The “saltatory search”
foraging strategy is defined by a stop-and-go movement pattern. It is a highly flexible active foraging strategy in fishes that varies to suit the environment (O’Brien et al. 1990). For example, White Crappie (*Pomoxis annularis*) and Arctic Grayling (*Thmillus arcticus*) pause briefly, swimming faster and farther, when foraging on larger prey than when feeding on small prey (O’Brien et al. 1990). The duration of pauses and length of movements during the “go” stage can vary so much that they make the saltatory foraging strategy nearly inseparable to either the ambush or cruising strategy depending (O’Brien et al. 1990). If Largemouth Bass forage using a saltatory strategy, then changes in the duration of pauses and length of movements during the “go” stage may be used to evaluate management actions in the short-term better than by evaluating changes in total movement distances, per se.

Habitat treatment sites could make good “stop” sites, or areas of decreased movement, because these areas would improve Largemouth Bass foraging. DeBoom and Wahl (2013) investigated the foraging success of Largemouth Bass in structural features of differing complexities and found Largemouth Bass benefit energetically from foraging in coarse woody habitat with high levels of structural complexity. Results revealed that Largemouth Bass can benefit from decreased predatory movements, like prey follows, when predating on Bluegills in highly complex structures. Others have also found improved foraging by predators near structural features (e.g. Savino and Stein 1982; Warfe and Barmuta 2004; Daugherty et al. 2014). Savino and Stein 1989 found that heterogeneous habitats are ideal for Largemouth Bass because they provide both ambush cover as well as open water areas that improve capture success. Largemouth Bass
foraging in the saltatory strategy in this environment could focus efforts on these areas for short periods before moving to new sites.

Prey dynamics in Grand Lake might further explain high overall Largemouth Bass activity rates even if short-term foraging behaviors change. Largemouth Bass may need to continually move to new areas to improve encounter rates with diverse prey. Prey abundances in Grand Lake increased following the habitat enhancement project (Chapter 2). Moreover, Grand Lake prey abundance was higher near the habitat treatments when compared to adjacent open water areas following the habitat enhancement project (personal observation, 2015-2016). The concentration of prey fish around physical structure is common (e.g., Prince and Maughan 1979; Wege and Anderson 1979; Brown 1986) and would favor Largemouth Bass focusing attention on these areas. Prey fishes often shift habitats to avoid predators (“predator-mediated habitat shifts”; Werner et al. 1983; Diehl and Eklöv 1995; Lima 1998). Movements increase encounter rates with prey for predators (O’Brien et al. 1990; Gendron and Staddon 1983; Dukas 2002) and would still likely be important for foraging Largemouth Bass because it may increase their chance of encountering prey using such an avoidance strategy. In addition, average prey size was generally larger away from the near shore littoral area (personal observation, 2015-2016). Prey observed near the habitat treatment sites and open-water areas during seasonal diet sampling were generally *Dorosoma* spp. and large-sized *Lepomis* spp. (personal observation, 2015-2016). As mentioned previously, O’Brien et al. (1990) showed that large-sized prey is often correlated to faster and farther movements during the “go” phase of saltatory search in other fishes. The same pattern may be expected in
Largemouth Bass if they forage using this adaptive strategy and could explain the results that Largemouth Bass movements remained large.

The results from this project suggest that habitat enhancement projects may provide more than just energetic benefits to Largemouth Bass in “aging” systems. Structural habitats may restore system dynamics by providing environments favorable to multiple behavioral strategies. Structural habitats can benefit “ambush” foragers by providing important cover that allows individuals to remain hidden and relatively inactive. It can also benefit “actively searching” foragers by providing environments conducive to improved capture success. Mittlebach et al. (2014) highlighted the advantages of increased behavioral variability within populations, noting the effects at the population, community, and ecosystem levels. Large-scale habitat enhancement projects affect animal behaviors and the benefits are likely underestimated in most evaluation projects. Habitat enhancements are valuable tools to fisheries managers combating “reservoir aging” and should be recommended as a primary management strategy in these systems.

