FISH COMMUNITY RESPONSE TO RESERVOIR HABITAT ENHANCEMENT ACROSS MULTIPLE SPATIO-TEMPORAL SCALES

BY

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THESIS

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ABSTRACT

Structural habitat enhancements, such as additions of natural and synthetic fish habitats, are a common management tool used to mitigate the loss of natural physical structure in aging lakes and reservoirs. While habitat additions can concentrate fish, how this concentration effect varies over the age and location of the structure and whether habitat additions increase prey and fish production are poorly understood. I conducted two studies to test for the effects of reservoir habitat additions at different spatial and temporal scales. In the first study, I tested for responses of fish populations and fish prey resources to a whole-reservoir habitat manipulation, where over 1500 trees were added to the littoral zone of a small (22 ha) reservoir, resulting in about 12 times more littoral coarse woody habitat (CWH) compared to pre-habitat enhancement conditions. The CWH addition increased bluegill (*Lepomis macrochirus*) and largemouth bass (*Micropterus salmoides*) size structure during the four-year evaluation period but did not increase fish abundance as measured by catch per unit effort (CPUE), prey resources (i.e., zooplankton and macroinvertebrates), and the reproductive output of *Lepomis* spp. In the second study, I tested whether fish occupancy and relative abundance at 50 synthetic habitat structures (PVC cubes) varied longitudinally within Lake Shelbyville, a 4500-ha reservoir, and with time since deployment, ranging in age from five months to almost five years. Structure location influenced fish relative abundance at PVC cubes, such that catch rates generally decreased from lower to upper reservoir cube locations, with fish present at cubes shifting from primarily crappie (*Pomoxis* spp.) and sunfishes (*Lepomis* spp.) at lower reservoir sites to mainly white crappie (*Pomoxis annularis*) and freshwater drum (*Aplodinotus grunniens*) at upper reservoir cubes. These studies indicated that understanding the effects of habitat additions at multiple scales is important for the guidance of habitat enhancement programs. For example, observed increases in size structure indicated that habitat additions at the scale of an entire reservoir may enhance fish productivity, while the location of added habitats within a reservoir can shape the types and numbers of fish aggregating at each added habitat patch.

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CHAPTER 1: LITERATURE REVIEW

The function and sustainability of reservoir ecosystem services decline as reservoirs age, affecting humans and aquatic biota (Tundisi et al. 2008). Reservoir aging is a descriptive measure of the amount of storage capacity lost to sedimentation over time (Juracek 2015). Erosive processes in upstream river reaches, in-reservoir wind and wave erosion, as well as soil and riverbank runoff during events of intense precipitation (Juracek 2015), deliver the sediment that accelerates reservoir aging (Fox et al. 2016). High inputs of suspended and deposited sediment can compromise the health of reservoir ecosystems by degrading water quality and aquatic habitat (Miranda et al. 2010; 2020). For example, accumulating sediment covers structural habitats, reduces substrate heterogeneity (Krogman and Miranda 2016), and alters fish species composition within reservoirs through time (Lenhardt et al. 2009; Loures and Pompeu 2019). The availability of structural habitat is also influenced by the construction and operational goals of the reservoir (Sass et al., 2022). Standing timber is often removed during reservoir construction, and the remaining coarse woody habitat (CWH) decays over time (Miranda 2017). Water level fluctuations and low water clarity typical of flood control reservoirs limit the establishment of aquatic vegetation (Agostinho et al. 1999) and often further reduces the amount of littoral habitat available for macroinvertebrates and juvenile fishes (Wiley et al. 1984).

