INFLUENCE OF PHYSICAL HABITAT MANAGEMENT STRATEGIES ON SPORTFISH AND FOOD-WEB PROCESSES

BY

ERIC JOHN GATES

THESIS

Submitted in partial fulfillment of the requirements
for the degree of Master of Science in Natural Resources and Environmental Sciences
in the Graduate College of the
University of Illinois at Urbana-Champaign, 2020

Urbana, Illinois

Master's Committee:

Adjunct Professor David H. Wahl, Director of Research
Assistant Professor Eric R. Larson
Associate Professor Anthony C. Yannarell

ABSTRACT

The addition of habitat structures is a popular management strategy in reservoirs meant to mitigate the negative effects of passive and anthropogenic physical habitat degradation on sportfish populations and angler satisfaction. However, mechanisms linking the direct effect of habitat management strategies on aquatic communities and predator/prey interactions, and the ability of habitat management strategies to meet objectives, remains unclear. We conducted a series of replicated pond experiments using plastic fish attractors (Artificial) and coarse woody habitat (CWH) to test hypotheses linking the direct impact of habitat material type and spatial arrangement on aquatic invertebrates and the growth, condition, and survival of largemouth bass (*Micropterus salmoides*) and bluegill (*Lepomis machrochirus*), independent of habitat amount. Patterns of invertebrate community colonization and daily secondary production were similar between ponds containing Artificial or CWH structures and was not influenced by habitat spatial arrangement. Moreover, the growth, condition, and survival of largemouth bass and bluegill sunfish were similar in ponds containing Artificial or CWH structures, and between ponds that differ in habitat spatial arrangement. Our results suggest that other factors such as habitat amount, or the presence of alternative physical habitats, are more important to fishes and aquatic invertebrates than habitat material type or spatial arrangement. Management agencies and stakeholders should focus on maintaining existing physical habitat abundance and diversity, and the relative cost and longevity of introducing different physical habitat types at the appropriate spatial extent may be more important than habitat material type or spatial arrangement.

ACKNOWLEDGMENTS

I would like to acknowledge my academic advisor, Dr. David H. Wahl for his guidance and direction in the development and implementation of this research project, as well as Drs. Eric R. Larson and Anthony C. Yannarell for their helpful suggestions during the project development and interpretation of results. I would also like to thank the staff, technicians, and interns at the Kaskaskia and Sam Parr Biological Stations for logistical support and use of facilities, particularly Drs. J. Parkos and M. Nannini. Dr. T. Detmer provided invaluable help with initial set up and use of the FlowCAM® for zooplankton processing. Thank you to Mossback Fish Habitat Company (Springdale, AR) for donating plastic fish attractors and Jake Wolf Memorial Fish Hatchery (Topeka, IL) for supplying juvenile largemouth bass. I especially thank all my undergraduate research assistants for their help in the field and in the laboratory: R. Corniuk, J. Nagle, J. Finlay, H. Capone, E. Copenhaver, E. Humphrey, and B. Hu. Funding for this research was provided in part by Federal Aid in Sport Fish Restoration Project F-185-R-7 and an NRES Educational Opportunity Grant (2018).

TABLE OF CONTENTS

CHAPTER 1: LITERATURE REVIEW

Substantial modification of natural ecosystems by humans has resulted in pervasive habitat degradation and loss, and has been identified as a primary driver of species extinction and declining biodiversity worldwide (Kovalenko et al. 2012). Habitat loss in lentic ecosystems can be attributed to direct anthropogenic disturbances such as lakeshore development and removal of littoral physical habitat (Schindler et al. 2000; Marburg et al. 2006). Degradation of physical habitat also occurs passively through physical breakdown by wind action and water abrasion (Czarnecka 2016) and chemical breakdown through nutrient leaching and decomposition by microbes and certain xylophagous invertebrate taxa (Harmon et al. 1986). Physical habitat, such as coarse woody habitat (CWH), can also become unavailable due to sedimentation and inundation by fine particle sediments that occurs as reservoirs age (Moring et al. 1986). These direct and indirect processes result in increasingly simplified and homogenous reservoir ecosystems that are capable of supporting fewer species and individuals, are more vulnerable to stochastic events, and are more susceptible to biological invasions that may accelerate species extinction and extirpation (McCann 2000). Moreover, substantial declines in ecosystem integrity and biodiversity can result in lost natural resources and ecosystem services that are economically beneficial to humans (Christensen et al. 1996).

Intentional removal and degradation of physical habitat in reservoir littoral zones is problematic for fisheries, as littoral zones contain physical habitat that is critical to fisheries (Lewin et al. 2004). Littoral zones within reservoirs are shallower and more protected than more exposed pelagic habitats, and are therefore important spawning areas for economically important species such as crappie (*Pomoxis spp.*), muskellunge (*Esox masquinongy*), and bluegill sunfish (*Lepomis machrochirus*) (Werner and Hall 1988; Zorn et al. 1998). Other species such as largemouth bass (*Micropterus salmoides*) and yellow perch (*Perca flavescens*) can spawn by utilizing littoral habitat directly (Wills et al 2004; Sass et al. 2006). As such, habitat degradation and loss negatively affect fishes and other aquatic communities because of the decoupling of the biological and physical conditions to which they are adapted. Moreover, natural recruitment of new sources of physical habitat in reservoirs, usually in the form of riparian CWH, occurs at a prohibitively slow rate (Guyette and Cole 1999).

Physical habitat introduction is one of only a few tools that fisheries managers have available to enhance fisheries because of low availability of littoral physical habitat. Both natural (e.g. trees, aquatic vegetation) and artificial (e.g. limestone rip-rap, tires, plastic fish attractors) habitat types are added to public and private waters by local, state, and federal agencies, universities, and other non-governmental organizations (Bassett 1994). Despite prolific use of habitat additions as a management tool based on knowledge that fish abundances are higher around habitats in reservoirs at certain times of the year, the effects of habitat additions on productivity and space use remain largely understudied. A wide variety of physical habitat types and strategies exist that differ in material type, complexity, land spatial extent and distribution. Moreover, many physical habitat introductions occur without *a priori* management objectives and without appropriate pre- and post-introduction monitoring (Bolding et al. 2004) making difficult to determine the effect of physical habitat management in reservoirs and to compare strategies across broad spatial and temporal scales (Wiens 1989).

There exists a need to understand whether physical habitat of differing material types and spatial arrangement have the same effect on colonizing macroinvertebrates and fishes. Physical habitats of differing material type vary in surface complexity and convolution (Sanson et al. 1995), three dimensional architecture (Jeffries 1993; Johnson et al. 1988) and rate of decomposition (Harmon et al. 1986), all of which interact to influence the quality and quantity food resources (Claflin 1968; Santos et al. 2011) and refuge space (Hesterberg et al. 2017) and have been shown to influence individual and community level responses by macroinvertebrates (Jeffries 1993; Magoulick 1998) and fishes (Johnson et al. 1988; Diehl 1992). How these mechanisms and responses interact to influence long term macroinvertebrate community dynamics and fish growth and survival remains speculative. Therefore, it would be useful to fisheries managers, and in situations where habitat management is a primary objective, to understand the relative ability of habitats that differ in material type to meet management goals in reservoirs.

Aquatic ecologists have confronted the ambiguity and confounding nature around definitions of physical habitat complexity by designing and testing metrics that attempt to objectively quantify physical habitat (Morse et al. 1985; Dibble, Killgore, and Dick 1996; Newbrey et al. 2005; Warfe, Barmuta, and Wotherspoon 2008). For example, Morse et al. (1985) estimated the fractal dimension of several plant species using a grid method. Fractal dimension is unitless and can be applied across multiple scales, and therefore may be useful when comparing structural complexity between habitat types at different scales of measure.

The qualitative and often study-dependent nature around how physical habitat complexity is defined poses significant barriers to valid quantitative comparisons among studies, which in turn makes the task of detecting mechanisms and interpreting broad-scale effects of physical habitat additions on aquatic ecosystems difficult. This poses obvious challenges for fisheries managers, who are expected to make difficult management decisions based on incomplete information and limited financial resources.

CHAPTER 2: INFLUENCE OF HABITAT MATERIAL TYPE ON MACROINVERTEBRATE COMMUNITIES AND LARGEMOUTH BASS GROWTH

A. Introduction

Lentic ecosystems, such as lakes and reservoirs, are important sources of outdoor recreation that attract millions of anglers and generate billions of dollars annually in the United States (FAO 2009). However, inland fisheries within these ecosystems, and the aquatic food-webs that sustain them, are threatened by declining physical habitat quantity and quality as a result of multiple passive and active mechanisms unrelated to fishing activities, including reservoir aging and sedimentation (Moring et al. 1986) and anthropogenic disturbance (Christensen et al. 1996). Physical habitat is important in reservoirs because physical habitat, such as aquatic vegetation and coarse woody habitat (CWH) influences fish distribution and activity (Scheuerell and Schindler 2004; Ahrenstorff, Sass, and Helmus 2009), predator and prey interactions (Savino and Stein 1982), and food resource availability (Pardue 1973). Collectively, these interactions between aquatic organisms and habitat drive fish growth (Schindler et al. 2000) and reproductive output (Wills et al. 2004). The importance of physical habitat is so great that loss of physical habitat poses a greater threat to inland fisheries sustainability than fishing pressure and harvest (Arlinghaus et al. 2016).

Some studies have demonstrated a positive effect of habitat introductions through increased fish growth (Pardue 1973; Wege and Anderson 1979) and increased attraction by fishes (Rold et al. 1996; Santos et al. 2008). Similarly, the removal of physical habitat has been shown to have negative effects on fish populations and fish growth in lakes (Sass et al. 2006) and in streams (Angermeier and Karr 1984). As such, physical habitat additions are a popular management strategy in lakes and reservoirs that seeks to mitigate the effects of habitat degradation and loss by providing refuge to juvenile sport fishes and forage organisms, increase angler satisfaction, provide spawning substrate, or reduce erosion (Bassett 1994; Tugend et al. 2002; Arlinghaus et al. 2016). Both natural (e.g. trees, aquatic vegetation) and artificial (e.g. limestone rip-rap, tires, plastic fish attractors) habitat types are added to public and private waters by multiple management agencies and stakeholder groups to meet various objectives (Santos et al. 2011).

Despite evidence for positive effects of physical habitat additions and negative effects of physical habitat removals in controlled experiments, the ability of physical habitat additions to meet management objectives or to provide long-term benefits to aquatic communities over relevant ecological scales has not been demonstrated in lakes and reservoirs (Bolding et al. 2004) or in stream ecosystems (Bernhardt et al. 2005; Palmer et al. 2010). The diversity of introduced structure types poses significant barriers to effective evaluation of physical habitat management strategies because responses to physical habitat is influenced by system-specific environmental conditions (Nilsen and Larimore 1973; Walters et al. 1991), fish species (DeBoom and Wahl 2013), interstitial space (Hesterberg et al. 2017), and the availability of alternative sources of physical habitat (Wills et al. 2004).   Furthermore, the benefits of habitat management strategies in lakes and reservoirs are often assumed or inferred in the absence of hypothesis-driven pre- or post-manipulation monitoring of aquatic communities at the appropriate spatial and temporal scales (Bolding et al. 2004; Tugend et al. 2002). As such there exists a need to isolate and evaluate the various interacting aspects of physical habitat quality (Tokeshi and Arakaki 2012) and subsequent responses by the target species or communities in order to make defendable conclusions pertaining to the effect of habitat management in inland fisheries.

The influence of habitat material type on responses by aquatic communities in lakes and reservoirs has received less attention compared to other aspects of physical habitat management, such as architectural complexity and physical habitat density (Crowder and Cooper 1982; Bettoli et al. 1992; DeBoom and Wahl 2013; Johnson et al. 1988). Habitat material type influences surface complexity and convolution as well as habitat surface area (Dibble et al. 1996; Thomaz et al. 2008) and has been shown to influence colonization dynamics by periphyton, fungi, and macroinvertebrates in streams (Dudley and D'Antonio 1991; Jeffries 1993; Sanson et al. 1995; Casartelli and Ferragut 2018) and in lentic habitats (Bowen et al. 1998; Smokorowski et al. 2006). Habitat material type also influences the rate at which habitat decays (Harmon et al. 1986) which can be an important mechanism regulating colonization by periphyton (Hax and Golladay 1993) and macroinvertebrates (Magoulick 1998) in stream ecosystems. Thus, habitat material type could influence ecosystem productivity because of the relative ability of different physical habitat types to provide food resources to fish species occupying higher trophic levels, such as bluegill (*L. machrochirus*) and largemouth bass (*M. salmoides*), which are popular sport fishes sought by anglers that occur in most reservoir ecosystems in the continental United States.

Several studies have observed differences in fish use of structures that differ in habitat material type (Rold et al. 1996; Magnelia et al. 2008; Santos et al. 2011). In a large reservoir in Brazil, fish colonization between artificial reefs constructed from PVC, ceramic, and concrete substrates was influenced by fish species, fish size, and time of year (Santos et al. 2011). Both Rold et al. (1996) and Magnelia et al. (2008) found more individuals across all fish species occupying cedar trees and juniper trees compared to plastic artificial attractors, respectively, in reservoirs in the United States. Differences in fish use were attributed to habitat-specific differences in periphyton and macroinvertebrate colonization (Santos et al. 2011) as well as differences in structural complexity and interstitial space (Magnelia et al. 2008; Rold et al. 1996).

These studies suggest that natural habitat types (e.g. CWH) are better at attracting fishes compared to artificial habitat types; however, the reasons attributed to these differences, such as differences in complexity and macroinvertebrate colonization, were not specifically tested. Therefore, manipulative experiments in controlled environments linking fish and macroinvertebrate responses to habitat material type may help identify the relative effectiveness of different habitat types to meet management objectives. This could provide useful information to managers in charge of physical habitat management that seek to maximize the effect of management decisions at the smallest cost (Bolding et al. 2004).

The objective of our experiment was to determine the effect of habitat material type on macroinvertebrate colonization and fish growth. Specifically, we introduced plastic fish attractors or natural CWH in ponds to compare (1) patterns in macroinvertebrate community colonization and structure between habitat material types through time, and (2) determine whether habitat material type influences largemouth bass growth, condition, and survival. We predicted macroinvertebrate community composition to differ and for macroinvertebrate community abundance and diversity to be greater among communities colonizing CWH structures compared to plastic fish attractors. We also predicted largemouth bass growth, condition, and survival would be greater in ponds with CWH structures compared to ponds with plastic fish attractors.

B. Methods

To test our predictions, we conducted a pond experiment at the Sam Parr Biological Station of the Illinois Natural History Survey (Kinmundy, IL) using ten 0.04 ha replicate drainable ponds during Summer/Fall 2017. We used a one-factor completely randomized experimental design. Five were ponds assigned the plastic fish attractor habitat type (Artificial) and five ponds were assigned a coarse woody habitat type (CWH).

Our plastic fish attractors were Safe Haven™ structures manufactured by the Mossback Fish Habitat Company (Springdale, AR). These artificial structures are made of recycled polyvinyl chloride and consist of a single hollow trunk (height: 1.3 m, diameter: 0.11 m) and 24 textured composite limbs (width: 1.3 m) radiating from the trunk horizontally. We selected white oak (*Quercus alba*) as our CWH source in order to control for differences among wood species and their potential to affect colonizing invertebrates (Nilsen and Larimore 1973; Magoulick 1998). Live *Q. alba* (bole diameter < 0.15 m) were harvested and the leaves were removed manually. Bare trees were cut and trimmed into sections (length: 1.3 m, width: 1.3 m) to correspond to the physical dimensions of the artificial structures. Each CWH structure consisted of three or four *Q. alba* sections fastened together with zip-ties. We also added two detachable sections of *Q. alba* to each CWH structure to facilitate macroinvertebrate sampling. The surface area provided by each habitat type was measured. Random branch sampling (Jessen 1955) was used to estimate CWH structure surface area and to keep available surface area for macroinvertebrate colonization consistent between habitat treatments. Six Artificial structures or six CWH structures were driven vertically into the bottom and spaced four meters apart in a 2 x 3 array in the center each pond. The estimated amount of habitat (m^2 ± SE) added to each pond did not differ by treatment (Artificial: 8.76 ± 0.26, CWH: 8.55 ± 0.21; $t_8 = 0.99$, $P = 0.35$). Filtered water (mesh size: 300 μm) was pumped from Stephen A. Forbes Reservoir into each pond until all structures were completely submerged. After ponds were filled, we allowed for a one month conditioning period to allow macroinvertebrate communities to develop and colonize the benthic zone and structures of each pond naturally prior to fish introduction.

Fifty juvenile largemouth bass obtained from Jake Wolfe Memorial Fish Hatchery (Topeka, IL) were introduced into each pond in August 2017 after the conditioning period. Mean initial total length of largemouth bass (mm ± SE) did not differ between treatments (Artificial: 94.3 ± 0.6, CWH: 94.6 ± 0.6; $t_8 = -0.25$, $P = 0.81$). Ponds were drained two months after fish introduction in October 2017 into a cement catch basin, where all surviving largemouth bass were counted, measured (mm), and weighed (g). We calculated mean daily growth rate ($mm \cdot day^{-1}$), mean condition (Fulton's K), and survival (# recovered/50) of largemouth bass for each pond.