The biggest limitation of the findings from this study is that there was no spatial or temporal replication. The project was conducted on an intensively managed private impoundment in eastern Texas and the same results may not occur in other systems since animal behaviors are flexible to environmental conditions. If Largemouth Bass movements are influenced by prey population dynamics as I have suggested, then systems with unmanaged prey communities may result in different changes in Largemouth Bass behavior following a habitat enhancement project. There is also potential for an unknown effect of weather. During the pre-habitat phase of the study
eastern Texas experienced a relatively hot dry period, and during the post-habitat phase eastern Texas experienced a relatively wet period (Chapter 1). Previous research indicates that movements decrease when water temperatures rise above 30°C (Messing and Wicker 1986), but we did not see the same pattern of decreased movements when temperatures rose above 30°C. Additionally we collected two summer seasons of data per evaluation period, providing temporal replication that did not indicate any abnormal Largemouth Bass movement patterns for any summer. All Largemouth Bass tracked during this movement study were large adults (likely female) and so other Largemouth Bass (juveniles and adult males) may have responded different behaviorally to the treatment. These movement results are likely limited in scope but the behavioral trends discovered are likely expected across systems.

Future research should focus on determining if Largemouth Bass forage using a “saltatory search” strategy. The temporal scale of our radio-telemetry data limited our ability to understand whether the stop-and-go dynamics exist in the Grand Lake Largemouth Bass population. This is a highly adaptable foraging strategy and would provide insights into their ability to respond behaviorally to fisheries management activities. I suggest an instantaneous tracking study using acoustic telemetry on Largemouth Bass of many sizes and sexes to understand individual behaviors and foraging strategies for the entire population. Additionally, future research should focus on understanding prey population dynamics in Grand Lake since many of the results discussed were based on personal observations. It would be beneficial to know differences in population characteristics (sizes, species, and relative abundances) between different habitats (open water, structural habitats, and nearshore areas). It would also be
good to know how prey react to predators in the different habitats. This could be achieved by fitting acoustic tags to different prey and looking at how behaviors change when predators enter similar habitats.
REFERENCES


Table 3.1. ANOVA results testing whether differences exist among 95% SUA size for Largemouth Bass because of habitat or season in Grand Lake, TX between June 2013 and November 2016. SUA sizes for the pre-habitat period (2013-2014) were used from Breeggemann (2016) and for the post-habitat period (2015-2016) were calculated from seasonal telemetry locations.

<table>
<thead>
<tr>
<th>Model</th>
<th>Numerator D.F.</th>
<th>Denominator D.F.</th>
<th>F-value</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Habitat</td>
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<td>174.83</td>
<td>3.72</td>
<td>0.06</td>
</tr>
<tr>
<td>Season</td>
<td>10</td>
<td>140.89</td>
<td>3.70</td>
<td>&lt;0.01</td>
</tr>
</tbody>
</table>
Table 3.2. Mixed effects model regression results to test how Largemouth Bass 95% SUA size differed among seasons in Grand Lake, TX between June 2013 and November 2016. Results are given on the log scale and not the response scale. Highlighted rows denote seasons with significant effects on Largemouth Bass SUA sizes.

| Parameter       | Estimate (SUA) | Standard Error | Lower 95% CI | Upper 95% CI | t-value | Pr(>|t|) |
|-----------------|----------------|----------------|--------------|--------------|---------|---------|
| (Intercept)     | 0.86           | 0.28           | 0.32         | 1.41         |         |         |
| Fall 2015       | 0.43           | 0.38           | -0.29        | 1.16         | 1.14    | 0.252   |
| Fall 2016       | 0.37           | 0.52           | -0.62        | 1.36         | 0.71    | 0.477   |
| Spring 2014     | -1.05          | 0.32           | -1.66        | -0.44        | -3.30   | <0.001  |
| Spring 2016     | 0.15           | 0.41           | -0.63        | 0.94         | 0.37    | 0.710   |
| Summer 2013     | 0.11           | 0.32           | -0.50        | 0.71         | 0.34    | 0.736   |
| Summer 2014     | 0.25           | 0.30           | -0.33        | 0.83         | 0.83    | 0.408   |
| Summer 2015     | 0.20           | 0.32           | -0.41        | 0.81         | 0.63    | 0.526   |
| Summer 2016     | 0.26           | 0.47           | -0.64        | 1.15         | 0.54    | 0.587   |
| Winter 2014     | -0.38          | 0.30           | -0.94        | 0.19         | -1.26   | 0.209   |
| Winter 2016     | -0.26          | 0.41           | -1.04        | 0.53         | -0.63   | 0.529   |
Table 3.3. ANOVA results testing whether differences exist among movement rates (m/h) for Largemouth Bass because of time of day or season in Grand Lake, TX between June 2015 and November 2016.