Structural habitat enhancements are used to maintain or restore ecosystem function by improving or replacing degraded aquatic habitat (Fisher et al. 2012) or reducing the physical effects of reservoir aging (Juracek 2015). The addition of artificial structural habitat structures is a common management strategy to mitigate habitat loss in aging reservoirs (Miranda 2017). Artificial habitat structures consist of natural or synthetic materials intentionally placed in an aquatic environment to enhance fish habitat and the fishery (Seaman and Sprague 1991). A variety of natural and synthetic materials are used as artificial fish habitats ranging from evergreen trees and brush piles to tires and plastics (Bolding et al. 2004). Many management agencies rely on artificial habitat structures based on the assumption that these structures increase fish production and angler catch rates (Bassett 1994; Tugend et al. 2002; Bolding et al. 2004). Although angling success near artificial structures is attributed to the increased concentration of fish (Wilbur 1978; Rogers and Bergersen 1999), objectives to increase fish production are thought to be achieved through the numerous fisheries benefits provided by improvements in habitat diversity (Bassett 1994; Sass et al. 2022).

Enhanced reproductive success, refuge from predation, and foraging opportunities are the mechanisms proposed to increase fish production from the addition of artificial habitat structures. Sportfish in reservoirs lacking structurally complex habitats can benefit from the use of artificial habitat structures because it can increase their nesting success. For example, largemouth bass (*Micropterus salmoides*) select nesting sites near brush shelters (Vogele and Rainwater 1975), CWH (Lawson et al. 2011; Weis and Sass 2011), and supplemental logs (Hoff 1991; Hunt and Annett 2002). Coarse woody habitats and other artificial habitat structures also provide refuge and foraging habitats for fishes (Newbrey et al. 2005; Sass et al. 2006*b*). Prey fish species concentrate in dense structure to avoid predation (Walters et al. 1991; Johnson et al. 1988; Lynch and Johnson 1989; Sass et al. 2006a), and the feeding efficiency of piscivores decreases at intermediate and high habitat complexities (Savino and Stein 1982; Sass et al. 2006*a*; DeBoom and Wahl 2013). Periphyton biomass and macroinvertebrate production increase on artificial habitat structures with increasing surface area and complexity (Pardue 1973; Casartelli and Ferragut 2018), thereby increasing foraging opportunities for small fishes. More specifically, macroinvertebrates have an affinity for decaying wood and colonize CWH with high surface complexity (Schmude et al. 1998; Smokorowski et al. 2006; Czarnecka 2016). These growth, reproduction, and survival benefits provided by artificial habitat additions, especially in systems that lack natural structure, are assumed to increase fish production. For example, bluegill (*Lepomis macrochirus*) and largemouth bass growth rates were positively influenced by CWH density in Wisconsin lakes (Schindler et al., 2000; Gaeta et al., 2011). However, the degree to which added structure increases system-wide fish production is still unclear (Smokorowski and Pratt 2007; Sass et al., 2019; Smokorowski et al., 2021).

Fish attraction and production are debated outcomes of artificial habitat additions (Bohnsack and Sutherland 1985; Polovina 1991; Brickhill et al., 2005; Miranda 2017). The attraction hypothesis is based on a behavioral response and suggests that newly added habitat redistributes fish biomass within an ecosystem by concentrating fishes to a localized area that results in no net increase in biomass (Brickhill et al. 2005). On the other hand, the production hypothesis is driven by the expected growth, survival, and recruitment benefits provided by habitat additions which increase total fish biomass (Brickhill et al. 2005; Miranda 2017). Fish responses to artificial habitat additions are likely a combination of attraction and production that falls along a gradient between the two extremes (Miranda 2017).

There is limited research on the attraction/production hypothesis, especially in freshwater ecosystems. Research regarding the attraction/production hypothesis of artificial habitat additions needs to be expanded beyond localized (site-specific) scales (Polovina 1991), with a critical need for whole-ecosystem assessments to test whether the addition of artificial structure increases fish biomass and production on a system-wide scale (Smokorowski and Pratt 2007). Currently, the only ecosystem-scale study of the effects of artificial habitat addition was a CWH manipulation in a natural lake (Sass et al. 2012; Sass et al. 2019). However, small reservoirs may serve as ideal locations to evaluate the outcomes of ecosystem-scale habitat additions because they are often in need of habitat enhancement and can expand the environmental context of our understanding of the effects of system-wide habitat additions. Fish productivity changes in ecosystems operate over varying time lags and are dynamic over time. Therefore, productivity responses to habitat manipulations require long-term data collection. Fish attraction, on the other hand, is a much more rapid response to habitat additions than productivity and is well-documented in freshwater ecosystems (Bassett 1994; Sass et al. 2012; Smith et al. 2022).