We conducted three temporal sampling events to document changes in macroinvertebrate community abundance and composition through time. Macroinvertebrates were sampled monthly beginning in August 2017 after the conditioning period and immediately prior to fish introduction (pre-fish introduction) and was repeated two more times in September and October 2017 (post-fish introduction). Benthic macroinvertebrates were sampled at three fixed locations in each pond using a stovepipe sampler (diameter: 0.19 m; Turner and Trexler 1997), filtered through a 250 μm sieve, and preserved in a solution of 0.1% Rose Bengal and 90 % ethanol for processing in the laboratory. Macroinvertebrates colonizing habitat structures were sampled from two limbs of two habitat structures in each pond during each sampling event (i.e. 4 habitat structure samples/pond/sampling event) by carefully sliding a mesh bag (mesh size: 300 μm) over a single detachable habitat limb to prevent macroinvertebrate escape and carefully removing the limb from the structure. The detached habitat limb was transported to the pond bank where the surface area contained inside the bag was scrubbed with a brush and rinsed with tap water into an enamel pan to dislodge and collect colonizing macroinvertebrates. The contents of the pan were transferred into a sample bottle and preserved in a solution of 0.1% Rose Bengal and 90% ethanol for processing in the laboratory. We also measured the surface area sampled of each habitat limb to derive standardized measures of macroinvertebrate abundance and biomass.

After colonizing macroinvertebrates were collected, all habitat limbs were returned to their respective habitat structures to prevent manipulation of available habitat surface area. We designed our temporal sampling schedule so that two limbs from each habitat structure were sampled, and that each habitat structure was sampled exactly once over the course three sampling events. Prior to macroinvertebrate sampling, we measured several abiotic parameters of each pond during each sampling event to characterize pond environmental conditions. Dissolved oxygen ($mg \cdot L^{-1}$) and water temperature (ºC) were measured with a YSI probe and water clarity (m) was measured with a Secchi disk. Dissolved oxygen, water temperature, and water clarity were averaged over the three sampling events for each pond to derive a single mean value for subsequent statistical analyses.

In the laboratory, macroinvertebrate samples were split by passing each sample through a 600 μm and a 250 μm sieve. Macroinvertebrates retained by the 600 μm sieve were separated from detritus with forceps and an enamel pan, identified, and counted using a dissecting microscope (12x magnification). Macroinvertebrates retained by the 250 μm sieve were subsampled (10% subsample), identified, and counted using a dissecting microscope (25x magnification). Only individuals with a head segment were counted. Macroinvertebrate taxa were typically identified to the family level, whereas non-insect taxa (e.g. ostracods, nematodes, leeches) were identified to the class/order level using keys from Merritt and Cummins (1996) and Thorp and Covich (1991). A maximum subsample of 20 individuals per taxonomic group were measured for total length (TL; mm) using a digitizing pad and ImageJ software (Schneider et al. 2012) for both the 600 μm and 250 μm samples. TL was converted to taxa-specific dry mass (DM; mg) using published length-to-dry mass regression equations (Eckblad 1971; Meyer 1989; Benke et al. 1999; Baumgärtner and Rothhaupt 2003; Edwards et al. 2009). Standardized measures of abundance and biomass were estimated for each structure and benthic sample by summing the counts and biomass estimates for the associated 600 μm and 250 μm samples corrected for subsample size and dividing by the area (m^2) sampled (Smokorowski et al. 2006). Aquatic worms (*Oligochaeta*), although highly abundant, were excluded from our analyses because our sampling and preservation methods precluded us from obtaining reliable estimates of abundance and biomass (Howmiller 1972). Abundance of *Oligochaeta* in macroinvertebrate samples did not noticeably differ between habitat types.

Mean abundance ($N \cdot m^{-2}$) and mean biomass ($mg \cdot m^{-2}$) of macroinvertebrates were estimated separately for benthic and structure communities in each pond by averaging the three stovepipe samples and four habitat structure samples, respectively, collected during each sampling event. We were also interested in comparing mean taxa richness between macroinvertebrate communities colonizing Artificial and CWH habitat structures; however, we sampled significantly more habitat area of Artificial habitat limbs compared to CWH habitat limbs (ANOVA habitat $F_{1,117} = 78.9$, $P < 0.001$). Therefore, we compared mean rarefied taxa richness ($E\ (S_n)$; Hurlbert 1971) between habitat types, which accounts for biases associated with differences in sampling effort (Gotelli and Colwell 2001). Taxa-specific counts were used to estimate mean diversity of macroinvertebrate communities colonizing habitat structures using Shannon's H' (Pielou 1966). Mean rarefied taxa richness and mean diversity were calculated in the same manner as mean abundance and biomass.

Statistical Analysis

A repeated measures analysis of variance (RM-ANOVA) using linear mixed models was used to test the effect of habitat material type on mean abundance, mean biomass, mean rarefied species richness, and mean diversity of macroinvertebrate communities through time. Sampling date and habitat type were fixed effects and individual ponds were the random effect in each model. Abundance was square root transformed to meet the assumptions of analysis of variance. If differences in response metrics were detected, Tukey's HSD was used to determine which groups differed. To visualize differences in macroinvertebrate community structure between habitat types through time, we used non-metric multidimensional scaling (NMDS; Minchin 1987) based on 4th root transformed Bray-Curtis dissimilarity matrices, and differences between macroinvertebrate community groups were determined using permutational multivariate analysis of variance (PERMANOVA; Anderson 2001) using 9999 permutations. If the PERMANOVA detected differences in community structure, we performed a similarity percentage analysis (SIMPER; Clarke 1993) to identify which macroinvertebrate taxa contribute most to changes in macroinvertebrate community structure.

Student's t-test was used to test the effect of habitat type on mean daily growth rate, condition, and survival of largemouth bass. Model selection was used to evaluate the ability of pond environmental conditions to explain additional variation in our fish response metrics by comparing simple and multiple linear regression models that included habitat type only against models that included habitat and one additional pond condition factor. We only included one additional pond condition factor in candidate models in order to avoid model overfitting. Candidate models were ranked for each fish response variable based on Akaike's Information Criterion (AIC_c) corrected for low sample size, and model weights (W_i) were calculated using methods described in Burnham and Anderson (2004). Pond environmental condition factors were mean temperature (Temperature, °C), mean Secchi depth (Secchi depth, m), mean dissolved oxygen (Dissolved Oxygen, $mg \cdot L^{-1}$), mean benthic macroinvertebrate biomass (Benthic biomass, $mg \cdot m^{-2}$), and mean structure macroinvertebrate biomass (Structure biomass, $mg \cdot m^{-2}$). Mean benthic macroinvertebrate biomass was estimated by averaging standardized measures of macroinvertebrate biomass of the three stovepipe samples collected in each pond over the three sampling periods. Mean structure macroinvertebrate biomass was estimated by averaging measures of macroinvertebrate biomass of the four limbs sampled in each pond over the three sampling periods. All analyses were performed in R (v. 3.6.2; R Core Team 2019) using the tidyverse, Rmisc, lmer, AICcmodavg, and vegan packages (Hope 2013; Bates et al. 2015; Oksanen et al. 2019; Wickham et al. 2019; Lenth 2020).

C. Results

Macroinvertebrates

A total of 34,501 macroinvertebrates were identified from pond benthic zones and habitat structures, and 13,721 individuals (40%) were measured to estimate biomass. Habitat structures were colonized by 23 macroinvertebrate taxa over the course of the experiment, three of which were the most dominant for both habitat types. By abundance, 93% of all individuals identified from habitat structures were non-biting midges (*Chironomidae*), ostracods (*Ostracoda*), and nematodes (*Nematoda*). Less dominant but still relatively common taxa included predatory midges (*Ceratopogonidae*), snails *(Physidae*), water scavenger beetles (*Hydrophilidae*), and leeches (*Hirudinea*). Almost all taxa were found colonizing both Artificial and CWH structures at some point during the experiment; *Caenid* mayflies (*Ephemeroptera*), water boatmen (*Corixidae*), and single specimens of both crawling water beetles (*Haliplidae*) and backswimmers (*Notonectidae*) were only found colonizing Artificial structures, while spread-winged damselflies (*Lestidae*) and a single whirligig beetle (*Gyrinidae*) were found only on CWH structures.

Macroinvertebrates colonized all habitat structures rapidly after ponds were filled and the structures submerged. Mean abundance in August prior to fish introduction was similar between habitat types ($P > 0.05$; Figure 2.1A). Mean abundance (square root transformed) changed through time on both habitat types (RM-ANOVA time $F_{2,22} = 52.27$, $P < 0.01$; Figure 2.1A); Abundance increased on both habitat types one month after fish introduction (Table 2.1, September), which was followed by a decrease in mean abundance on both habitat types two months after fish introduction (Table 2.1, October). The interaction between time and habitat was significant (RM-ANOVA habitat × time $F_{2,22} = 5.25$, $P < 0.01$; Figure 2.1A), indicating that patterns in mean abundance differed between habitat types through time. Mean abundance did not differ between habitat types before fish introduction (August, $P > 0.05$; Figure 2.1A) or one month after fish introduction (September, $P > 0.05$; Figure 2.1A), but macroinvertebrate communities were more abundant on CWH structures compared to Artificial structures two months after fish introduction (October, $P = 0.01$; Figure 2.1A).

Mean biomass followed a similar pattern compared to mean abundance. Mean biomass in August prior to fish introduction was similar between habitat types ($P > 0.05$; Figure 2.1A) and changed significantly through time for both habitat types (RM-ANOVA time $F_{2,22} = 21.06$, $P < 0.001$; Figure 2.1B). Mean biomass increased on both habitat types one month after fish introduction (Table 2.1, September) and decreased on both habitat types two months after fish introduction (Table 2.1, October). However, unlike abundance, patterns in mean biomass did not differ between habitat types (RM-ANOVA habitat × time $F_{2,22} = 2.52$, $P = 0.08$; Figure 2.1B).

Diverging patterns between mean abundance and mean biomass of macroinvertebrates in October may be driven by differences the relative size of certain macroinvertebrate taxa between habitat types. For example, *Hirudinea* and *Physidae* were more abundant on CWH structures compared to the Artificial structures two months after fish introduction (Table 2.1), but individual *Hirudinea* (5.53 mg) and *Physidae* (0.81 mg) colonizing Artificial structures were larger than *Hirudinea* (0.35 mg) and *Physidae* (0.55 mg) colonizing CWH structures (Table 2.1).

Rarefied taxa richness was similar between habitat types in August prior to fish introduction ($P > 0.05$) and changed significantly through time (RM-ANOVA time $F_{2,22} = 119.5$, $P < 0.001$; Figure 2.1C). Overall, rarefied taxa richness was higher on Artificial structures compared to CWH structures (RM-ANOVA habitat $F_{1,22} = 21.9$, $P < 0.01$; Figure 2.1C). Rarefied taxa richness increased significantly on both habitat types one month after fish introduction ($P < 0.01$), which was driven by the colonization of habitat structures by *Baetidae, Caenidae*, *Coenagrionidae*, and *Lestidae*, and to a lesser degree by the appearance of a few individuals of *Dytiscidae, Haliplidae,* and *Corixidae* (Table 2.1). Rarefied taxa richness was higher among macroinvertebrate communities colonizing Artificial structures compared to CWH structures one month after fish introduction ($P < 0.01$). Patterns of change in rarefied taxa through time differed between habitat types (RM-ANOVA habitat × time $F_{2,22} = 3.69$, $P = 0.04$; Figure 2.1C); rarefied taxa richness decreased slightly on Artificial structures in October two months after fish introduction, whereas rarefied taxa richness increased slightly on CWH structures during the same time period, although two months after fish introduction differences were not significant between habitat types ($P > 0.05$). Despite converging patterns in rarefied taxa richness between habitat types, rarefied taxa richness remained higher on Artificial structures compared to CWH structures in October two months after fish introduction ($P = 0.04$).

Like rarefied taxa richness, diversity of macroinvertebrate communities was similar between habitat types in August prior to fish introduction ($P = 0.96$; Figure 2.1D). Community diversity generally increased through time (RM-ANOVA time $F_{2,22} = 6.94$, $P < 0.01$; Figure 2.1D). These changes were the result of the combined effects of increasing taxa richness, decreasing relative abundance of *Ostracoda*, and increasing relative abundance of *Physidae* through time for both habitat types (Table 2.1). Despite changing community diversity through time, patterns of change were somewhat different between habitat types (RM-ANOVA time $F_{2,22} = 3.15$, $P = 0.07$; Figure 2.1D). Community diversity on Artificial structures increased significantly between the beginning and end of the experiment (Tukey's HSD, $P < 0.01$), whereas the change in community diversity on CWH structures was similar before and after fish introduction (Tukey's HSD, $P = 0.86$).

Macroinvertebrate community structure changed through time (PERMANOVA; time pseudo-$F_{2,24} = 16.0$, $P < 0.001$). The NMDS ordination plot shows clear separation between sampling events, and rates of change in macroinvertebrate community structure appear to decrease over time (Figure 2.2). Changes in macroinvertebrate community structure in September one month after introduction were primarily driven by increases in abundance of *Ostracoda, Physidae, Chironomidae*, and *Ceratopogonidae*, respectively (SIMPER: 43% observed cumulative dissimilarity), whereas changes in community structure in October two months after fish introduction were driven by decreasing abundance of *Ostracoda, Nematoda*, and *Chironomidae*, and increasing abundances of *Leptoceridae* and *Hydracarina* (SIMPER: 42% observed dissimilarity) compared to September one month after fish introduction. After accounting for changes through time, macroinvertebrate communities differed between habitat types (PERMANOVA; habitat pseudo-$F_{2,24} = 2.78$, $P = 0.04$). Differences in macroinvertebrate community structure between habitat types in August prior to fish introduction were driven primarily by *Ostracoda*, *Collembola*, and *Hydracarina* (SIMPER: 38% observed dissimilarity) whereas differences were driven by *Baetidae*, *Hydracarina*, and *Physidae* in September one month after fish introduction (SIMPER: 22% observed dissimilarity) and by *Chironomidae, Nematoda*, and *Leptoceridae* in October two months after fish introduction (SIMPER: 31% observed dissimilarity). NMDS does show some separation between habitat types within sampling events, but the difference is less extreme than differences between sampling events (Figure 2.2). Moreover, the difference in macroinvertebrate community structure between habitat types within sampling events did not change (PERMANOVA; habitat × time pseudo-$F_{2,24}$ =, P = 0.10) and is supported by NMDS (Figure 2.2). A permutational test of homogeneity of multivariate dispersion between groups was insignificant ($F_{5,24}$ = 0.42 P = 0.85) suggesting that differences in community structure between habitat types were not related to differences in group dispersion (Warton et al. 2012).

Largemouth Bass

Mean daily growth of largemouth bass was similar between ponds with Artificial habitat structures compared to ponds with CWH structures (t_8 = 0.36, P = 0.73; Figure 2.3A). Mean condition of largemouth bass also did not differ between habitat types (t_8 = 0.36, P = 0.73; Figure 2.3B). The number of largemouth bass recovered from each pond was highly variable (mean: 34, range: 23–43), but was not influenced by habitat type (t_8 = -0.77, P = 0.46; Figure 2.3C). Pond environmental conditions were generally poor predictors of largemouth bass growth, condition, and survival. Our AICc analysis showed the greatest support for candidate models that included habitat type only as a fixed effect for each fish response variable (Table 2.2) and all candidate models that included an additional pond condition factor as a fixed effect showed significantly less support (all $\Delta AIC_c > 2$, $W_i > 0.6$; Burnham and Anderson 2004). After habitat type, candidate models including mean pond temperature showed the next best support for largemouth bass growth and condition, while a candidate model including mean dissolved oxygen showed the next best support for largemouth bass survival (Table 2.2).

D. Discussion

Macroinvertebrates

We found that macroinvertebrate communities colonizing a plastic fish attractor were very similar to macroinvertebrate communities colonizing CWH structures. These results contrast with our original hypotheses that predicted macroinvertebrate abundance, biomass, and diversity of macroinvertebrates would be higher among communities colonizing CWH structures. Previous research has shown differences in periphyton (Dudley and D'Antonio 1991; Hax and Golladay 1993) and macroinvertebrate colonization (Hax and Golladay 1993; Magoulick 1998) as a function of habitat material. However, these studies were conducted in streams rather than ponds. Multiple studies have shown differences in macroinvertebrate colonization as a function of water velocity (Hax and Golladay 1993; Nilsen and Larimore 1973) which may in part explain why our results diverged from work in streams. Moving water accelerates physical habitat decomposition due to physical abrasion that increases surface area available for colonization (Hax and Golladay 1993) and increases light penetration and oxygen transport which may further accelerate decomposition by colonizing organisms (Harmon et al. 1986). Moreover, moving water increases rates of dispersion and encounters of novel habitats through macroinvertebrate drift (Stoneburner and Smock 1979) that does not occur in lentic habitats.