<table>
<thead>
<tr>
<th>Model</th>
<th>Numerator D.F.</th>
<th>Denominator D.F.</th>
<th>F-value</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Time of Day</td>
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<td>490.4</td>
<td>4.33</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Season</td>
<td>4</td>
<td>500</td>
<td>4</td>
<td>&lt;0.01</td>
</tr>
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</table>
Table 3.4. Mixed effects model regression results to compare how time of day affected Largemouth Bass movement rates (m/hr) in Grand Lake, TX during the pre-habitat (2013-2014) and post-habitat period (2015-2016). Results are given on the log scale and not the response scale. Highlighted rows denote times of day with significant effects on Largemouth Bass movement rate.

| Parameter | Estimate | Standard Error | Lower 95% CI | Upper 95% CI | t-value | Pr(>|t|) |
|-----------|----------|----------------|--------------|--------------|---------|---------|
| (Intercept) | 2.63     | 0.19           | 2.25         | 3.01         |         |         |
| 12-16     | -0.16    | 0.21           | -0.57        | 0.26         | -0.74   | 0.460   |
| 16-20     | 0.25     | 0.21           | -0.17        | 0.66         | 1.17    | 0.243   |
| 20-00     | -0.40    | 0.21           | -0.81        | 0.01         | -1.90   | 0.057   |
| 00-04     | -0.40    | 0.21           | -0.81        | 0.02         | -1.88   | 0.060   |
| 04-08     | 0.46     | 0.21           | 0.05         | 0.87         | 2.19    | 0.028   |

| Parameter | Estimate | Standard Error | Lower 95% CI | Upper 95% CI | t-value | Pr(>|t|) |
|-----------|----------|----------------|--------------|--------------|---------|---------|
| (Intercept) | 2.66     | 0.16           | 2.35         | 2.98         |         |         |
| 12-16     | -0.33    | 0.20           | -0.72        | 0.06         | -1.66   | 0.098   |
| 16-20     | -0.30    | 0.20           | -0.69        | 0.09         | -1.52   | 0.129   |
| 20-00     | 0.07     | 0.20           | -0.32        | 0.46         | 0.36    | 0.719   |
| 00-04     | 0.08     | 0.20           | -0.31        | 0.47         | 0.40    | 0.686   |
| 04-08     | 0.47     | 0.20           | 0.08         | 0.86         | 2.34    | 0.019   |
Table 3.5. Mixed effects model regression results to compare how season affected Largemouth Bass movement rates (m/hr) in Grand Lake, TX during the pre-habitat (2013-2014) and post-habitat period (2015-2016). Results are given on the log scale and not the response scale. Highlighted rows denote seasons with significant effects on Largemouth Bass movement rate.

### Pre-habitat Period:

| Parameter       | Estimate | Standard Error | Lower 95% CI | Upper 95% CI | t-value | Pr(>|t|) |
|-----------------|----------|----------------|--------------|--------------|---------|---------|
| (Intercept)     | 2.42     | 0.22           | 1.99         | 2.85         |         |         |
| Spring 2014     | -0.84    | 0.32           | -1.47        | -0.20        | -2.63   | 0.009   |
| Summer 2013     | 0.17     | 0.22           | -0.26        | 0.61         | 0.79    | 0.429   |
| Summer 2014     | 0.51     | 0.23           | 0.05         | 0.98         | 2.19    | 0.028   |
| Winter 2014     | -0.02    | 0.26           | -0.53        | 0.50         | -0.07   | 0.942   |