Although there is a great deal of evidence supporting the ability of artificial habitats to attract and concentrate fish, additional questions remain regarding spatial and temporal variation in the fish attraction function of habitat additions. Successional patterns of fish colonization of artificial structure have not typically been addressed in studies of temperate, freshwater ecosystems, likely due to the seasonal patterns and low fish richness characteristic of temperate regions (Santos et al. 2011). Evaluating artificial structures in temperate ecosystems over varying colonization times (i.e., time since deployment) could provide empirical evidence to support the hypothesized lack of successional patterns of fish colonization or document previously unrecorded patterns of fish colonization. The use of habitat structures composed of synthetic materials is being widely adopted by anglers, stakeholder groups, and management agencies due to their longevity compared to organic woody material (Tugend et al. 2002; Bolding et al. 2004; Sass et al. 2022); however, there have not been tests of their effectiveness over long time periods (i.e., > 2 years). In addition to temporal variation in fish concentration patterns at artificial habitats, the use of habitat patches can also be influenced by their location within an aquatic landscape (Parkos et al., 2011). Large reservoirs can be used to test for the effects of the spatial distribution of synthetic structures on fish attraction because large reservoirs often have longitudinal gradients in chemical, water quality, habitat, and sedimentation conditions that shape the spatial distribution of biota within these ecosystems (Miranda 2017).

Environmental conditions may alter fish behavior and their distribution throughout large reservoirs; therefore, it is important to understand whether the environmental longitudinal gradient affects fish use of artificial habitat structures (Daugherty et al. 2014). Large reservoirs can be divided into different ecological zones: the lacustrine (maximum depth, adjacent to dam), transitional (middle portion), and riverine (shallowest, adjacent to inflow; Thornton 1990). Coarse sediment settles in the riverine zone as inflowing current velocities slow, while fine silts and clays are transported farther depending on current hydrological conditions (Schleiss et al. 2016; Miranda 2017). Because of the relatively high-water velocity and transport of materials from inflowing tributaries, the riverine zone of reservoirs is characterized by low water clarity and high nutrient concentrations (Soares et al. 2012). Increased turbidity reduces light intensity with depth and therefore limits primary production, such as the growth of submerged macrophytes and phytoplankton (Anderson et al. 2002; Soares et al. 2012) despite high nutrient levels. The effects of turbidity on fish include reduced feeding efficiency of planktivores (Gardner 1981), reduced prey selectivity of piscivores (Shoup and Wahl 2009), altered predator-prey interactions (Lynch and Johnson 1989; Abrahams and Kattenfeld 1997), and disrupted sexual selection and mating behavior from reduced visual cues (Helfman et al. 2009). Sediment-bound and dissolved nutrients from runoff accelerate eutrophication in reservoirs, especially in agricultural regions (Miranda 2017). In contrast to the riverine zone, the lacustrine zone typically has lower nutrient concentrations, but higher primary productivity as more sediment settles from the lack of flow (Soares et al. 2012). In addition to the potential for longitudinal variation in fish use of artificial structures, the depth of artificial structures can also influence fish use (Walters et al. 1991), with structure use correlated with the depth of the metalimnion (Johnson and Lynch 1992). An understanding of location effects could provide guidance for management agencies when selecting appropriate sites for artificial structure deployment.