The effect of habitat decomposition and conditioning on macroinvertebrate colonization of CWH structures was likely not an important factor influencing macroinvertebrate colonization in our experiment (Bowen et al. 1998; Smokorowski et al. 2006). Oak (*Quercus* spp.) is a very hard wood species relative to other common deciduous species, such as maple (*Acer* spp.) and elm (*Ulmus* spp.) and is primarily composed of lignin and cellulose that are not easily metabolized by most fungi and unicellular organisms (Scheffer 1966). Moreover, deciduous hardwoods such as oak contain organic compounds that initially provide resistance to colonization by fungi and microbes, which are not only important drivers of wood decay, but are themselves food resources for many scraping and collecting macroinvertebrate taxa (Dudley and Anderson 1982). Chemical and physical breakdown of CWH also releases nitrogen and dissolved organic carbon compounds that are readily usable by aquatic organisms (Harmon et al. 1986), although the net effect of these two competing mechanisms on our macroinvertebrate community metrics is unknown. Our CWH structures did not exhibit symptoms of decomposition (separation of bark from the cambium layer, bark softening, etc.) which may in part explain the general lack of differences in macroinvertebrate communities colonizing the Artificial and CWH structures. However, we did find some evidence of diverging patterns between macroinvertebrate communities colonizing Artificial and CWH structures related to differences in abundance and size structure in the final month of the experiment.

Both habitat types represent a hard and stable substrate that are important subsidies in aquatic ecosystems where physical habitat is lacking (Schneider and Winemiller 2008) such as the clay and silt dominated experimental ponds used in this experiment. As such, all habitat structures were colonized rapidly by periphyton and opportunistic macroinvertebrates, and at least initially, may not have been subject to the intra- and interspecific competitive mechanisms that are mediated by various physical and chemical properties of the substrate being colonized (Harmon et al. 1986; Hax and Golladay 1993). Moreover, macroinvertebrate taxa differ in their ability to disperse and colonize new habitat sources because of differences in life-history characteristics and feeding habits (Thorp and Covich 1991). This may explain in part the observed increase in taxa richness and diversity through time, as certain taxa such as *Trichoptera* and *Ephemeroptera*, as well as predatory *Odonata* and *Coleoptera* became more abundant as time progressed. Stochastic variability inherent to natural ecosystems may also have influenced the lack of detectable differences between our habitat treatments. Variability in our estimates of abundance, biomass, and diversity among ponds, and between structures within ponds, was high (Table 2.1). Ten experimental units combined with the short time frame of the experiment may have had low statistical power to detect changes in macroinvertebrate communities colonizing the two habitat types (Peterman 1990).

Largemouth Bass

Our results do not support the contention that habitat material type influenced the growth, condition, and survival of largemouth bass. Thus, physical habitat amount/complexity may be more important to largemouth bass than the material from which it is constructed or composed. The majority of studies evaluating the impact of physical habitat on fishes focused on manipulating physical habitat abundance/complexity (Pardue and Nielsen 1979; Crowder and Cooper 1982; Bettoli et al. 1992; Miranda and Hubbard 1994; Sass et al. 2006). Experiments evaluating fish use of different habitat material types while attempting to control for habitat amount have primarily focused on observational studies via scuba and snorkeling surveys (Bryant 1992; Santos et al. 2011) and sonar (Baumann et al. 2016); no studies have evaluated the direct effect of habitat material type on largemouth bass growth, condition, and survival while attempting to control for habitat amount/complexity.

Others have suggested differences in primary production and food resource quality between different habitat material types in lakes (Bowen et al. 1998; Smokorowski et al. 2006), which could influence largemouth bass growth, condition, and survival (Ludsin and DeVries 1997). We did not detect systematic differences in abundance and biomass of macroinvertebrate prey between habitat types, and food resource availability would have been similar between habitat types. Mean TL and growth rate of all largemouth bass by the end of our experiment (133 mm, 0.61 $\text{mm}\cdot\text{day}^{-1}$) was generally less than that reported by others evaluating young-of-year largemouth bass growth (Stone and Modde 1982; Miller and Storck 1984; Maceina and Isely 1986) but was similar to non-piscivorous young-of-year largemouth bass (Ludsin and DeVries 1997). This suggests largemouth bass growth was more related to food resource quality or quantity. Alternatively, largemouth bass were not able to optimally exploit the food resources available to them. We found that macroinvertebrate prey biomass on habitat structures was higher compared to numbers reported by others in lakes (Bowen et al. 1998; Smokorowski et al. 2006) and macroinvertebrate food resources may have been higher than what is typically reported in the field; however, that models included Benthic Biomass or Structure Biomass of macroinvertebrates showed very little support (Table 2.2). This suggests that largemouth bass were not able to optimally exploit the macroinvertebrate prey resources available to them. The largemouth bass were sufficiently large to make an ontogenetic shift to piscivory at the time of introduction (Bettoli et al. 1992; Ludsin and DeVries 1997). Moreover, fish prey are a more energy dense food resource than macroinvertebrates (Keast and Eadie 1985) and would have been preferred if they had been available. Lack of optimal forage may also explain why mean condition of all largemouth bass declined from 145 to 117 by the end of the experiment (Anderson 1984). Decreasing condition through time may have also contributed to the relatively high mortality rate of largemouth bass (Miranda and Hubbard 1994).

Growth and colonization by American Pondweed (*Potamogeton nodosus*) occurred rapidly during our experiment and densities were highly variable between experimental ponds; some experimental ponds had over 50% pond surface area coverage, while other experimental ponds had little to no colonization (personal observation by the authors). Aquatic macrophytes are another important source of physical habitat in aquatic ecosystems and has important implications for growth and survival of largemouth bass (Bettoli et al. 1992; Olson et al. 1998). We did not control nor account for the growth of this physical habitat subsidy, which may have contributed to the variability in our fish and macroinvertebrate response metrics and potentially masked the effect of our physical habitat introductions.

Management implications

Our results suggest, at least in the short term, that habitat material type has little effect on macroinvertebrate abundance and diversity. In eutrophic reservoirs characteristic of agricultural watersheds in the midwestern United States, it is likely that all physical habitat introductions will be colonized quickly by biofilm and other primary producers, followed quickly by opportunistic macroinvertebrates (Bowen et al. 1998). Within a matter of months, these habitats could provide an important local food subsidy and refuge to prey fishes and early life-stage sport fishes (Tugend et al. 2002). However, physical habitat usually occupies a small proportion of reservoir area relative to open water habitats, and the effect of localized changes in primary and secondary production on system-level productivity of macroinvertebrates (Smokorowski and Pratt 2007;

Helmus and Sass 2008) and fishes (Sass et al. 2012) over broad spatial and temporal scales has not been reliably demonstrated (Lodge et al. 1998).

The effects of habitat introductions may not be beneficial in reservoirs where habitat, whether in the form of aquatic vegetation, CWH, or benthic substrate may not be limiting (Wills et al. 2004). Thus, knowledge of each water body and surveys of available physical habitat should be performed prior to any habitat introduction in order to allocate limited money and resources to reservoirs where physical habitat management is likely to produce the greatest effect.

If physical habitats of differing material type provide comparable resources for macroinvertebrates and sport fishes, the decision to add either habitat type may become a matter of cost-benefit analysis. CWH is a relatively cheap and readily obtainable renewable resource that can be introduced quickly and efficiently. However, the complex branching structure of CWH that influences its value as a food resource and refuge for fishes can degrade quickly (i.e. within a few years depending on the wood species) due to chemical, biological, and physical breakdown due to wind and wave action (Czarnecka 2016). Relatively hard woods, such as oak (*Quercus* spp.) and cedar (*Cedrus* spp.), may be more cost-effective alternatives to soft woods such as Christmas trees (*Pinus*, *Abies* spp.) that are common sources of CWH introductions in reservoirs (Bassett 1994; Bolding et al. 2004). If longevity of physical habitat is of primary concern, CWH introductions may be most cost-effective in coves and inlets that are more protected from wind and wave action, potentially reducing the rate of habitat degradation compared to more exposed main channel littoral habitats. On the other hand, physical habitat constructed from artificial materials (e.g. plastic, PVC, drain tile, etc.) is far more resistant to chemical and biological degradation and is likely to be more robust to physical breakdown compared to organic CWH. However, artificial substrates are more expensive (e.g. our Mossback Safe Haven™ structures are currently listed at $100 retail) and require more effort and resources to construct and introduce relative to natural sources of physical habitat (Pardue and Nielsen 1979; Tugend et al. 2002). Considering the size of large reservoirs in the United States, the budgetary requirements necessary to introduce physical habitat at the appropriate spatial scale may not be feasible for many fisheries management agencies.

E. Figures and Tables

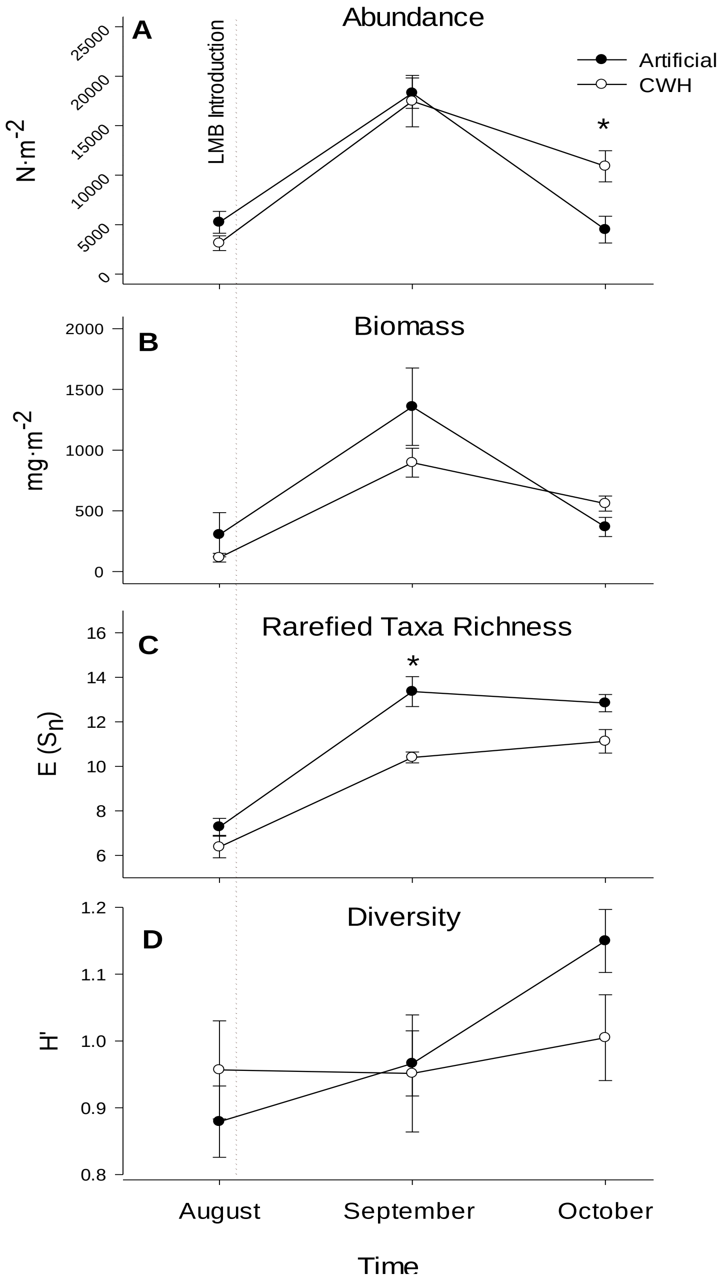

Figure 2.1. Mean (± SE) abundance, biomass, rarefied taxa richness, and diversity of macroinvertebrates communities colonizing Artificial habitat structures (solid circles) and CWH habitat structures (open circles) over time. The vertical dotted line represents the time of largemouth bass introduction. Asterisks represent significant differences between habitat types based on Tukey's HSD (α = 0.05).

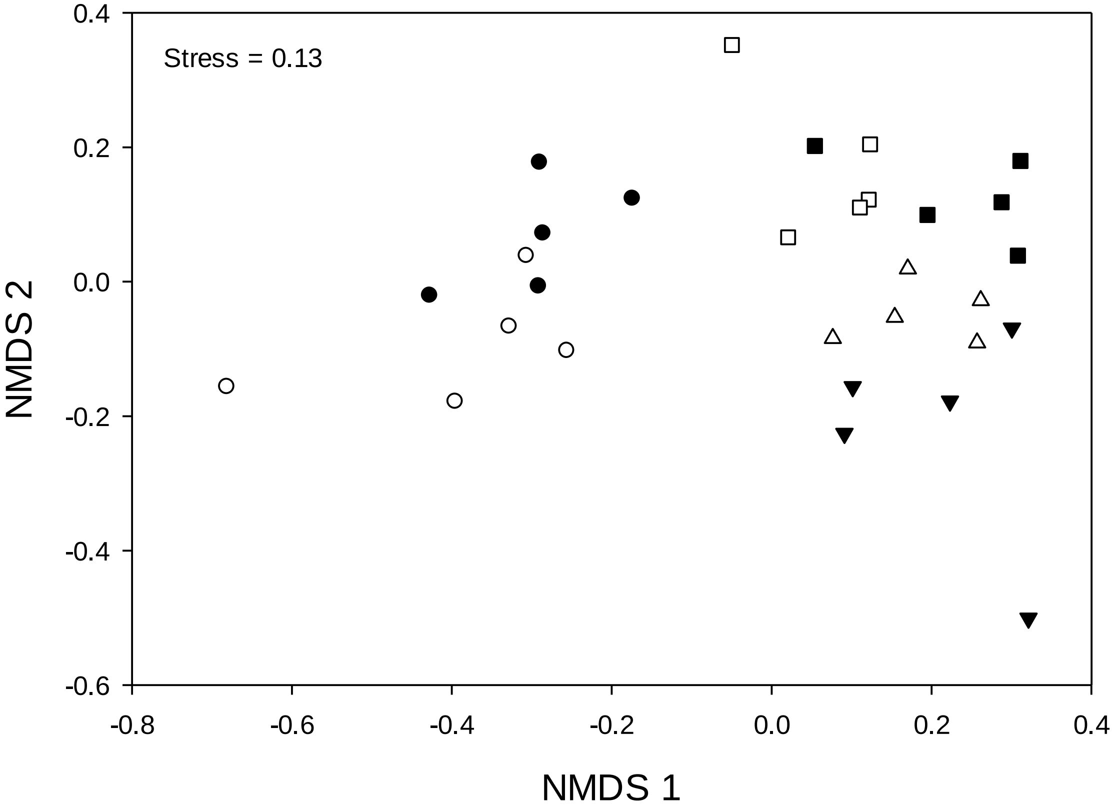

Figure 2.2. NMDS plot of macroinvertebrate community structure based on 4th root transformed Bray-Curtis distances. Closed symbols represent communities colonizing Artificial habitat structures and open symbols represent communities colonizing CWH habitat structures during August (circles), September (squares) and October (triangles).

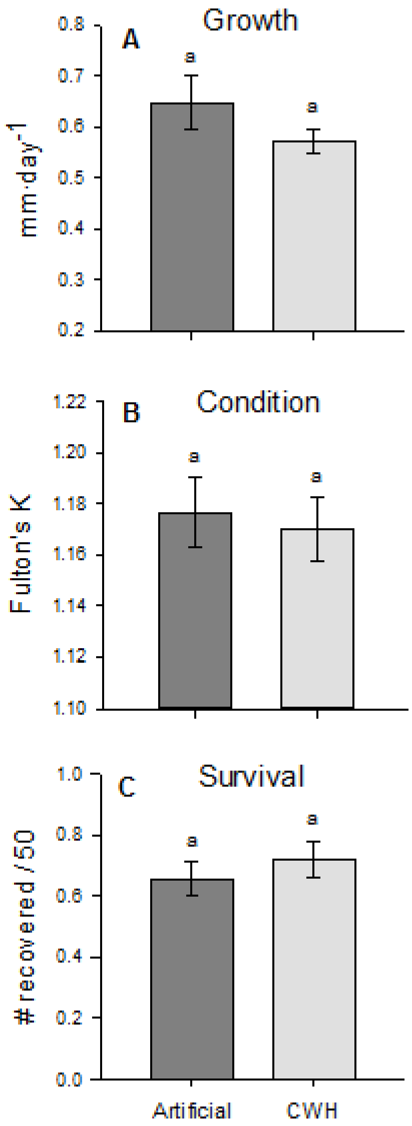

Figure 2.3. Mean (± SE) growth, condition, and survival of largemouth bass stocked in ponds with Artificial habitat structures (dark-grey bars) and ponds with CWH habitat structures (light-grey bars). Bars with the same letter are not significantly different ($\alpha = 0.05$).