### Post-habitat Period:

| Parameter       | Estimate | Standard Error | Lower 95% CI | Upper 95% CI | t-value | Pr(>|t|) |
|-----------------|----------|----------------|--------------|--------------|---------|---------|
| (Intercept)     | 2.77     | 0.27           | 2.24         | 3.31         |         |         |
| Spring 2016     | -0.72    | 0.32           | -1.35        | -0.09        | -2.25   | 0.025   |
| Summer 2015     | -0.08    | 0.27           | -0.61        | 0.45         | -0.29   | 0.772   |
| Summer 2016     | 0.23     | 0.31           | -0.36        | 0.83         | 0.77    | 0.443   |
| Winter 2016     | -0.63    | 0.42           | -1.45        | 0.19         | -1.50   | 0.134   |
Table 3.6. Results from the first two axes of the outlying means index (OMI) habitat selectivity analyses for Largemouth Bass and seven habitat features in Grand Lake, TX during each season of the pre-habitat period (2013-2014). Highlighted columns correspond to the results from the second axis for each season. Marginality is the squared Euclidean distance between habitat features used and mean features available within Grand Lake, TX. The Cumulative marginality accounted for by the first two axes each season is equivalent to the sum between the two axes.

<table>
<thead>
<tr>
<th>Pre-habitat Period:</th>
<th>Summer 2013</th>
<th>Fall 2013</th>
<th>Winter 2014</th>
<th>Spring 2014</th>
<th>Summer 2014</th>
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<tbody>
<tr>
<td></td>
<td>Axis 1</td>
<td>Axis 2</td>
<td>Axis 1</td>
<td>Axis 2</td>
<td>Axis 1</td>
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<tr>
<td>% of Marginality</td>
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<td>25.40</td>
<td>39.34</td>
<td>20.72</td>
<td>34.71</td>
</tr>
<tr>
<td>Docks</td>
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<td>0.00</td>
<td>-0.34</td>
<td>0.05</td>
</tr>
<tr>
<td>Brush Bundles</td>
<td>0.41</td>
<td>-0.29</td>
<td>-0.23</td>
<td>-0.09</td>
<td>0.40</td>
</tr>
<tr>
<td>Laydown Logs</td>
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<td>-0.44</td>
<td>-0.24</td>
<td>0.08</td>
<td>0.13</td>
</tr>
<tr>
<td>Upright Trees</td>
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<td>-0.47</td>
<td>0.37</td>
<td>0.61</td>
<td>-0.35</td>
</tr>
<tr>
<td>Stumps</td>
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<td>-0.36</td>
<td>-0.76</td>
<td>0.34</td>
<td>0.19</td>
</tr>
<tr>
<td>Vegetation</td>
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<td>-0.19</td>
<td>0.37</td>
<td>0.36</td>
<td>-0.78</td>
</tr>
<tr>
<td>Open Water</td>
<td>-0.08</td>
<td>0.58</td>
<td>0.20</td>
<td>-0.49</td>
<td>0.22</td>
</tr>
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</table>
Table 3.7. Results from the first two axes of the outlying means index (OMI) habitat selectivity analyses for Largemouth Bass and eight habitat features in Grand Lake, TX during each season of the post-habitat period (2015-2016). Highlighted columns correspond to the results from the second axis for each season. Marginality is the squared Euclidean distance between habitat features used and mean features available within Grand Lake, TX. Cumulative marginality accounted for by the first two axes each season is equivalent to the sum between the two axes.