Artificial habitat additions are being used in an effort to enhance recreational fisheries in reservoirs but without sufficient knowledge of their effects at an ecosystem scale. Based on previous research, some knowledge has been acquired as to how CWH separately influences periphyton and macroinvertebrate growth, as well as fish growth and reproduction at localized scales. Moreover, research regarding CWH additions is often restricted by time and space (Minns et al. 1996), such that studies are not conducted for a long enough time period or at a large enough scale to elicit responses. I tested for the effects of a whole-lake CWH addition in a small, eutrophic reservoir using response variables from multiple trophic levels. Studies at this spatial scale are rare; therefore, my research provides an important contribution to the understanding of whether CWH additions influence productivity within reservoir ecosystems. Eutrophic reservoirs are frequently limited by the availability of CWH; however, this system type has not been previously studied within the context of a whole-lake CWH addition.

Additionally, I tested for potential spatial and temporal variation in the efficacy of synthetic habitat structures. Synthetic structures are long-lasting physically, but how long they maintain their ability to attract fish and whether fish assemblage composition at these structures changes over time is unknown. My research addresses these questions by assessing fish use of plastic cube structures that vary in time since deployment and location along a longitudinal gradient of physical and biological conditions within a large reservoir. Due to the relatively rapid degradation of CWH in aquatic ecosystems (Sass et al. 2009), the effects and benefits of CWH are likely short-lived, making synthetic structures a favorable option for some resource managers. Further evaluation of synthetic habitat structures under these spatio-temporal factors will inform resource managers about their effectiveness through time and provide guidance for structure placement in similar ecosystems.

CHAPTER 2: ECOSYSTEM RESPONSE TO A WHOLE-RESERVOIR COARSE WOODY HABITAT ADDITION

Introduction

Natural physical structures become increasingly scarce as reservoirs age due to the loss of aquatic macrophytes and coarse woody habitat (CWH) (Agostinho et al. 1999; Miranda et al. 2010), with subsequent, adverse effects on reservoir fisheries (Agostinho et al. 1999; Cowx 2002). In reservoirs devoid of physical structure, many management agencies rely on the addition of CWH to enhance structural habitat complexity (Bassett 1994; Tugend et al. 2002). The goals of CWH additions (e.g., felled trees, fish cribs, “fish sticks”, brush piles, evergreen tree clusters, and stumps) targeting lake and reservoir fisheries are to improve angler success through the concentration of fish and increase fish production (Bassett 1994; Tugend et al. 2002).

Coarse woody habitat in the littoral zone increases the availability of food resources and mediates predator-prey interactions (Sass et al. 2006a; Sass et al. 2012), potentially leading to increased transfer of energy to upper trophic levels (Crowder et al. 1998; Schindler et al. 2000; Sass et al. 2006b, 2019, 2022; Carey et al. 2010). Coarse woody habitat in the littoral zone creates a foundation for aquatic food webs by providing an additional attachment surface for periphyton (Vadeboncoeur and Lodge 2000; Vadeboncoeur et al. 2006; Sass 2009, 2019, 2022; Carey et al. 2010). This basal food resource attracts scraper and grazer invertebrates that feed on the epixylic algae (Smokorowski et al. 2006; Sass 2009; Czarnecka 2016). In turn, predacious macroinvertebrates and insectivorous fishes forage on invertebrate prey attracted to the CWH (Crowder et al. 1998, Sass 2009). Larval and early juvenile life stages of many lacustrine fishes are also concentrated in the littoral zone (Claramunt et al. 2005), where they feed on zooplankton and insect larvae (Lemly and Dimmick 1982; Whiteside et al. 1985) and shelter in structurally complex habitats (Gotceitas and Colgan 1990; Newbrey et al. 2005; Sass et al. 2006b). The littoral habitat continues to provide resources throughout fish ontogeny (Whiteside et al. 1985). Ultimately, CWH concentrates lower trophic organisms in the littoral zone where top predators, such as piscivorous fishes, can take advantage of the foraging opportunities (DeBoom and Wahl 2013). The attraction of multiple trophic levels to structural habitat in the littoral zone has the potential to increase fish production (Miranda 2017). Despite the potential benefits of CWH additions for fishery management, the effects of CWH additions at an ecosystem scale are largely unevaluated.