Table 2.1. Mean abundance ($N \cdot m^{-2}$) and biomass ($mg \cdot m^{-2}$) of the most abundant macroinvertebrate taxa collected from each habitat type over the three sampling events in 2017. Numbers in parentheses are standard errors of the means. Means were computed from the estimated abundance and biomass of four limbs sampled within each pond (i.e. experimental unit) within each habitat treatment (n = 5 ponds per treatment). Instances where taxa-specific abundance was estimated, but not biomass, were a result of individuals that could not be accurately measured to estimate biomass. Taxa not listed but were occasionally present in small numbers were *Gyrinidae, Haliplidae, Culicidae, Corixidae,* and *Notonectidae.*

Taxon	Pre-fish introduction				Post-fish introduction							
	August				September				October			
	Artificial		CWH		Artificial		CWH		Artificial		CWH	
	Abundance	Biomass	Abundance	Biomass	Abundance	Biomass	Abundance	Biomass	Abundance	Biomass	Abundance	Biomass
Crustacea *Ostracoda*	2753.7 (623.9)	24.40 (7.061)	564.9 (131.3)	9.84 (2.389)	9337.6 (1454)	247.68 (58.958)	8711.1 (2733.2)	186.89 (56.8)	925.6 (274.6)	14.69 (3.42)	1712.4 (522.9)	39.82 (10.97)
Gastropoda *Physidae*	--	--	0.5 (0.5)	0.44 (0.44)	328 (119.8)	78.9 (41.6)	293 (100.1)	79.3 (37.9)	221.1 (59.2)	180.3 (32.4)	550 (74.6)	303.1 (55.8)
Hirudinea	22.8 (10)	26.0 (7.3)	4.2 (1.7)	7.9 (4.9)	109.1 (25.2)	640.5 (214.4)	30.1 (11.2)	177.3 (45.1)	19.5 (7.1)	107.9 (41.5)	30.8 (23.1)	10.772 (7.34)
Hydracarina	28.3 (20.8)	0.001 (0.001)	--	--	43.6 (24.9)	0.002 (0.001)	34.6 (24.7)	--	56.2 (22.6)	0.002 (0.001)	75.9 (31.2)	0.004 (0.002)
Insecta												
Coleoptera												
Dytiscidae	--	--	--	--	1.3 (1.1)	0.02 (0.0)	16.8 (15.3)	--	3.3 (1.4)	0.17 (0.14)	6.4 (4.8)	0.01 (0.01)
Hydrophilidae	54.7 (30.9)	6.2 (1.4)	58 (22.6)	26.7(13.2)	42.2 (16.4)	48.6 (33.0)	100.1 (21.0)	68.6 (22.7)	13 (5.1)	5.3 (2.1)	18.1 (4.2)	15.8 (7.3)
Diptera												
Ceratopogonidae	43.5 (27.1)	3.4 (2.6)	79 (39.1)	3.1 (1.7)	283.4 (67.7)	7.8(4.9)	375.3 (69.3)	5.8 (1.4)	84.7 (39.4)	9.2 (5.9)	267.8 (146.7)	12.9 (4.3)
Chironomidae	1856.3 (839.5)	13.9 (4.3)	1716.5 (417.4)	54.7(19.3)	7518.1 (1629.7)	303.0 (95.7)	7166.7 (1870.5)	364.1 (103.4)	2896.4 (1095.7)	30.3 (9.9)	7357.3 (1029.6)	119.6 (19.8)
Ephemeroptera												
Baetidae	--	--	--	--	43.3 (13.1)	2.4 (1.1)	6.6 (4.1)	0.5 (0.4)	15.3 (14.6)	0.96 (0.96)	1.9 (1.2)	0.3 (0.2)
Caenidae	--	--	--	--	7.5 (6.8)	0.05 (0.04)	--	--	1.2 (1.2)	0.2 (0.2)	1.0 (1.0)	--
Odonata												
Aeshnidae	1.6 (1.6)	182 (181.8)	--	--	0.6 (0.6)	--	2.4 (2.3)	--	0.4 (0.4)	1.6 (1.6)	1.9 (1.2)	1.9 (1.9)
Libellulidae	3.2 (2.1)	40.1 (33.8)	13.4 (11.9)	0.5 (0.3)	19.9 (7.8)	18.1(17.5)	22.7 (20.5)	12.5 (15.5)	17.9 (8.8)	6.2 (4.6)	18.9 (6.4)	20.9 (14.1)
Coenagrionidae	--	--	--	--	44.5 (16.6)	0.9 (0.3)	8 (3.5)	0.3 (0.2)	15 (5.1)	6.0 (1.8)	41.5 (12.2)	22.6 (8.4)
Lestidae	--	--	--	--	--	--	3.2 (3)	0.3 (0.3)	--	--	3.4 (2.4)	0.3 (0.3)
Trichoptera												
Hydroptilidae	--	--	0.7 (0.7)	--	81.4 (45.2)	1.5 (1.0)	24.6 (13.7)	0.4 (0.3)	77.8 (16.9)	1.5 (0.5)	149.3 (32.4)	2.7 (0.9)
Leptoceridae	--	--	--	--	35.1 (21.5)	0.1 (0.05)	--	--	47.9 (21.6)	0.3 (0.08)	62.5 (38.2)	0.2 (0.2)
Nematoda	439.5 (161.9)	7.6 (2.8)	652.9 (305.4)	11.2 (5.4)	400.3 (167.9)	6.26 (2.9)	790.6 (340.3)	13.6 (6.037)	93.8 (64.4)	1.6 (1.121)	530 (157.9)	8.3 (2.4)
Turbellaria	--	--	--	--	0.6 (0.6)	0.2 (0.2)	--	--	1.1 (0.7)	0.05 (0.03)	4.1 (2.7)	0.6 (0.4)
Total	5204.1 (1107.5)	303.4 (181.5)	3095.6 (742.4)	114.5 (35.7)	18300.5 (1535.7)	1357.1 (318.7)	17601.7 (2598.2)	909.7 (118.6)	4493.9 (1350.7)	367.3 (78.8)	10844.8 (1573.2)	559.6 (62.2)

Table 2.2. Results of AIC analysis comparing simple linear regression models describing the relationship between fish response metrics (Growth; mm·day^{-1}, Condition; Fulton's K, Survival; percent recovered) and pond environmental characteristics (Temperature; ºC, Secchi Depth; m, Dissolved Oxygen; mg·L^{-1}, Benthos Biomass; mg·m^{-2}, Structure Biomass; mg·m^{-2}).

Fish Response	Model	AIC_c	ΔAIC_c	Rel Lik	W_i
Growth	Habitat	-11.65	0.00	1.00	0.69
	Habitat + Temperature	-7.89	3.76	0.15	0.1
	Habitat + Dissolved Oxygen	-7.87	3.78	0.15	0.1
	Habitat + Benthic Biomass	-5.71	5.94	0.05	0.04
	Habitat + Structure Biomass	-5.70	5.95	0.05	0.04
	Habitat + Secchi Depth	-5.69	5.97	0.05	0.03
Condition	Habitat	-34.16	0.00	1.00	0.61
	Habitat + Temperature	-31.96	2.20	0.33	0.20
	Habitat + Benthic Biomass	-30.28	3.88	0.14	0.09
	Habitat + Dissolved Oxygen	-28.36	5.80	0.05	0.03
	Habitat + Secchi Depth	-28.25	5.91	0.05	0.03
	Habitat + Structure Biomass	-28.22	5.94	0.05	0.03
Survival	Habitat	-4.34	0.00	1.00	0.61
	Habitat + Dissolved Oxygen	-1.49	2.85	0.24	0.15
	Habitat + Secchi Depth	-0.81	3.54	0.17	0.10
	Habitat + Benthic Biomass	-0.03	4.32	0.12	0.07
	Habitat + Structure Biomass	1.36	5.70	0.06	0.04
	Habitat + Temperature	1.41	5.75	0.06	0.03

CHAPTER 3: THE ROLE OF HABITAT SPATIAL ARRANGEMENT ON PREDATOR-PREY INTERACTIONS AND FOOD-WEB RESPONSES

A. Introduction

Physical habitat and its arrangement in space is an important factor influencing the structure and function of aquatic food webs in lentic habitats (Bell et al. 1991). Physically complex habitats create unique microhabitats and niche spaces and is often positively correlated with population abundance and community diversity of reservoir ecosystems across multiple trophic levels (Crowder and Cooper 1982; Schneider and Winemiller 2008). Mechanisms evoked to explain the importance of physical habitat complexity in aquatic ecosystems include the regulation of predator-prey encounters and behavior among fishes (Walters et al. 1991; DeBoom and Wahl 2013) and increased surface area and surface convolution that provides substrate for colonization and refuge for primary producers (Casartelli and Ferragut 2018) and macroinvertebrates (France 1997).

Despite observational and experimental evidence supporting the importance of physical habitat complexity, the effect of the physical habitat complexity is often context-specific and is dependent on how physical habitat complexity is defined and quantified (Warfe et al. 2008). This ambiguity suggests that physical habitat complexity is itself complex and is influenced by multiple interacting components that operate along multiple spatial and temporal scales. This presents a significant barrier to effective management of physical habitat in aquatic ecosystems, particularly in reservoirs, because of the wide variety of habitat management strategies that exist across political and geographic boundaries (Bassett 1994; Bolding et al. 2004). Recognizing the need for a more comprehensive understanding of habitat complexity, Tokeshi and Arakaki (2012) proposed a framework that included five components that should be considered when investiging physical habitat complexity: 1) scale of habitat complexity, 2) diversity of complexity generating elements, 3) spatial arrangement of elements, 4) sizes of elements, and 5) abundance/density of elements. A majority field and laboratory studies investigating the effect of physical habitat on fishes and invertebrates have focused on manipulating the abundance/density of physical habitat (Crowder and Cooper 1982; Savino and Stein 1982; Bettoli et al. 1992; Diehl 1992; Everett and Ruiz 1993; Sass et al. 2006; Helmus and Sass 2008; Ahrenstorff et al. 2009; DeBoom and Wahl 2013) while other components of physical habitat complexity, such as spatial arrangement of elements, have received far less attention.

As such, there exists a need to understand how the arrangement of physical habitat across the landscape influences long term aquatic community dynamics in reservoirs.

Habitat spatial arrangement has been shown to be important to population persistence and community diversity in terrestrial ecosystems (Bowman et al. 2002; Fahrig 2017) but has received comparatively less attention in aquatic ecosystems. Field and laboratory studies that did investigate habitat spatial arrangement in aquatic ecosystems have primarily focused on the effects interstitial space (Johnson et al. 1988; Walters et al. 1991) and the vertical arrangement/orientation of habitat (Slack et al. 1988; Johnson 1993; Santos et al. 2008). Few studies have attempted to determine the influence of physical habitat spatial arrangement across broader spatial scales; Bryant (1992) observed differences in the use of three different spatial arrangements of brush structures by young-of-year, juvenile, and adult largemouth bass (*M. salmoides*) and smallmouth bass (*M. dolemieu*) in a California reservoir over two years. This study found that a “discrete-open” habitat arrangement was preferred by all life-stages of both fish species during both years, and responses were attributed to differences in food resources and alternative habitats adjacent to brush structures (Bryant 1992). Controlled manipulative experiments designed to evaluate mechanisms linking physical habitat spatial arrangement and reservoir food-web dynamics are noticeably lacking.

Understanding the effect of physical habitat spatial arrangement across broad spatial scales is crucial to developing effective habitat management strategies that meet conservation and management objectives in reservoirs and other aquatic ecosystems. Specifically, effects of physical habitat spatial arrangement could be integrated with knowledge of system-specific aquatic community structure, existing physical habitat quantity and quality, and management objectives to more efficiently allocate limited financial and personnel resources required by management actions.

We conducted a replicated pond experiment designed to evaluate the effect of physical habitat spatial arrangement on predator/prey interactions and food-web processes. Specifically, we manipulated the placement of physical habitat structures to create a "clumped" habitat arrangement, in which habitat structures are grouped together in a cluster, and a "uniform" habitat arrangement, in which habitat structures are dispersed in order to evaluate the effect of habitat spatial arrangement on the production of macroinvertebrates and zooplankton as well as predator-prey dynamics between adult largemouth bass and young-of-year bluegill. We predicted that prey growth and survival and predator growth would differ between habitat spatial arrangements as a result of differences in predator-prey encounter rates and feeding strategies, and that the magnitude of this response would be mediated by the relative differences in the production of macroinvertebrate and zooplankton communities between habitat spatial arrangements.

B. Methods

We conducted a pond experiment using ten rectangular experimental ponds (0.04 ha; 16 x 25 m) at the Sam Parr Biological Station, Illinois Natural History Survey, Kinmundy, IL, USA. Plastic fish attractors (Safe Haven™, Mossback Fish Habitat, Springdale, AR) were used as physical habitat because these structures are easily constructed, and habitat surface area and complexity are virtually identical between individual structures. These structures are made of recycled polyvinyl chloride and consist of a single hollow trunk (height: 1.3 m, diameter: 0.11 m) and 24 textured composite limbs (width: 1.3 m) radiating from the trunk horizontally. Ponds were randomly assigned one of two habitat treatments (n = 5 ponds/treatment). One habitat arrangement consisted of placing six habitat structures in a 2 x 3 array with structures placed 5 m apart in the center of the pond (i.e. Uniform). The second habitat arrangement consisted of placing six habitat structures in the same 2 x 3 array as the Uniform treatment, except habitat structures were placed directly adjacent to each other with no overlap between structures (i.e. Clumped). Thus, only habitat spatial arrangement was manipulated while keeping the amount and complexity of habitat consistent between treatments (Tokeshi and Arakaki 2012).

We selected largemouth bass (*M. salmoides*) and bluegill (*L. machrochirus*) as the predator and prey species, respectively, because both species are popular sportfish and often associate with physical habitat (Johnson et al. 1988). In August 2018, 4000 young-of-year bluegill (mean TL ± SE: 52 ± 0.3 mm) seined from 0.4 ha ponds at the Sam Parr Biological Station were divided equally among ponds (n = 400 Bluegill/pond). Dead bluegill were counted and replaced one day after stocking to account for initial stocking mortality. Thirty adult largemouth bass (mean TL ± SE: 310 ± 6 mm) collected by electrofishing from Stephen A. Forbes reservoir were tagged with FLOY T-bar tags and divided equally among ponds (n = 3 largemouth bass per pond). Mean total length of bluegill ($F_{9,490} = 1.45$; $P = 0.17$) and largemouth bass ($F_{9,20} = 0.61$; $P = 0.78$) did not differ between ponds at the time of introduction.

Temporal sampling of ponds began immediately after fish introduction. Macroinvertebrates were sampled monthly from habitat structures and the benthic zone of each pond. Macroinvertebrates colonizing habitat structures were sampled from one limb of two randomly selected structures in each pond during each of the three sampling events; thus, each habitat structure was sampled exactly once over the course of the experiment. Structure colonizing macroinvertebrates were sampled by sliding a mesh bag (mesh size: 300 μm) over the structure limb, removing the limb, and scraping the limb and the mesh bag with a brush and tap water to dislodge macroinvertebrates, passed through a 250 μm sieve, and preserved in 0.1% Rose Bengal and 90% ethanol for laboratory processing. Concurrently, benthic macroinvertebrates were sampled from three fixed sites within each pond with a stovepipe sampler (diameter: 0.19 m; Turner and Trexler 1997), passed through a 250 μm sieve, and preserved in 0.1% Rose Bengal and 90% ethanol for laboratory processing. Zooplankton communities were sampled bimonthly beginning two weeks after fish stocking with an integrated tube sampler (diameter: 70 mm, length: 0.5 m; DeVries and Stein 1992) from four sites within each pond; two sites were located away from the habitat structures (> 3 m away) and two sites were located directly adjacent to habitat structures (within 10 cm). Zooplankton sampling sites were arranged such that one "away from habitat" and one "adjacent to habitat" site were located on each side of the habitat structures in each pond. Three tube samples were taken consecutively at each site and combined to constitute one sample, passed through a 63 μm sieve, and preserved in Lugol's solution for laboratory processing.

Several abiotic metrics were measured in each pond during each sampling event. Water temperature (ºC) and dissolved oxygen ($mg \cdot L^{-1}$) were measured with a YSI meter. Water clarity was measured with a Secchi disk (m). Percent coverage by submerged aquatic vegetation (% SAV) was estimated visually by standing at end of the walkway found in each pond. We included submerged terrestrial vegetation (e.g. cut-grass), which formed a ring around the wetted area in most of the ponds, in our calculation of percent SAV because this habitat subsidy could have been used as habitat by the fish and invertebrate communities. Aquatic and terrestrial vegetation was periodically thinned with a vegetation rake to keep aquatic and terrestrial vegetation density low relative to the introduced habitat structures. All abiotic metrics were averaged over the entire experiment to derive a single mean value of each abiotic metric for each pond.

Ponds were drained individually beginning in October 2018 into a concrete catch basin where surviving largemouth bass and bluegill were counted, measured (mm) and weighed (g). Unexpectedly, introduced bluegill successfully spawned in nine of the ten ponds. Spawned bluegill were collected in the catch basin and were placed in plastic bags and frozen. The number of spawned bluegill were counted in the laboratory, and a maximum subsample of 200 random individuals were measured (mm) and bulk weighed (g) to estimate the abundance of spawned bluegill in each pond because these bluegill were a potential food resource for the stocked largemouth bass.