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>% of Marginality</td>
<td>42.26</td>
<td>20.65</td>
<td>42.59</td>
<td>21.76</td>
<td>71.28</td>
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<tr>
<td>Docks</td>
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<td>0.87</td>
<td>-0.41</td>
<td>0.00</td>
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</tr>
<tr>
<td>Brush Bundles</td>
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<td>0.08</td>
<td>0.02</td>
<td>0.35</td>
<td>-0.04</td>
<td>0.41</td>
</tr>
<tr>
<td>Laydown Logs</td>
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<td>0.24</td>
<td>0.02</td>
<td>0.38</td>
<td>-0.12</td>
<td>-0.24</td>
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<tr>
<td>Mossback Habitat</td>
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<td>-0.13</td>
<td>0.35</td>
<td>0.73</td>
<td>0.84</td>
<td>0.27</td>
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<tr>
<td>Upright Trees</td>
<td>0.10</td>
<td>-0.35</td>
<td>-0.11</td>
<td>-0.19</td>
<td>-0.09</td>
<td>-0.08</td>
</tr>
<tr>
<td>Stumps</td>
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<td>Vegetation</td>
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<td>0.02</td>
<td>0.44</td>
<td>0.65</td>
</tr>
<tr>
<td>Open Water</td>
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<td>-0.21</td>
<td>-0.31</td>
<td>-0.28</td>
<td>-0.18</td>
</tr>
</tbody>
</table>
Figure 3.1. Bathymetric map and location of Grand Lake in eastern Texas.
Figure 3.2. Maps of Grand Lake, Texas showing available structural habitat during the pre-habitat period (left; 2013-2014) and post-habitat period (right; 2015-2016).
Figure 3.3. Maps of Grand Lake, Texas showing availability of aquatic vegetation during the pre-habitat period (left; 2012-2014) and post-habitat period (right; 2015-2016).
Figure 3.4. Graphical design of each “fish city” placed around the shoreline of Grand Lake, Texas during the large-scale habitat enhancement project completed between September and November of 2014.
Figure 3.5. Maps of Grand Lake, Texas showing minimum (left) and maximum (right) observed Largemouth Bass seasonal use areas during the post-habitat period.
Figure 3.6. Largemouth Bass least-squares mean SUA size (ha) for the pre-habitat enhancement period (2013-2014) and post-habitat period (2015-2016) in Grand Lake, TX. SUA sizes for the pre-habitat period were copied from Breeggemann (2016) and were calculated from seasonal telemetry locations for the post-habitat period. Error bars represent 95% confidence intervals.
Figure 3.7. Largemouth Bass least-squares mean SUA size (ha) for Grand Lake, TX between June, 2013 and November, 2016. SUA sizes for the 2013-2014 seasons were borrowed from Breeggemann (2016) and were calculated from seasonal telemetry locations for the 2015-2016 seasons. Error bars represent 95% confidence intervals and letters indicate significant groups.
Figure 3.8. Map of Grand Lake, Texas showing maximum observed Largemouth Bass daily movement distance during the post-habitat period.
Figure 3.9. Largemouth Bass least-squares mean movement rate (m/h) for Grand Lake, TX for different times of day (A) and seasons (B). Movement rates for the pre-habitat period were copied from Breeggemann (2016) and were calculated from 24-hr radiotelemetry locations for the post-habitat period. Error bars represent 95% confidence intervals. The two periods were not compared directly so numbers refer to significant groups during the pre-habitat period and letters indicate significant groups during the post-habitat period.
Figure 3.10. Outlying means index (OMI) habitat selectivity analyses results for Largemouth Bass in Grand Lake, Texas during six seasons of the pre-habitat period. The origins of the graphs correspond to the means of the available habitat conditions during each season. Points indicate the means of the utilized habitat conditions for individual Largemouth Bass, with distance from origin indicating deviation from mean use. Habitat features are shown as boxes with text describing feature type and arrows indicating the strength of the habitat variable at explaining the first two OMI axes.
Figure 3.11. Outlying means index (OMI) habitat selectivity analyses results for Largemouth Bass in Grand Lake, Texas during six seasons of the post-habitat period. The origins of the graphs correspond to the means of the available habitat conditions during each season. Points indicate the means of the utilized habitat conditions for individual Largemouth Bass, with distance from origin indicating deviation from mean use. Habitat features are shown as boxes with text describing feature type and arrows indicating the strength of the habitat variable at explaining the first two OMI axes.