Fish production associated with CWH has not been thoroughly explored in temperate reservoirs, likely due to the temporal and spatial scale necessary for this type of investigation (Minns et al. 1996; Smokorowski and Pratt 2007). Whole-lake habitat manipulations require long-term assessments and become increasingly difficult with lake surface area (Tugend et al. 2002; Sass et al. 2019). With increasing spatial scale, the challenges in estimating fish abundance and identifying potential mechanisms driving patterns of fish growth, distribution, and the variability of fish recruitment increase (Tugend et al. 2002, Sass 2009). Coarse woody habitat increases prey availability (Smokorowski et al. 2006) and acts as habitat for foraging and refuge (Newbrey et al. 2005; Sass et al. 2006a; Sass 2009), but these effects may not directly translate into increased fish production despite the assumption that CWH increases fish production in freshwater ecosystems (Sass et al. 2019).

Habitat manipulations conducted along an entire shoreline (lake-scale) are rare, and so each case study can provide valuable insight into influences on lake productivity. Sass et al. (2012) added more than 300 treetops to the littoral zone of an oligotrophic, seepage lake in

Northern Wisconsin to test whether reversing the effects of lakeshore residential development (i.e., physical removal of CWH; Christensen et al. 1996; Jennings et al. 1999; Francis and Schindler 2006; Marburg et al. 2006) influenced fish population dynamics. Additionally, Sass et al. (2019, 2022) described an ongoing, long-term experiment on a Wisconsin glacial lake to address some of the unanswered questions regarding the fish production response to CWH additions. All of the published whole-lake CWH manipulations to date have been conducted within natural lakes in Wisconsin; thus a recent lake-scale addition of CWH into a small reservoir in central Illinois provided an opportunity to test for the effects of this type of habitat manipulation under a new environmental context, that of a eutrophic, reservoir ecosystem at a lower latitude.

In this study, I tested whether a large-scale habitat enhancement had a positive bottom-up effect on zooplankton biomass and density, macroinvertebrate biomass, fish size structure, fish relative abundance, and fish reproduction in a reservoir ecosystem by using a before-after-control-impact (BACI) design (Stewart-Oaten et al. 1986) that compared responses in the treatment reservoir to two unmanipulated reference reservoirs. I hypothesized that the whole-lake CWH addition would increase the abundance of the lower trophic levels that provide prey for fish (i.e., macroinvertebrates and zooplankton), with a subsequent increase in factors associated with fish production such as size, abundance, and reproduction.

Methods

Study Sites

Walnut Point Lake (Douglas County, Illinois), the treatment reservoir in the BACI design, was constructed in 1967 by impounding an unnamed stream that flows into the Embarras