In the laboratory, macroinvertebrates samples were split by passing each sample through a 600 μm and a 250 μm sieve. Macroinvertebrates retained by the 600 μm sieve were separated from detritus with forceps and an enamel pan. A dissecting microscope (12x magnification) was used to identify and count all macroinvertebrates in the 600 μm sample. Macroinvertebrates retained by the 250 μm sieve were subsampled (10% subsample), identified, and counted using a dissecting microscope (25x magnification). Only individuals with a head segment were counted. Macroinvertebrate taxa were typically identified to the family level, whereas non-insect taxa (e.g. ostracods, nematodes, leeches) were identified to the class/order level using keys from Merritt and Cummins (1996) and Thorp and Covich (1991). A maximum subsample of 20 individuals per taxonomic group were measured for total length (mm) using a digitizing pad and ImageJ software (Schneider et al. 2012) for both the 600 μm and 250 μm samples. Published length to dry mass regression equations were used to estimate biomass of macroinvertebrates (Eckblad 1971; Meyer 1989; Benke et al. 1999; Baumgärtner and Rothhaupt 2003; Edwards et al. 2009). In instances where only a partial segment of larger individuals was present (e.g. Odonata), head-width was measured to obtain estimates of biomass. Standardized measures of abundance ($\#\cdot m^{-2}$) and biomass ($mg\cdot m^{-2}$) were estimated for each structure and benthic site by summing the biomass estimates for the associated 600 μm and 250 μm samples, correcting for subsample size, and dividing by the area (m^2) sampled. Mean abundance and biomass of macroinvertebrates was then calculated separately for benthic and structure colonizing macroinvertebrate communities for each pond over each sampling event by averaging sample estimates (i.e. 2 Structure samples/pond; 3 Benthic samples/pond).

Zooplankton samples were processed using a FlowCAM®, a semi-automated device used to enumerate and identify particles using an algorithm-derived particle image analysis (see Detmer et al. 2019 for a detailed description of the device configuration and sample processing method). The device is semi-automated because it requires the user to post-process particle images to ensure zooplankton were classified into the correct taxonomic group and converted to corrected lengths (Detmer et al. 2019). Zooplankton lengths were then converted to biomass (μg) using length to dry mass regression equations (Bottrell et al. 1976; Dumont et al. 1975; Pace and Orcutt 1981; Rosen 1981) and were combined with corrected density estimates to estimate zooplankton biomass per sample ($\mu g \cdot L^{-1}$).

We also estimated daily secondary production of macroinvertebrate and zooplankton communities in each pond to evaluate patterns in energy-flow between habitat spatial arrangements. We calculated daily secondary production for three separate invertebrate community groups: benthic colonizing macroinvertebrates (Benthic Production), habitat structure colonizing macroinvertebrates (Structure Production), and Zooplankton (Zooplankton Production) for each pond. Daily secondary production in each pond was estimated using the following equation (Plante and Downing 1989):

$$\log(P) = 0.06 + 0.79\log(B) - 0.16\log(Wm) + 0.05\,T$$

where production (P; $g \cdot m^{-2} \cdot day^{-1}$, $g \cdot L^{-1} \cdot day^{-1}$) is a function of mean population biomass (B; $g \cdot m^{-2}$, $g \cdot L^{-1}$), maximum individual body mass (Wm; mg), and mean water temperature (T; °C). Mean population biomass was estimated for each pond by averaging the mean biomass of invertebrate community groups across all sampling periods. We used the 95th percentile maximum observed length in each invertebrate community group for each pond as our estimate of Wm, in order to remove the effect of large-bodied outliers on our production estimates. Mean water temperature was estimated for each pond by averaging water temperatures across all sampling periods.

Statistical Analysis

A two-factor repeated measures analysis of variance (RM-ANOVA) was used to evaluate patterns in macroinvertebrate and zooplankton community abundance between habitat spatial arrangements through time. Sampling date and habitat spatial arrangement served as fixed effects and individual ponds served as the random effect in each model. Models were fit using taxa-specific abundances of the most abundant taxa within each invertebrate community group as well as for Total Macroinvertebrates and Total Zooplankton. Separate analyses were conducted for Benthic and Structure community macroinvertebrates because each respective macroinvertebrate community was sampled with different gears. If a significant interaction effect was detected, differences between groups were determined using contrasts and Tukey's Honestly Significant Difference test.

Student's t-test was used to evaluate the effect of habitat spatial arrangement on largemouth bass growth (LMB growth; $mm \cdot d^{-1}$), bluegill growth (BG growth; $mm \cdot d^{-1}$), bluegill survival (BG survival; number of bluegill recovered/number of bluegill introduced), structure colonizing macroinvertebrate production (Structure Production; $mg \cdot m^{-2} \cdot day^{-1}$), benthic colonizing Macroinvertebrate Production (Benthic Production; $mg \cdot m^{-2} \cdot day^{-1}$), Zooplankton Production ($ug \cdot L^{-1} \cdot day^{-1}$), and the number of spawned BG collected (Spawned BG).

We used a model selection approach (Akaike's Information Criterion; AIC) to determine whether pond conditions better explain the variation in our fish response metrics. Models were limited to one predictor variable in addition to the grand mean and error terms in order to avoid model overfitting because we had only ten observations to fit a model (i.e. ponds were the experimental unit). Models were ranked based on AIC_c scores corrected for small sample sizes, and model weights were calculated according to Burnham and Anderson (2004). We considered models with $\Delta AICc < 2$ to have equal support (Burnham and Anderson 2004). All analyses were performed in R (v. 3.6.2) using the tidyverse, Rmisc, lme4, emmeans, and AICcmodavg packages (Hope 2013; Bates et al. 2015; Mazerolle 2019; R Core Team 2019; Wickham et al 2019; Lenth 2020).

C. Results

Twenty-seven of the original thirty largemouth bass were recovered at the end of the experiment. All largemouth bass mortalities occurred in different ponds; one mortality occurred in a pond with the clumped habitat arrangement, while two mortalities occurred in two ponds with the uniform habitat arrangement. Largemouth bass grew similarly in ponds with the uniform and clumped habitat arrangements (Figure 3.2; t_8= -1.95, p = 0.09). Bluegill growth was also not different between habitat spatial arrangements (Figure 3.2; t_8= 0.87, P = 0.41). Bluegill survival was highly variable between ponds (range: 8% - 44% recovered) and did not differ between habitat spatial arrangements. (t_8= -0.38, P = 0.72; Figure 3.2). Introduced bluegill successfully spawned in nine of the ten experimental ponds. Spawned bluegill abundance varied between ponds, with observed abundances ranging from as few as 50 in one pond to nearly 5,000 in another. Spawned bluegill abundance did not differ between habitat arrangements (t_8 = -0.23, P = 0.82).

Benthic colonizing macroinvertebrate communities (i.e. Benthic communities) were dominated by nematodes (*Nematoda*), midges (*Ceratopogonidae, Chironomidae*), and ostracods (*Ostracoda*), which comprised 94% of all benthic macroinvertebrates collected. Less abundant but relatively commonly encountered taxa included water scavenger beetles (*Hydrophilidae*), fingernail clams (*Sphaeridae*), and leeches (*Hirudinea*). Structure colonizing macroinvertebrate communities (i.e. Structure communities) were dominated by non-biting midges (*Chironomidae*), ostracods (*Ostracoda*), biting midges (*Ceratopogonidae*), water scavenger beetles (*Hydrophilidae*), and snails (*Physidae*), which comprised 96% of all structure macroinvertebrates collected. Less numerically dominant but still relatively common taxa included leeches (*Hirudinea*), water mites (*Hydracarina*), and long-horned caddisflies

(*Leptoceridae*). Darner dragonflies (*Aeshnidae*), giant water bugs (*Belostomatidae*), crayfish (*Decapoda*), backswimmers (*Notonectidae*, *Pleidae*), and horseflies (*Tabanidae*) were only found colonizing Benthic communities, whereas phantom midges (*Chaoboridae*), hydra (*Cnidaria*), tube-making caddisflies (*Polycentropodidae*), spongeflies (*Sisyridae*), and a single pyralid moth (*Pyralidae*), and soldier fly (*Stratiomyidae*) were only found among Structure communities.

Benthic community abundance changed through time (RM-ANOVA time $F_{2,22} = 4.45$, $P = 0.03$; Figure 3.3). Benthic community abundance generally decreased between week 1 and week 4, followed by an increase in abundance in week 8 of the experiment (Figure 3.3). Overall, changes in total Benthic community abundance through time were similar between habitat spatial arrangements (RM-ANOVA habitat × time $F_{2,22} = 1.67$, $P = 0.21$; Figure 3.3). Taxa-specific patterns in Benthic community abundance through time were also similar between habitat spatial arrangements for *Diptera* larvae (RM-ANOVA habitat × time $F_{2,22} = 0.51$, $P = 0.61$; Figure 3.3), *Ostracoda* (RM-ANOVA habitat × time $F_{2,22} = 0.01$, $P = 0.99$; Figure 3.3), and *Nematoda* (RM-ANOVA habitat × time $F_{2,22} = 1.38$, $P = 0.27$; Figure 3.3). Structure community abundance also differed through time (RM-ANOVA time $F_{2,22} = 35.2$, $P < 0.001$; Figure 3.3) and followed a similar pattern compared to Benthic community abundance, with a decrease in abundance between week 1 and week 4 of the experiment (except in the uniform spatial arrangement), followed by an increase in abundance in week 8 of the experiment (Figure 3.3). Taxa-specific patterns in Structure community abundance through time were also similar between habitat spatial arrangements for *Diptera* larvae (RM-ANOVA habitat × time $F_{2,22} = 0.73$, $P = 0.49$; Figure 3.3) and *Nematoda* (RM-ANOVA habitat × time $F_{2,22} = 0.18$, $P = 0.84$; Figure 3.3). Patterns in abundance of *Ostracoda* differed between habitat spatial arrangements (RM-ANOVA habitat × time $F_{2,22} = 3.96$, $P = 0.03$; Figure 3.3) because the abundance of *Ostracoda* was greater in the clumped spatial arrangement compared to the uniform spatial arrangement only during the week 1 of the experiment (contrast: “Clumped_Structure – Uniform_Structure”, $P < 0.05$; Figure 3.3). Overall, changes in total Structure community abundance through time were similar between habitat spatial arrangements (RM-ANOVA habitat × time $F_{2,22} = 2.74$, $P = 0.09$ Figure 3.3). Daily secondary production of macroinvertebrates did not differ between habitat arrangements among Benthic ($t_8 = -0.08$, $P = 0.94$; Figure 3.5) and Structure ($t_8 = -0.59$, $P = 0.57$; Figure 3.5) macroinvertebrate communities.

Zooplankton communities were dominated by copepod *Nauplii*, *Calanoida*, and *Rotifera* in both habitat arrangements, which together comprised 87% and 90% of all individuals collected in the clumped and uniform spatial arrangements, respectively. Less numerically dominate yet relatively common taxa included *Sididae*, *Ceriodaphnia*, and *Cyclopoida*. Zooplankton abundance changed significantly through time (RM-ANOVA time $F_{3,30} = 24.26$, $P < 0.001$; Figure 3.4) with zooplankton abundance decreasing from $726 \cdot L^{-1}$ and $882 \cdot L^{-1}$ in the 2nd week to $270 \cdot L^{-1}$ and $274 \cdot L^{-1}$ in the 4th week for the clumped and uniform habitat arrangements, respectively (Figure 3.4). After the 4th week, zooplankton abundance remained relatively stable at around $200 \cdot L^{-1}$ in both habitat arrangements for the remainder of the experiment (Tukey’s HSD, $P > 0.05$; Figure 3.4). Patterns in total zooplankton community abundance through time were similar between our habitat arrangements (RM-ANOVA habitat × time $F_{3,30} = 2.46$, $P = 0.08$; Figure 3.4). Taxa-specific abundances were also similar between habitat spatial arrangements through time for copepod *Nauplii* (RM-ANOVA habitat × time $F_{3,30} = 1.37$, $P = 0.27$; Figure 3.4), and *Calanoida* (RM-ANOVA habitat × time $F_{3,30} = 0.34$, $P = 0.80$; Figure 3.4), which generally decreased in abundance through time. *Rotifera* was the only zooplankton taxa that was more abundant in ponds with the clumped spatial arrangement (RM-ANOVA habitat $F_{1,30} = 8.39$, $P < 0.01$; Figure 3.4), and unlike all other zooplankton taxa, generally increased in abundance through time (Figure 3.4). Moreover, patterns in *Rotifera* abundance through time differed between habitat spatial arrangements (RM-ANOVA habitat × time $F_{3,30} = 7.95$, $P < 0.01$; Figure 3.4) as a result of *Rotifera* being more abundant in the clumped spatial arrangement compared to the uniform spatial arrangement during the 6th week of the experiment (contrast: "Clumped_6th – Uniform_6th", $P < 0.05$; Figure 3.4). Zooplankton production was marginally greater in ponds with the clumped habitat spatial arrangement compared to ponds with the uniform spatial arrangement ($t_8 = 2.25$, $P = 0.06$; Figure 3.5).

The AIC analysis showed that pond environmental conditions as well as invertebrate production and spawned bluegill abundance were not able to account for the variation in our fish response metrics relative to habitat spatial arrangement. A model that included habitat spatial arrangement showed greater support than any other predictor variable for LMB growth and BG growth, but not for BG survival (Table 3.1). Moreover, habitat spatial arrangement showed the greatest support compared to any other model for LMB growth ($\Delta AICc > 2$; Table 3.1), while all other models showed equal support compared to habitat spatial arrangement for BG growth $\Delta AICc < 2$; Table 3.1). The best supported model for BG survival included Dissolved Oxygen; however, all other models showed comparable support ($\Delta AICc < 2$; Table 3.1).

D. Discussion

We provide the first manipulative experiment designed to determine the effect of physical habitat spatial arrangement on aquatic food-webs, independent of physical habitat amount or density. We show that habitat spatial arrangement had little effect on food web processes within our ponds. Bluegill grew at similar rates in both habitat arrangements, although mean bluegill growth was slightly faster in the clumped habitat arrangement compared to the uniform habitat arrangement. Differences in bluegill growth between individual ponds were driven by variability in bluegill survival. Bluegill growth is often negatively related to bluegill density because higher densities increases the frequency of interaction with conspecifics and competition for limited food resources (Olson et al. 2003). Our results support this observation, as bluegill growth was strongly related to bluegill survival within individual ponds during our experiment.

Largemouth bass growth was similar in the uniform habitat arrangement compared to the clumped habitat arrangement. Several explanations exist to explain the variation in largemouth bass growth between ponds. Variation in largemouth bass growth could be attributed to differences in survival between treatments (i.e. density-dependent growth). However, largemouth bass survival differed between treatments because of a single individual, and the loss of this individual is unlikely to explain the observed variation in largemouth bass growth. Moreover, the mean growth rate of largemouth bass in the two ponds with the uniform habitat arrangement that experienced mortalities was less (0.33 $mm \cdot day^{-1}$) than overall mean largemouth growth among the three ponds with the uniform habitat arrangement that experienced no mortalities (0.38 $mm \cdot day^{-1}$), which does not support the idea of density-dependent growth of largemouth bass. An alternative explanation is that variation in largemouth bass growth was more related to variation in pond environmental conditions as well as invertebrate production and spawned bluegill abundance. Our multiple linear regression analysis supports this explanation, as bluegill growth was negatively correlated with largemouth bass growth and was the best predictor of largemouth bass growth compared to any other predictor variable. It is not intuitively obvious why this was the case but considering the strong density-dependent growth of stocked bluegill in our experiment, largemouth bass growth may have been more directly related to stocked bluegill survival. However, we did not detect a significant relationship between bluegill survival and largemouth bass growth. The lack of evidence for a relationship appears to be driven by a single pond that experienced relatively high bluegill survival and slow largemouth growth. The largemouth bass introduced in this pond were larger at the time of introduction (mean TL: 336 mm) and at the time of recovery (mean TL: 362 mm) than any other pond, which may explain the slow relative growth of largemouth bass in this pond because largemouth bass growth rate is size-dependent (citation). Removal of this pond from the analysis yields a significant positive correlation between bluegill survival and largemouth bass growth, and considering the high initial mortality of stocked bluegill in both habitat arrangements, growth of largemouth bass may be best explained by the abundance of available forage of stocked bluegill after initial stocking mortality.

Patterns in total macroinvertebrate abundance through time was similar between habitat spatial arrangements. Changes in macroinvertebrate abundance through time appear to be driven by increasing abundance of *Diptera* larvae and decreasing abundance of *Ostracoda* in both the Benthic and Structure macroinvertebrate communities. Abundance of *Nematoda* remained similar though time in both macroinvertebrate community types and between spatial arrangements. Similarly, changes in total zooplankton abundance through time was similar between habitat spatial arrangements. Except for *Rotifera*, all zooplankton taxa experienced steady and sustained reductions in abundance for both habitat spatial arrangements. Reductions in zooplankton abundance were likely driven by predation by bluegill (Mittelbach 1981; Detmer and Wahl 2019), which may explain the observed increases in *Rotifera* abundance for both habitat spatial arrangements because of reduced predation pressure by carnivorous zooplankton (Thorp and Covich 1991). Despite localized differences among certain invertebrate taxa, macroinvertebrate and zooplankton production were similar between habitat types, which may in part explain why bluegill growth and survival were similar between habitat arrangements, because zooplankton and macroinvertebrates are crucial food resources for bluegill (Olson et al. 2003). Despite the importance of macroinvertebrates and zooplankton to bluegill diets, we did not find strong evidence that bluegill were influenced by macroinvertebrate or zooplankton production. Bluegill density by the end of the experiment was low compared to similar experiments in ponds (Shoup et al. 2012) and thus may have been unable to exploit macroinvertebrate and zooplankton food resources at detectable rates.

With the exceptions of relationships among our fish response metrics (i.e. largemouth bass growth, bluegill growth, bluegill survival), we did not find that pond environmental conditions, invertebrate production, and spawned bluegill abundance were able to account for variation in fish response metrics compared to habitat spatial arrangement. One possible explanation is that these predictors were unrelated to our fish response metrics. However, other studies have documented changes in fish growth, behavior, or survival as a function of vegetation density (Savino and Stein 1982), temperature (Strawn 1961), and water clarity (Hoxmeier, Aday, and Wahl 2009). The observed range of some of our abiotic predictor variables, including temperature and dissolved oxygen, was small and did not differ between ponds (one-way ANOVA, $p > 0.05$), making it difficult to detect relationships through linear regression analysis. The observed range in water clarity and vegetation density was sufficiently large to detect differences between ponds (one-way ANOVA, $p < 0.05$), yet neither of these predictor variables explained a significant proportion of variation in our fish response metrics. Our attempts to control aquatic vegetation growth with a vegetation rake likely mitigated its influence on our habitat arrangements.

An observational study of fish use of physical habitat showed differences in the number of largemouth bass of all age classes congregating around submerged trees arranged in three different designs (Bryant 1992). Thus, our habitat arrangements could influence year-to-year reproductive output and recruitment of largemouth bass and bluegill. Because stocked bluegill successfully spawned in nine ponds, our study could shed light on the relative potential of our habitat arrangements to influence reproduction of bluegill. We did not find a difference in spawned bluegill abundance between our habitat arrangements, and therefore bluegill reproduction may be unrelated to our physical habitat arrangements. However, we did not expect nor account for the possibility of our stocked bluegill to spawn, and more rigorous testing of hypotheses related to habitat spatial arrangement and reproductive potential of fishes would be valuable.

Management Implications

Independent of physical habitat amount, we did not find that habitat spatial arrangement any detectable food-web effects in our experimental ponds. Thus, general responses of aquatic communities to physical habitat introductions and management may be more related to the absolute abundance/density of physical habitat (Bettoli et al. 1992; Schindler et al. 2000; Sass et al. 2006; Ahrenstorff et al. 2009) than by how that physical habitat is arranged across the landscape. In systems where physical habitat management is a primary objective, we recommend that managers determine “how much” physical habitat is needed as opposed to “where” the physical habitat is located in space. Before any action is taken, managers should have an idea of how much available physical habitat is present (e.g. aquatic macrophyte density), or first quantify the amount of available physical habitat through habitat surveys, because responses to physical habitat management is influenced by the amount of physical habitat already present (Bryant 1992;

Wills et al. 2004). This would allow managers to more effectively allocate limited financial and personnel resources to systems where physical habitat management has been identified *a priori* as most likely to have the greatest effect (Bolding et al. 2004; Everett and Ruiz 1993). Furthermore, this could reduce the probability of adding too much physical habitat, which would not only represent a waste of limited resources, but potentially be counterproductive (Savino and Stein 1982; Gotceitas and Colgan 1989).

E. Figures and Table

Figure 3.1. Photographs of the two habitat spatial arrangements. The top panel (A) is a pond with a uniform habitat spatial arrangement with structures placed apart. The bottom panel (B) is a pond with a clumped habitat spatial arrangement with structures placed adjacent to each other without overlap.

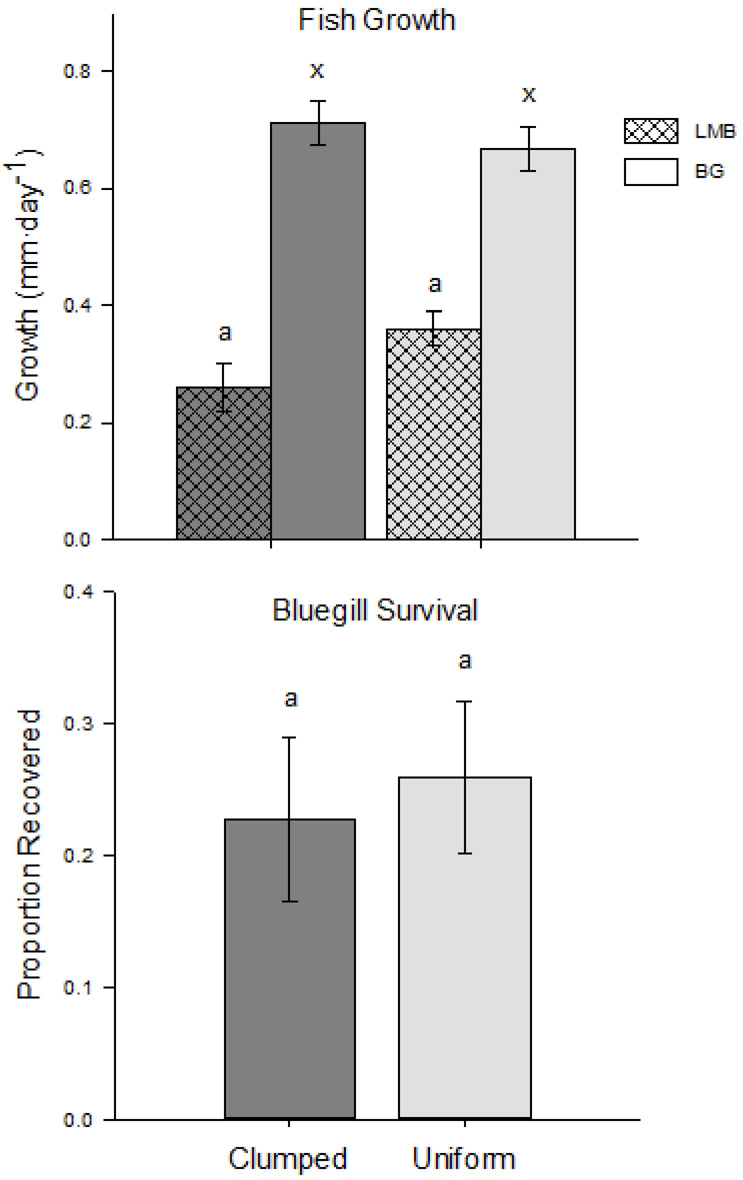

Figure 3.2. Mean (± SE) growth of stocked fishes (top panel) and mean (± SE) survival of stocked bluegill (bottom panel) between habitat spatial arrangements. LMB, Largemouth bass (textured bars); BG, Bluegill (solid bars). Bars with the same letter are not significantly different ($\alpha = 0.05$).

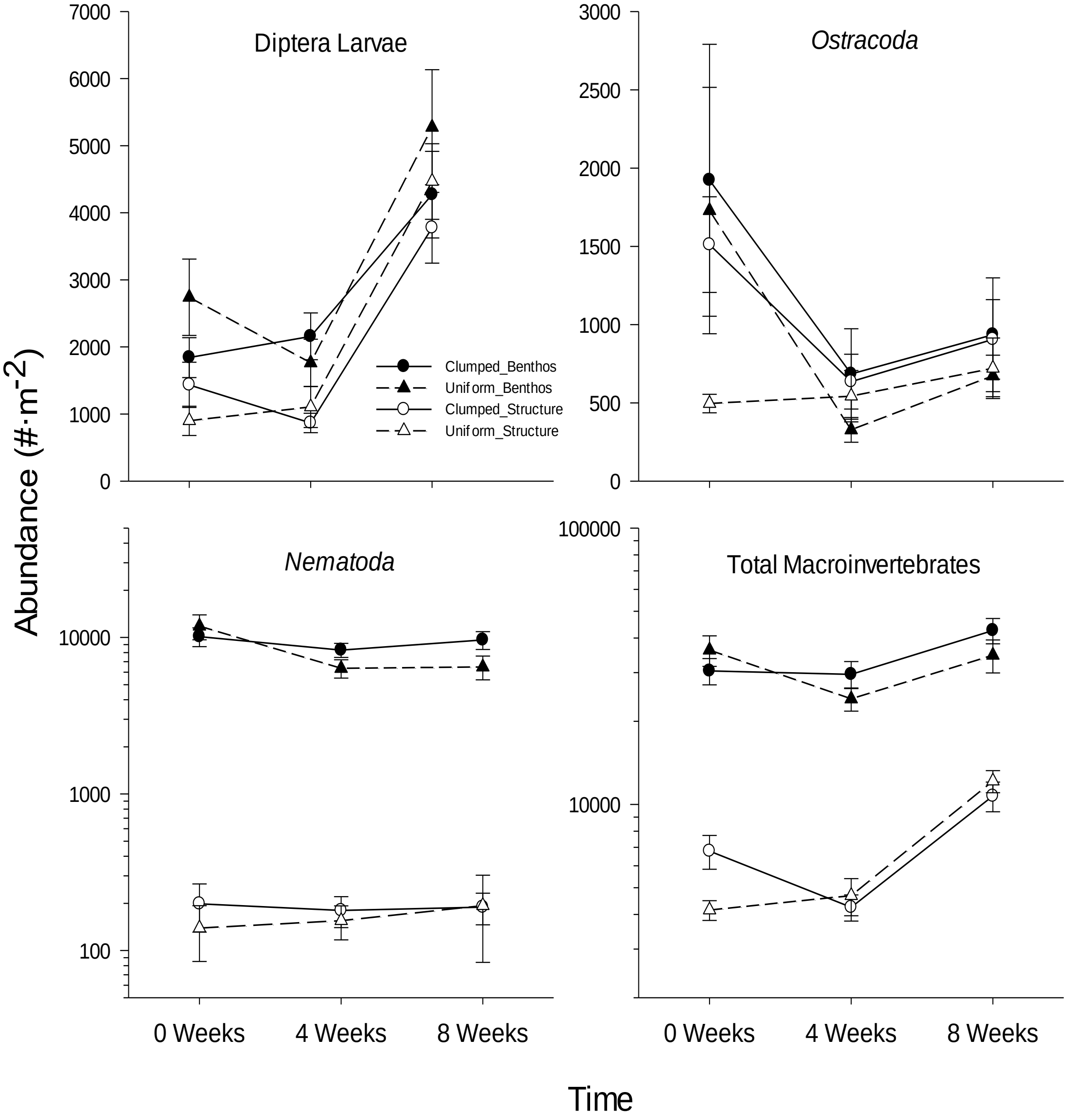

Figure 3.3. Mean (± SE) taxa abundance of *Diptera* larvae (*Chironomidae* + *Ceratopogonidae*), *Ostracoda*, *Nematoda*, and Total Macroinvertebrates. Mean taxa abundance is partitioned between individuals colonizing the pond benthos in the clumped spatial arrangement (solid circles, solid line) and the uniform spatial arrangement (solid triangles, dashed line) and individuals colonizing habitat structures in the clumped spatial arrangement (open circles, solid line) and the uniform spatial arrangement (open triangles, dashed line) through time. Note that y-axes are on a $\log_{10}$ scale for *Nematoda* and Total Macroinvertebrates.

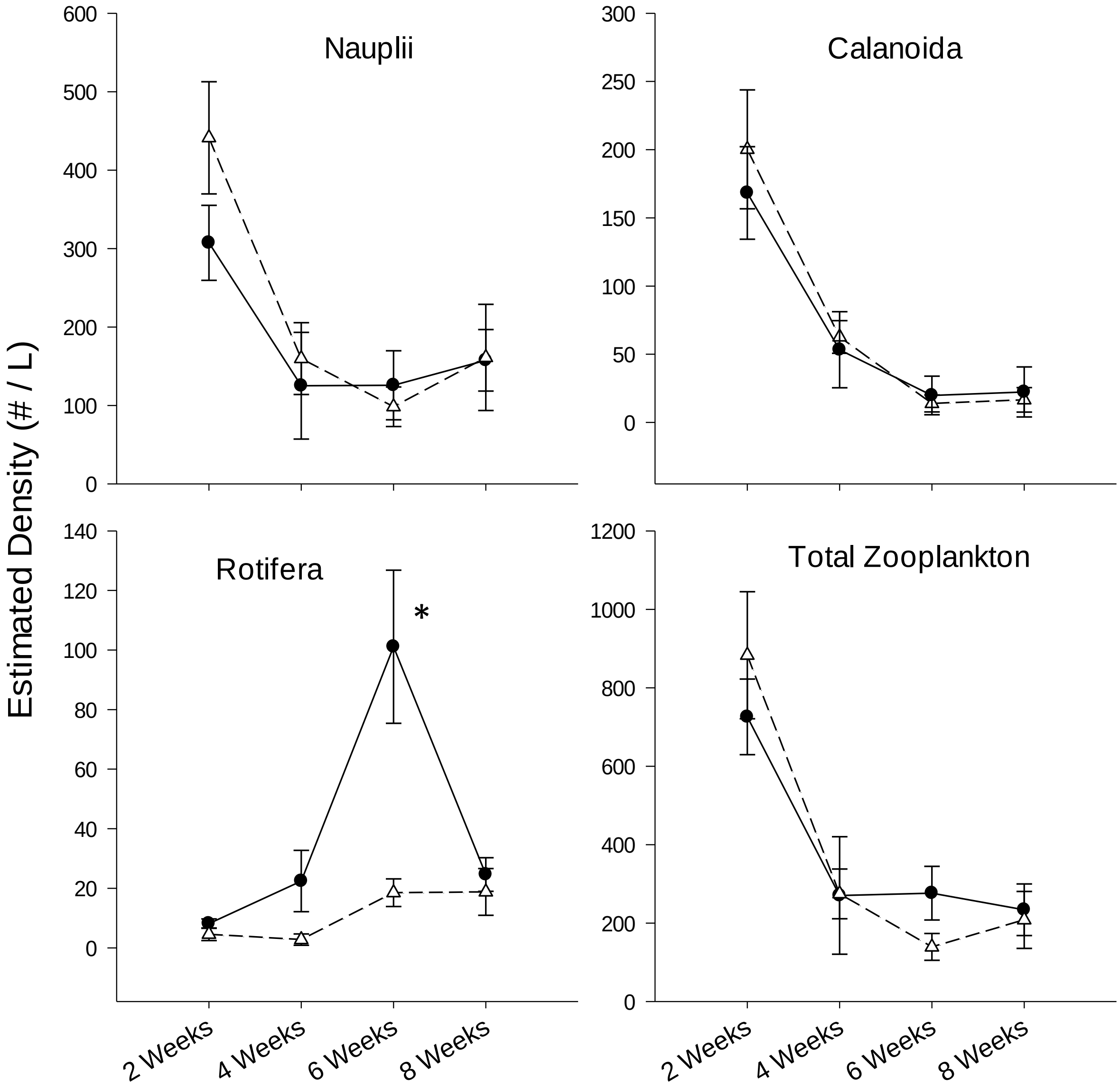

Figure 3.4. Mean (± SE) density of copepod nauplii, *Calanoida*, *Rotifera*, and Total Zooplankton in ponds with the clumped habitat spatial arrangement (black circles, solid line) and the uniform habitat spatial arrangement (open triangles, dotted line) through time. Zooplankton were not sampled at the time of introduction. Asterisks indicated significant differences between habitat spatial arrangements (α = 0.05).

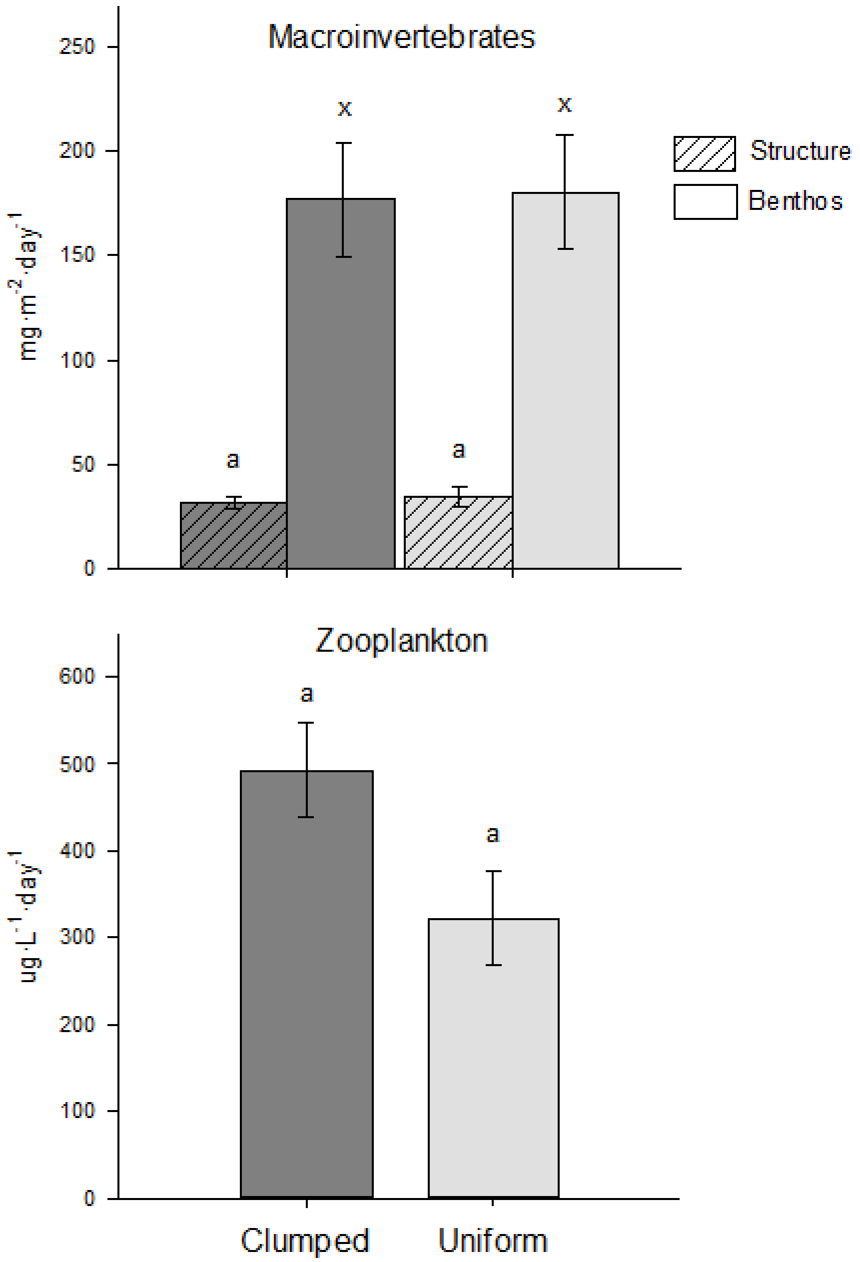

Figure 3.5. Mean production (± SE) of macroinvertebrates (top panel) and zooplankton (bottom panel) between habitat spatial arrangements. Macroinvertebrate production was separated between production of macroinvertebrates colonizing physical structures (textured bars) and benthic habitats (solid bars) within each habitat spatial arrangement. Bars with the same letter are not significantly different ($\alpha = 0.05$).