River (Figure 2.1) and has a surface area of 21 ha. In January 2018, the Illinois Department of Natural Resources (IDNR) felled about 1,500 trees into the littoral zone of Walnut Point Lake to provide fish habitat and increase light penetration to the riparian zone. Prior to the habitat manipulation, there were about 14 logs/km of shoreline in Walnut Point Lake. Pre-period log counts in the littoral zone were estimated using side-scan sonar in August 2016. Log counts were divided by shoreline length to obtain the tree density for each reservoir. The felled trees resulted in a 12-fold increase in CWH post-manipulation (Table 2.1). Lincoln Trail Lake (Clark County, Illinois) and Homer Lake (Champaign County, Illinois) served as unmanipulated reference systems in this study (Figure 2.1). Lincoln Trail Lake is a 55-ha reservoir that was constructed in 1956 by impounding the Sandy Branch near its Mill Creek outlet, and Homer Lake is a 33-ha reservoir that was built in 1969 where the impounded Conkey Branch flows into the Salt Fork River. Both reference reservoirs are similar to Walnut Point Lake; however, Homer Lake is shallower, has lower water clarity, and has a lower mean tree density compared to Walnut Point Lake and Lincoln Trail Lake (Table 2.1). All three reservoirs have high primary productivity and are considered eutrophic to hypereutrophic (Illinois Natural History Survey, unpublished data; Parkos and Wahl 2010). The fish assemblages of the control reservoirs are similar to Walnut Point Lake, with a few differences, such as the presence of white crappie (*Pomoxis annularis*), warmouth (*Lepomis gulosus*), and bullhead (*Ameiurus spp.*) in the control reservoirs (Table 2.2). The most notable fish assemblage difference among the reservoirs is the presence of gizzard shad (*Dorosoma cepedianum*) in Homer Lake. The presence of gizzard shad is notable due to the influence of this species on nutrient dynamics and zooplankton assemblages in reservoirs (Dettmers and Stein 1992; Schaus and Vanni 2000). The shorelines of Walnut Point Lake and Lincoln Trail Lake are undeveloped, with low to moderate levels of vegetation and fallen timber

(Table 2.1). Most of the shoreline of Homer Lake is undeveloped except for some areas cleared of trees and shrubs for access by recreational anglers. Homer Lake also experiences excessive algal and vegetation growth on a seasonal basis in the shallow upper reservoir.

Field Collections and Laboratory Processing

Zooplankton

Three offshore and three nearshore zooplankton samples were collected monthly in each reservoir from May-October 2014-2021 using a 0.5-m diameter, 1.5-m long conical, vertical tow net with 63-µm mesh. To account for differences in the spatial distribution of zooplankton (Pothoven and Fahnenstiel 2015; Detmer 2019), each reservoir was divided into three zones (closest to the dam, mid-lake, and upper) where one offshore and one nearshore sample was collected from a stationary boat at a fixed site in each zone (Figure 2.2). Some zooplankton sampling sites varied by location between the pre-and post-period but remained within the same reservoir zone except for one nearshore site in Lincoln Trail Lake. Offshore samples were collected above the oxycline, and so tow depth of offshore samples was dependent upon the depth at which the dissolved oxygen concentration dropped below 3 mg/L (Detmer et al. 2019). Nearshore samples were collected at tow depths of 1 m. Zooplankton were preserved with 4% Lugol’s solution in the field and stored in a dark location until processing.

In the laboratory, macrozooplankton (cladocerans, non-naupliar copepods, *Chaoborus* larvae) were identified and enumerated using a stereo microscope until either a minimum of 400 individuals were identified or 10% by volume of the sample was examined. Rotifers were counted until either a minimum of 400 individuals were identified or 1% by volume of the sample was processed. The number of copepod nauplii was also counted for all samples. For each taxon present in a sample, 15 randomly chosen individuals were measured for body length to calculate biomass from length-mass regressions (Dumont et al. 1975; Bottrell et al. 1976; Pace and Orcutt 1981; Rosen 1981; Anderson et al. 1998; Burgess et al. 2015). For the Homer Lake reference reservoir, only three years of pre-manipulation data (2015-2017) were available for offshore zooplankton biomass. Furthermore, nearshore zooplankton samples collected from the upper reservoir zone were not available during 2019-2021. Zooplankton abundance was indexed as area under the curve (AUC) using the MESS package in R. The area below monthly mean biomass or density curves for each year were integrated using the composite trapezoid rule to account for the temporal variability of abundance throughout each growing season (Rice et al. 1987; Goldman 1988; Durant et al. 2005).