Table 3.1. Results of AIC analysis comparing simple linear regression models describing the relationship between fish response metrics (LMB Growth; mm·day^{-1}, BG Growth; mm·day^{-1}, BG Survival; percent recovered) and pond environmental characteristics (Habitat Spatial Arrangement, Temperature; ºC, Secchi Depth; m, Dissolved Oxygen; mg·L^{-1}, Vegetation Density; % SAV, Benthic Production; mg·m^{-2}·day^{-1}, Structure Production; mg·m^{-2}·day^{-1}, and Zooplankton Production; ug·L^{-1}·day^{-1}. Only the top five most supported models are included for each fish response metric.

Fish Response	Model	AIC_c	ΔAIC_c	Rel Lik	W_i
LMB Growth	Habitat	-14.06	0.00	1.00	0.41
	Secchi Depth	-11.55	2.51	0.29	0.12
	Temperature	-10.82	3.24	0.20	0.08
	Spawned BG	-10.79	3.27	0.19	0.08
	Zooplankton Production	-10.49	3.57	0.17	0.07
BG Growth	Habitat	-14.38	0.00	1.00	0.15
	Dissolved Oxygen	-14.28	0.10	0.95	0.14
	Spawned BG	-13.95	0.42	0.81	0.12
	Temperature	-13.89	0.49	0.78	0.11
	Benthic Production	-13.65	0.73	0.70	0.10
BG Survival	Dissolved Oxygen	-4.80	0.00	1.00	0.15
	Benthic Production	-4.63	0.17	0.92	0.14
	Spawned BG	-4.55	0.25	0.88	0.13
	Temperature	-4.19	0.62	0.73	0.11
	Structure Production	-3.98	0.83	0.66	0.10

CHAPTER 4: SUMMARY AND CONCLUSIONS

The modification and disturbance of natural habitats resulting from anthropogenic activities has been identified, and will continue to be, a primary threat to biodiversity and ecosystem integrity worldwide. Reservoir ecosystems, although characterized as highly modified ecosystems themselves, are subject to the same ecological mechanisms that regulate the distribution and abundance of aquatic organisms across broad spatial and temporal scales. Furthermore, reservoirs and impoundments are important sources of recreation that generate billions of dollars annually. As such, reservoirs represent a nexus between the natural environment and human activity, and therefore are important laboratories for the development of multiple-use management strategies that simultaneously meet the needs of society and mitigate the negative effects of anthropogenic disturbance on ecosystem integrity.

Reservoir ecosystems experience declining habitat quality and quantity as a result of several passive and active mechanisms over time, which negatively affect reservoir ecosystems leading to declining ecosystem services provided by these ecosystems. The introduction of new sources of physical habitat is a popular management strategy in the United States in order to mitigate the loss and degradation of physical habitat in reservoirs; however, several barriers exist that preclude the development of effective multiple-use physical habitat management strategies. The objectives of my thesis research were to identify and test hypotheses linking the direct effect of (1) habitat material type and (2) spatial distribution of physical habitat independent on habitat amount on food-web interactions and the growth and survival of largemouth bass (*M. salmoides*) and bluegill (*L. machrochirus*), which are two popular sportfishes in the United States that require physical habitat to complete their life histories. My research hypotheses were tested using a series of replicated pond experiments in order to control the effect of extraneous variables on my research hypotheses, while retaining some comparability between larger reservoir ecosystems.

In my first chapter, I used plastic fish attractors (Artificial) and natural coarse woody habitat (CWH) structures to identify the influence of habitat material type on macroinvertebrate community colonization through time, and to determine the influence of habitat material type on the growth, condition, and survival of juvenile largemouth bass. I predicted that macroinvertebrate community abundance and diversity would be greater on CWH structures compared to Artificial structures and that the growth, condition, and survival of largemouth bass would be greater in ponds with CWH structures as a result of relative differences in food resource quality and quantity provided by my habitat structures. I show in my first chapter that macroinvertebrate community abundance and composition through time was similar between the two habitat types, and that largemouth bass growth, condition, and survival were unrelated to physical habitat material type.

In my second chapter, I manipulated the distribution of plastic fish attractors into “clumped” and “uniform” arrangements to determine the effect of habitat spatial arrangement, independent of habitat amount, on (1) predator-prey interactions in a largemouth bass and bluegill fish assemblage and (2) the abundance and production of three different invertebrate communities. I also attempted to determine links between invertebrate community production and pond conditions on my fish response metrics. My results show that the growth of largemouth bass and bluegill, as well as the survival of bluegill prey, were not influenced by habitat spatial arrangement. I also show that habitat spatial arrangement did not influence the production of invertebrate communities in the experimental ponds, and environmental conditions were unrelated to my fish response metrics.

My two research experiments demonstrate that independent of habitat amount, habitat material type and habitat spatial arrangement had little effect on pond communities and trophic interactions. My results suggests that other factors, such as the absolute abundance of physical habitat, or the availability of alternative sources of physical habitat, may be more important to aquatic communities and fish growth than from what material the habitat is composed of, or how the habitat is spatially distributed. Fisheries managers and stakeholders in charge of physical habitat introduction should have some idea of the amount of physical habitat already present via habitat surveys, I recommend that managers identify specific reservoir ecosystems where physical habitat may be limiting. If habitat material type and spatial arrangement are unrelated to aquatic ecosystem dynamics, other factors such as the financial cost or relative differences in temporal longevity of different physical habitat types may be more relevant to fisheries management agencies tasked with producing the greatest effect at the least financial cost.

REFERENCES

Ahrenstorff, T. D., G. G. Sass, and M. R. Helmus. 2009. The Influence of Littoral Zone Coarse Woody Habitat on Home Range Size, Spatial Distribution, and Feeding Ecology of Largemouth Bass (Micropterus Salmoides). Hydrobiologia 623(1):223–33.

Anderson, M. J. 2001. “A New Method for Non-Parametric Multivariate Analysis of Variance.” *Austral Ecology* 26(1):32–46.

Anderson, O. 1984. “Optimal Foraging by Largemouth Bass in Structured Environments.” *Ecology* 65(3):851–61.

Angermeier, P. L., and J. R. Karr. 1984. “Relationships between Woody Debris and Fish Habitat in a Small Warmwater Stream.” *Transactions of the American Fisheries Society* 113:716–26.

Arlinghaus, R., K. Lorenzen, B. M. Johnson, S. J. Cooke, and I. G. Cowx. 2016. “Management of Freshwater Fisheries: Addressing Habitat, People and Fishes.” *Freshwater Fisheries Ecology* 557–79.

Bassett, C. E. 1994. “Use and Evaluation of Fish Habitat Strcutres in Lakes of the Eastern United States.” *Bulletin of Marine Science* 55:1137–48.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. “Fitting Linear Mixed-Effects Models Using Lme4.” *Journal of Statistical Software* 67(1):1–48.

Baumann, J. R., N. C. Oakley, and B. J. McRae. 2016. “Evaluating the Effectiveness of Artificial Fish Habitat Designs in Turbid Reservoirs Using Sonar Imagery.” *North American Journal of Fisheries Management* 36(6):1437–44.

Baumgärtner, D., and K. Rothhaupt. 2003. “Predictive Length–Dry Mass Regressions for Freshwater Invertebrates in a Pre-Alpine Lake Littoral.” *International Review of Hydrobiology* 88(5):453–63.

Bell, S. S., E. D. McCoy, and H. R. Mushinsky, eds. 1991. *Habitat Structure: The Physical Arrangement of Objects in Space*. Dordrecht: Springer Netherlands.

Benke, A. C., A.D. Huryn, L. A. Smock, and J. B. Wallace. 1999. “Length-Mass Relationships for Freshwater Macroinvertebrates in North America with Particular Reference to the Southeastern United States.” *Journal of the North American Benthological Society* 18(3):308–43.

Bernhardt, E. S., M. A. Palmer, J. D. Allan, G. Alexander, K. Barnas, S. Brooks, J. Carr, S. Clayton, C. Dahm, J. Follstad-Shah, D. Galat, S. Gloss, P. Goodwin, D. Hart, B. Hassett, R. Jenkinson, S. Katz, G. M. Kondolf, P. S. Lake, R. Lave, J. L. Meyer, T. K. O’Donnell, L. Pagano, B. Powell, and E. Sudduth. 2005. “Synthesizing U.S. River Restoration Efforts.” *Science* 308(5722):636–37.

Bettoli, P. W., M. J. Maceina, R. L. Noble, and R. K. Betsill. 1992. “Piscivory in Largemouth Bass as a Function of Aquatic Vegetation Abundance.” *North American Journal of Fisheries Management* 12:509–16.

Bolding, B., S. Bonar, and M. Divens. 2004. “Use of Artificial Structure to Enhance Angler Benefits in Lakes, Ponds, and Reservoirs: A Literature Review.” *Reviews in Fisheries Science* 12(1):75–96.

Bottrell, H., A. Duncan, M. Gliwicz, E. Grygierek, A. Herzig, A. Hillbricht-Ilkowska, H. Kurasawa, P. Larsson, and T. Weglenska. 1976. “A Review of Some Problems in Zooplankton Production Studies.” *Norwegian Journal of Zoology* 24:419–56.

Bowen, K. L., N. K. Kaushik, and A. M. Gordon. 1998. “Macroinvertebrate Communities and Biofilm Chlorophyll on Woody Debris in Two Canadian Oligotrophic Lakes.” *Archiv Fur Hydrobiologie* 141:257–81.

Bowman, J., N. Cappuccino, and L. Fahrig. 2002. “Patch Size and Population Density: The Effect of Immigration Behavior.” *Conservation Ecology* 6(1).

Bryant, G. J. 1992. “Direct Observations of Largemouth and Smallmouth Bass in Response to Various Brush Structure Designs in Ruth Reservoir, California.” *Fish Habitat Relationship Technical Bulletin No. 10. USDA Forest Service, Pacific Southwest Region*.

Burnham, K. P., and D. R. Anderson. 2004. “Multimodel Inference: Understanding AIC and BIC in Model Selection.” *Sociological Methods & Research* 33(2):261–304.

Casartelli, M. R., and C. Ferragut. 2018. “The Effects of Habitat Complexity on Periphyton Biomass Accumulation and Taxonomic Structure during Colonization.” *Hydrobiologia* 807(1):233–46.

Christensen, D. L., B. R. Herwig, D. E. Schindler, and S. R. Carpenter. 1996. “Impacts of Lakeshore Residential Development on Coarse Woody Debris in North Temperate Lakes.” *Ecological Applications* 6(4):1143–49.

Claflin, T. O. 1968. “Reservoir Aufwuchs on Inundated Trees.” *Transactions of the American Microscopical Society* 87(1):97.

Clarke, K. R. 1993. “Non-Parametric Multivariate Analyses of Changes in Community Structure.” *Australian Journal of Ecology* 18(1):117–43.

Crowder, L. B., and W. E. Cooper. 1982. “Habitat Structural Complexity and the Interaction Between Bluegills and Their Prey.” *Ecology* 63(6):1802.

Czarnecka, M. 2016. “Coarse Woody Debris in Temperate Littoral Zones: Implications for Biodiversity, Food Webs and Lake Management.” *Hydrobiologia* 767(1):13–25.

DeBoom, C. S., and D. H. Wahl. 2013. “Effects of Coarse Woody Habitat Complexity on Predator–Prey Interactions of Four Freshwater Fish Species.” *Transactions of the American Fisheries Society* 142(6):1602–14.

Detmer, T. M., K. J. Broadway, C. G. Potter, S. F. Collins, J. J. Parkos, and D. H. Wahl. 2019. “Comparison of Microscopy to a Semi-Automated Method (FlowCAM®) for Characterization of Individual-, Population-, and Community-Level Measurements of Zooplankton.” *Hydrobiologia* 838(1):99–110.

Detmer, T. M., and D. H. Wahl. 2019. “Trophic Cascade Strength Is Influenced by Size Frequency Distribution of Primary Consumers and Size-Selective Predation: Examined with Mesocosms and Modeling.” *Aquatic Sciences* 81(3).

DeVries, D. R., and R. A. Stein. 1992. “Complex Interactions between Fish and Zooplankton: Quantifying the Role of an Open-Water Planktivore.” *Canadian Journal of Fisheries and Aquatic Sciences* 49(6):1216–27.

Dibble, E. D., and S. L. Harrel. 1997. “Largemouth Bass Diets in Two Aquatic Plant Communities.” *J. Aquat. Plant Manage.* 35:74–78.

Dibble, E. D., K. J. Killgore, and G. O. Dick. 1996. “Measurement of Plant Architecture in Seven Aquatic Plants.” *Journal of Freshwater Ecology* 11(3):311–18.

Diehl, S. 1992. “Fish Predation and Benthic Community Structure: The Role of Omnivory and Habitat Complexity.” *Ecology* 73(5):1646–61.

Dudley, T. L., and N. H. Anderson. 1982. “A survey of invertebrates associated with wood debris in aquatic habitats.” *Melanderia* 39:1-21.

Dudley, T. L., and C. M. D'Antonio. 1991. "The Effects of Substrate Texture, Grazing, and Disturbance on Macroalgal Establishment in Streams." *Ecology* 72(1):297–309.

Dumont, H. J., I. Van de Velde, and S. Dumont. 1975. "The Dry Weight Estimate of Biomass in a Selection of Cladocera, Copepoda and Rotifera from the Plankton, Periphyton and Benthos of Continental Waters." *Oecologia* 19(1):75–97.

Eckblad, J. W. 1971. "Weight-Length Regression Models for Three Aquatic Gastropod Populations." *American Midland Naturalist* 85(1):271.

Edwards, F. K., R. B. Lauridsen, L. Armand, H. M. Vincent, and I. J. Jones. 2009. "The Relationship between Length, Mass and Preservation Time for Three Species of Freshwater Leeches (Hirudinea)." *Fundamental and Applied Limnology / Archiv Für Hydrobiologie* 173(4):321–27.

Everett, R. A., and G. M. Ruiz. 1993. "Coarse Woody Debris as a Refuge from Predation in Aquatic Communities: An Experimental Test." *Oecologia* 93(4):475–86.

Fahrig, L. 2017. "Ecological Responses to Habitat Fragmentation Per Se." *Annual Review of Ecology, Evolution, and Systematics* 48(1):1–23.

FAO. 2009. "The state of world fisheries and aquaculture 2008." Rome, Italy: United Nations FAO Fisheries and Aquaculture Department.

France, R. L. 1997. "Macroinvertebrate Colonization of Woody Debris in Canadian Shield Lakes Following Riparian Clearcutting." *Conservation Biology* 11(2):513–21.

Gotceitas, V., and P. Colgan. 1989. "Predator Foraging Success and Habitat Complexity: Quantitative Test of the Threshold Hypothesis." *Oecologia* 80(2):158–66.

Gotelli, N. J., and R. K. Colwell. 2001. "Quantifying Biodiversity: Procedures and Pitfalls in the Measurement and Comparison of Species Richness." *Ecology Letters* 4(4):379–91.

Guyette, R. P., and W. G. Cole. 1999. “Age Characteristics of Coarse Woody Debris (Pinus Strobus) in a Lake Littoral Zone.” *Canadian Journal of Fisheries and Aquatic Sciences* 56:12.

Harmon, M. E., J. F. Franklin, F. J. Swanson, P. Sollins, S. V. Gregory, J. D. Lattin, N. H. Anderson, S. P. Cline, N. G. Aumen, J. R. Sedell, G. W. Lienkaemper, K. Cromack, and K. W. Cummins. 1986. “Ecology of Coarse Woody Debris in Temperate Ecosystems.” Pp. 133–302 in *Advances in Ecological Research*. Vol. 15. Elsevier.

Hax, C. L., and S. W. Golladay. 1993. “Macroinvertebrate Colonization and Biofilm Development on Leaves and Wood in a Boreal River.” *Freshwater Biology* 29(1):79–87.

Helmus, M. R., and G. G. Sass. 2008. “The Rapid Effects of a Whole-Lake Reduction of Coarse Woody Debris on Fish and Benthic Macroinvertebrates.” *Freshwater Biology* 53(7):1423–33.

Hesterberg, S. G., C. C. Duckett, E. A. Salewski, and S. S. Bell. 2017. “Three-Dimensional Interstitial Space Mediates Predator Foraging Success in Different Spatial Arrangements.” *Ecology* 98(4):1153–62.

Hope, R. M. 2013. “Rmisc: Rmisc: Ryan Miscellaneous.” R package version 1.5. https://CRAN.R-project.org/package=Rmisc.

Howmiller, R. P. 1972. “Effects of Preservatives on Weights of Some Common Macrobenthic Invertebrates.” *Transactions of the American Fisheries Society* 101(4):743–46.

Hoxmeier, J. H., D. D. Aday, and D. H. Wahl. 2009. “Examining Interpopulation Variation in Bluegill Growth Rates and Size Structure: Effects of Harvest, Maturation, and Environmental Variables.” *Transactions of the American Fisheries Society* 138(2):423–32.

Hurlbert, S. H. 1971. “The Nonconcept of Species Diversity: A Critique and Alternative Parameters.” *Ecology* 52(4):577–86.

Jeffries, M. 1993. “Invertebrate Colonization of Artificial Pondweeds of Differing Fractal Dimension.” *Oikos* 67(1):142.

Jessen, R. J. 1955. “Determining the Fruit Count on a Tree by Randomized Branch Sampling.” *Biometrics* 11(1):99.

Johnson, D. L., R. A. Beaumier, and W. E. Lynch. 1988. “Selection of Habitat Structure Interstice Size by Bluegills and Largemouth Bass in Ponds.” *Transactions of the American Fisheries Society* 117(2):171–79.

Johnson, S. L. 1993. “Cover Choice by Bluegills: Orientation of Underwater Structure and Light Intensity.” *Transactions of the American Fisheries Society* 122(1):148–54.

Keast, A., and J. M. Eadie. 1985. “Growth Depensation in Year-0 Largemouth Bass :” *Transactions of the American Fisheries Society* 114(2):204–13.

Kovalenko, K. E., S. M. Thomaz, and D. M. Warfe. 2012. “Habitat Complexity: Approaches and Future Directions.” *Hydrobiologia* 685(1):1–17.

Lenth, R. 2020. “emmeans: Estimated Marginal Means, aka Least-Squares Means.” R package version 1.4.5. https://CRAN.R-project.org/package=emmeans.

Lewin, W., N. Okun, and T. Mehner. 2004. “Determinants of the Distribution of Juvenile Fish in the Littoral Area of a Shallow Lake.” *Freshwater Biology* 49(4):410–24.

Lodge, D. M., R. A. Stein, K. M. Brown, A. P. Covich, C. Brönmark, J. E. Garvey, and S. P. Klosiewskt. 1998. “Predicting Impact of Freshwater Exotic Species on Native Biodiversity: Challenges in Spatial Scaling.” *Australian Journal of Ecology* 23(1):53–67.

Ludsin, S. A., and D. R. DeVries. 1997. “First-Year Recruitment of Largemouth Bass: The Interdependency of Early Life Stages.” *Ecological Applications* 7(3):1024–38.

Maceina, M. J., and J. J. Isely. 1986. “Factors Affecting Growth of an Initial Largemouth Bass Year Class in a New Texas Reservoir.” *Journal of Freshwater Ecology* 3(4):485–92.

Magnelia, S. J., M. J. De Jesus, J. W. Schlechte, G. C. Cummings, and J. L. Duty. 2008. “Comparison of Plastic Pipe and Juniper Tree Fish Attractors in a Central Texas Reservoir.” *Proc. Annu. Conf. Southeast. Assoc. Fish and Wildl. Agencies* 62:183–88.

Magoulick, D. D. 1998. “Effect of Wood Hardness, Condition, Texture and Substrate Type on Community Structure of Stream Invertebrates.” *The American Midland Naturalist* 139(2):187–200.

Mazerolle, M. J. 2019. “AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c).” R package version 2.2-2. https://cran.r-project.org/package=AICcmodavg.

McCann, K. S. 2000. “The Diversity–Stability Debate.” *Nature* 405(6783):228–33.

Merritt, R. W., and K. W. Cummins. 1996. *An Introduction to the Aquatic Insects of North America*. Third. Dubuque, Iowa, USA: Kendall-Hunt.

Meyer, E. 1989. “The Relationship between Body Length Parameters and Dry Mass in Running Water Invertebrates.” *Archiv Fur Hydrobiologie* 117(2):191–203.

Miller, S. J., and T. Storck. 1984. “Temporal Spawning Distribution of Largemouth Bass and Young-of-Year Growth, Determined from Daily Otolith Rings.” *Transactions of the American Fisheries Society* 115:571–78.

Minchin, P. R. 1987. “An Evaluation of the Relative Robustness of Techniques for Ecological Ordination.” *Vegetatio* 69(1–3):89–107.

Miranda, L. E., and W. D. Hubbard. 1994. “Winter Survival of Age-0 Largemouth Bass Relative to Size, Predators, and Shelter.” *North American Journal of Fisheries Management* 14(4):790–96.

Mittelbach, G. G. 1981. “Foraging Efficiency and Body Size: A Study of Optimal Diet and Habitat Use by Bluegills.” *Ecology* 62(5):1370–86.

Moring, J. R., P. D. Eiler, M. T. Negus, and E. Gibbs. 1986. “Ecological Importance of Submerged Pulpwood Logs in a Maine Reservoir.” *Transactions of the American Fisheries Society* 115(2):335–42.

Morse, D. R., J. H. Lawton, M. M. Dodson, and M. H. Williamson. 1985. “Fractal Dimension of Vegetation and the Distribution of Arthropod Body Lengths.” *Nature* 314(6013):731–33.

Newbrey, M. G., M. A. Bozek, M. J. Jennings, and J. E. Cook. 2005. “Branching Complexity and Morphological Characteristics of Coarse Woody Structure as Lacustrine Fish Habitat.” *Canadian Journal of Fisheries and Aquatic Sciences* 62(9):2110–23.

Nilsen, H. C., and R. W. Larimore. 1973. “Establishment of Invertebrate Communities on Log Substrates in the Kaskaskia River, Illinois.” *Ecology* 54(2):366–74.

Oksanen, J., F. G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, E. Szoecs, and H. Wagner. 2019. “vegan: Community Ecology Package.” R package version 2.5-6. https://CRAN.R-project.org/package=vegan.

Olson, M. H., S. R. Carpenter, P. Cunningham, S. Gafny, B. R. Herwig, N. P. Nibbelink, Tom Pellett, C. Storlie, A. S. Trebitz, and K. A. Wilson. 1998. “Managing Macrophytes to Improve Fish Growth: A Multi-Lake Experiment.” *Fisheries* 23(2):6–12.

Olson, N. W., C. P. Paukert, D. W. Willis, and J. A. Klammer. 2003. "Prey Selection and Diets of Bluegill Lepomis Macrochirus with Differing Population Characteristics in Two Nebraska Natural Lakes." *Fisheries Management and Ecology* 10(1):31–40.

Pace, M. L., and J. D. Orcutt. 1981. "The Relative Importance of Protozoans, Rotifers, and Crustaceans in a Freshwater Zooplankton Community." *Limnology and Oceanography* 25(5):822–30.

Palmer, M. A., H. L. Menninger, and E. Bernhardt. 2010. "River Restoration, Habitat Heterogeneity and Biodiversity: A Failure of Theory or Practice?" *Freshwater Biology* 55(s1):205–22.

Pardue, G. B. 1973. "Production Response of the Bluegill Sunfish, Lepomis Macrochirus Rafinesque, to Added Attachment Surface for Fish-Food Organisms." *Transactions of the American Fisheries Society* 102:622–26.

Pardue, G. B. and L. A. Nielsen. 1979. "Invertebrate biomass and fish produc-tion in ponds with added attachment surface." pp. 34-43. in: D. L. Johnson and R. A. Stein (eds*.). Response of fish to habitat structure in standing water*. American Fisheries Society, North Central Division, Special Publication 6. Bethesda, MD.

Peterman, R. M. 1990. "Statistical Power Analysis Can Improve Fisheries Research and Management." *Canadian Journal of Fisheries and Aquatic Sciences* 47(1):2–15.

Pielou, E. C. 1966. "Shannon's Formula as a Measure of Specific Diversity: Its Use and Misuse." *The American Naturalist* 100(914):463–65.

Plante, C., and J. A. Downing. 1989. "Production of Freshwater Invertebrate Populations in Lakes." *Canadian Journal of Fisheries and Aquatic Sciences* 46(9):1489–98.

Rold, R. E., T. S. McComish, and D. E. Van Meter. 1996. “A Comparison of Cedar Trees and Fabricated Polypropylene Modules as Fish Attractors in a Strip Mine Impoundment.” *North American Journal of Fisheries Management* 16(1):223–27.

Rosen, R. A. 1981. “Length-Dry Weight Relationships of Some Freshwater Zooplankton [a].” *Journal of Freshwater Ecology* 1(2):225–29.

Sanson, G. D., R. Stolk, and B. J. Downes. 1995. “A New Method for Characterizing Surface Roughness and Available Space in Biological Systems.” *Functional Ecology* 9(1):127.

Santos, L. N., F. G. Araújo, and D. S. Brotto. 2008. “Artificial Structures as Tools for Fish Habitat Rehabilitation in a Neotropical Reservoir.” *Aquatic Conservation: Marine and Freshwater Ecosystems* 18(6):896–908.

Santos, L. N., E. García-Berthou, A. A. Agostinho, and J. D. Latini. 2011. “Fish Colonization of Artificial Reefs in a Large Neotropical Reservoir: Material Type and Successional Changes.” *Ecological Applications* 21(1):251–62.

Sass, G. G., S. R. Carpenter, J. W. Gaeta, J. F. Kitchell, and T. D. Ahrenstorff. 2012. “Whole-Lake Addition of Coarse Woody Habitat: Response of Fish Populations.” *Aquatic Sciences* 74(2):255–66.

Sass, G. G., J. F. Kitchell, S. R. Carpenter, T. R. Hrabik, A. E. Marburg, and M. G. Turner. 2006. “Fish Community and Food Web Responses to a Whole-Lake Removal of Coarse Woody Habitat.” *Fisheries* 31(7):321–30.

Savino, J. F., and R. A. Stein. 1982. “Predator-Prey Interaction between Largemouth Bass and Bluegills as Influenced by Simulated, Submersed Vegetation.” *Transactions of the American Fisheries Society* 111(3):255–66.

Scheffer, T. C., G. H. Englerth, and C. G. Duncan. 1949. Decay resistance of seven native oaks. J. Agric. Res. 78, 129–152.

Scheffer, T. C. 1966. “Natural Resistance of Wood to Microbial Deterioration.” *Annual Review of Phytopathology* 4(1):147–68.

Scheuerell, M. D., and D. E. Schindler. 2004. “Changes in the Spatial Distribution of Fishes in Lakes Along a Residential Development Gradient.” *Ecosystems* 7(1):98–106.

Schindler, Daniel E., Sean I. Geib, and Monica R. Williams. 2000. “Patterns of Fish Growth along a Residential Development Gradient in North Temperate Lakes.” *Ecosystems* 3(3):229–37.

Schneider, C. A., W. S. Rasband, and K. W. Eliceiri. 2012. “NIH Image to ImageJ: 25 Years of Image Analysis.” *Nature Methods* 9(7):671–75.

Schneider, K. N., and K. O. Winemiller. 2008. “Structural Complexity of Woody Debris Patches Influences Fish and Macroinvertebrate Species Richness in a Temperate Floodplain-River System.” *Hydrobiologia* 610(1):235–44.

Shoup, D. E., M. A. Nannini, and D. H. Wahl. 2012. “The Effect of Vegetation Density on Juvenile Bluegill Diet and Growth.” *Journal of Freshwater Ecology* 27(2):199–209.

Slack, K. V., R. F. Ferreira, R. C. Averert, and S. S. Kennelly. 1988. “Effects of Spatial Orientation of Multiple Plate Artificial Substrates on Invertebrate Colonization1.” *JAWRA Journal of the American Water Resources Association* 24(4):781–89.

Smokorowski, K. E., and T. C. Pratt. 2007. “Effect of a Change in Physical Structure and Cover on Fish and Fish Habitat in Freshwater Ecosystems – a Review and Meta-Analysis.” *Environmental Reviews* 15:15–41.

Smokorowski, K. E., T. C. Pratt, W. G. Cole, L. J. McEachern, and E. C. Mallory. 2006. "Effects on Periphyton and Macroinvertebrates from Removal of Submerged Wood in Three Ontario Lakes." *Canadian Journal of Fisheries and Aquatic Sciences* 63(9):2038–49.

Stone, C. C., and T. Modde. 1982. "Growth and Survival of Largemouth Bass in Newly Stocked South Dakota Ponds." *North American Journal of Fisheries Management* 4:326–233.

Stoneburner, D. L., and L. A. Smock. 1979. "Seasonal Fluctuations of Macroinvertebrate Drift in a South Carolina Piedmont Stream." *Hydrobiologia* 63(1):49–56.

Strawn, K. 1961. "Growth of Largemouth Bass Fry at Various Temperatures." *Transactions of the American Fisheries Society* 90(3):334–35.

Thomaz, S. M., E. D. Dibble, L. R. Evangelista, J. Higuti, and L. M. Bini. 2008. "Influence of Aquatic Macrophyte Habitat Complexity on Invertebrate Abundance and Richness in Tropical Lagoons." *Freshwater Biology* 53(2):358–67.

Thorp, J. H., and A. P. Covich. 1991. *Ecology and Classification of North American Freshwater Invertebrates*. San Diego, CA: Academic Press, Inc.

Tokeshi, M., and S. Arakaki. 2012. "Habitat Complexity in Aquatic Systems: Fractals and Beyond." *Hydrobiologia* 685(1):27–47.

Tugend, K. I., M. S. Allen, and M. Webb. 2002. "Use of Artificial Habitat Structures in U.S. Lakes and Reservoirs: A Survey from the Southern Division AFS Reservoir Committee." *Fisheries* 27(5):22–27.

Turner, A. M., and J. C. Trexler. 1997. "Sampling Aquatic Invertebrates from Marshes: Evaluating the Options." *Journal of the North American Benthological Society* 16(3):694–709.

Walters, D. A., W. E. Lynch, and D. L. Johnson. 1991. “How Depth and Interstice Size of Artificial Structures Influence Fish Attraction.” *North American Journal of Fisheries Management* 11(3):319–29.

Warfe, D. M., L. A. Barmuta, and S. Wotherspoon. 2008. “Quantifying Habitat Structure: Surface Convolution and Living Space for Species in Complex Environments.” *Oikos* 117(12):1764–73.

Warton, D. I., S. T. Wright, and Y. Wang. 2012. “Distance-Based Multivariate Analyses Confound Location and Dispersion Effects: Mean-Variance Confounding in Multivariate Analysis.” *Methods in Ecology and Evolution* 3(1):89–101.

Wege, G. J. and R. O. Anderson. 1979. “Influence of Artificial Structures on Largemouth Bass and Bluegills in Small Ponds.” pp. 59-69. in: D. L. Johnson and R. A. Stein (eds.). *Response of fish to habitat structure in standing water*. American Fisheries Society, North Central Division, Special Publication 6. Bethesda, MD.

Werner, E. E., and D. J. Hall. 1988. “Ontogenetic Habitat Shifts in Bluegill: The Foraging Rate-Predation Risk Trade-Off.” *Ecology* 69(5):1352–66.

Wickham, H., M. Averick, J. Bryan, W. Chang, L. D. McGowen, R. Francois, G. Grolemund, A. Hayes, L. Henry, J. Hester, M. Kuhn, T. L. Pedersen, E. Miller, S. M. Bache, K. Muller, J. Ooms, D. Robinson, D. P. Seidel, V. Spinu, K. Takahashi, D. Vaughan, C. Wilke, K. Yoo, and H. Yutani. 2019. “Welcome to the Tidyverse.” *Journal of Open Source Software* 4:1686.

Wiens, J. A. 1989. “Spatial Scaling in Ecology.” *Functional Ecology* 3(4):385–97.

Wills, T. C., M. T. Bremigan, and D. B. Hayes. 2004. “Variable Effects of Habitat Enhancement Structures across Species and Habitats in Michigan Reservoirs.” *Transactions of the American Fisheries Society* 133(2):399–411.

Zorn, S. A., T. L. Margenau, J. S. Diana, and C. J. Edwards. 1998. “The Influence of Spawning Habitat on Natural Reproduction of Muskellunge in Wisconsin.” *Transactions of the American Fisheries Society* 127(6):995–1005.