Macroinvertebrates

Benthic macroinvertebrates were sampled with a stovepipe sampler (Parkos and Wahl 2010) during the pre-manipulation period (2014-2017) and with a petite Ponar dredge during the post-manipulation period (2018-2021). In 2018, simultaneous collections of stovepipe and petite Ponar dredge samples verified that macroinvertebrate biomass estimates did not differ between the two gear types (Parkos et al. 2019). In each reservoir, six samples (stovepipe cores 2014-2017 and petite Ponar dredges 2018-2021) were taken once per month in June and August each year at a 1 m water depth or twice the Secchi depth, whichever was shallower. All benthic samples were sieved through a 500-µm mesh bucket. To test for potential successional changes in macroinvertebrate community structure on woody habitat after the CWH addition (Czarnecka et al. 2014), two to eight D-net sweeps were collected along 1-m transects within randomly selected CWH patches each year during 2018-2021. Sample contents were preserved in 95% ethanol and stained with Rose Bengal.

In the laboratory, a minimum of 30% of the sample was processed and a minimum of 100 individuals were enumerated and identified (family as the lowest taxonomic resolution) using a stereo microscope. Ten random macroinvertebrates were measured for length from each taxonomic group present to calculate biomass from length-mass regressions (Rosen 1981; Anderson et al. 1998; Poepperl 1998; Benke et al. 1999; Sabo et al. 2002; Baumgartner and Rothhaupt 2003; Methot et al. 2012; Rosati et al. 2012; Mroczynski and Daliga 2016). Annelid fragments were separated, dried at 65°C for two hours, and then weighed to obtain a dry-weight biomass for each sample. Annelid biomasses were only calculated for D-net samples, and decapods were removed from all analyses. Mean annual biomass/m^2 was calculated by combining June and August samples each year, with counts converted to densities by dividing by the area of the stovepipe (0.0324 m^2) and the petite Ponar dredge (0.0235 m^2).

Fish

Mean monthly densities (individuals/m^3) of larval *Lepomis* were collected to estimate the reproductive success of *Lepomis* species to test whether increased availability of food resources led to an increase in energy for reproduction. To quantify fish reproduction, six ichthyoplankton samples were collected every other week during May-June and monthly during July-October using a 0.5-m diameter conical, bow-mounted push net with 0.5-mm mesh (Claramunt et al. 2005). The net was pushed parallel to the shoreline for 5 minutes, 2.5 minutes in one direction and the remaining 2.5 minutes in the opposite direction to create a U-shaped, non-overlapping transect. To estimate the volume of water sampled, a calibrated flowmeter was mounted within the opening of the push net and the boat was driven at a speed of 3.2 – 4 km/h to target 10,000 revolutions for a sample volume of 52.7 m^3. The collected larval fish were preserved in 95% ethanol until they were counted and identified to genus using a dissecting microscope in the laboratory. Larval fish counts were converted to density estimates by dividing counts by the volume of water filtered through the push net. The same AUC approach used for zooplankton abundance (i.e., area under curve connecting mean monthly densities) was also used as an index of larval fish relative abundance.

Adult and juvenile fishes were collected using pulsed-DC boat electrofishing and fyke netting. Pulsed-DC boat electrofishing and fyke netting are complementary sampling methods due to interspecific differences in gear-specific catchability (Hubert et al. 2012; Reynolds and Kolz 2012). For example, electrofishing effectively samples largemouth bass and has a general bias toward larger individuals and species, while fyke nets are selective for *Pomoxis* and *Lepomis* species (Porreca et al. 2013). Three 15-minute electrofishing transects (one in each reservoir zone) were conducted each September with a pulse rate of 60 Hz and duty cycle of 25% with the power goal set according to water temperature and conductivity conditions during sampling events (Burkhardt and Gutreuter 1995). After 15-minutes of continuous power, all collected fish were identified to species, measured to total length (mm), and released. Modified fyke net surveys were conducted annually in October. Net locations were based on a stratified random sampling design, with each reservoir zone having three to four net locations selected from a larger set of fixed positions. Ten fyke nets (91 x 183 cm frame, 13 mm bar mesh, four 61 cm hoops, 15 m lead line) were set at each reservoir for two consecutive net nights with soak times ranging from 20 – 26.5 hours. The nets were deployed perpendicular to the shoreline at depths < 3 m. After about 24 hours, the nets were retrieved and all fish collected were identified to species, measured for total length, and released back into the water away from the net location. Nets were re-deployed at the same location for the second net-night. Proportional size distribution (PSD) of bluegill from fyke net surveys and largemouth bass from electrofishing surveys was calculated as:

$$PSD = \frac{number\ of\ fish \geq minimum\ quality\ length}{number\ of\ fish \geq minimum\ stock\ length} \times 100$$

where the stock length is 80 mm for bluegill and 200 mm for largemouth bass and the quality length is 150 mm for bluegill and 300 mm for largemouth bass (Gabelhouse 1984; Neumann et al. 2012).

Statistical Analysis

To test for effects of the CWH addition, I used a two-way analysis of variance (ANOVA) where ecological response = lake type + period + (period x lake type), with lake type being either a control or treatment reservoir, period being before (4 years; 2014-2017) and after (4 years; 2018-2021) the addition of CWH to Walnut Point Lake, and the interaction term being the test of whether a response was due to the CWH addition (Stewart-Oaten et al. 1986; Underwood 1992; Stewart-Oaten and Bence 2001). Separate BACI analyses were conducted for each reservoir treatment-reference pair to assess the robustness of treatment responses across the presence/absence of gizzard shad. Responses were ln(x), $\sqrt{x}$, or $x^{2.5}$ transformed to meet the assumptions of ANOVA. If transformed responses still violated the normality and/or homoscedasticity assumptions of ANOVA, then a nonparametric Wilcoxon Signed Rank test was used to test for treatment effects on annual differences between paired treatment and reference systems. The following responses were analyzed using the Wilcoxon Signed Rank test: macroinvertebrate total biomass (Homer Lake comparison only), Diptera biomass (Homer Lake comparison only), and Ephemeroptera biomass (Homer Lake comparison only). I tested the null hypotheses that there was no interaction between lake type and period for zooplankton density, macroinvertebrate biomass, larval *Lepomis* density, and catch-per-unit effort and proportional size distribution of bluegill and largemouth bass populations. Statistical significance for all null hypotheses was set at $\alpha = 0.05$. I computed a non-metric multidimensional scaling (NMDS) plot to visually assess macroinvertebrate assemblages collected from D-net sweeps on wood substrate. Length-frequency distributions of bluegill and largemouth bass were compared between the pre- and post-treatment periods for each reservoir using a Kolmogorov-Smirnov (K-S) cumulative distribution test. All analyses were conducted in RStudio software version 4.2.1.

Results

The CWH addition in Walnut Point Lake had no detectable effect on prey resources. The lake type x period interaction was not significant for density (Table 2.3; Lincoln Trail Lake $F_{1,12} = 0.21$, $P = 0.65$, Homer Lake $F_{1,12} = 0.04$, $P = 0.84$) or biomass (Table 2.4; Lincoln Trail Lake $F_{1,12} = 0.12$, $P = 0.73$, Homer Lake $F_{1,12} = 0.12$, $P = 0.73$) of total offshore zooplankton (all taxa combined), nor for taxa-specific mean density of Cladocera, *Chaoborus* larvae, Copepoda, copepod nauplii, and Rotifera, and mean biomass of Cladocera, Copepoda, and Rotifera. Densities of Cladocera and *Chaoborus* larvae were higher in Walnut Point Lake than in the two reference reservoirs before and after the addition of CWH to Walnut Point Lake. Overall, Cladocera, Copepoda, *Chaoborus* larvae, copepod nauplii, and Rotifera densities increased after the CWH addition across all three reservoirs except for *Chaoborus* larvae in Homer Lake which showed a slight decrease in density between the pre- and post-manipulation periods (Figure 2.3). On average, Cladocera biomass was similar between Walnut Point Lake and Lincoln Trail Lake between study periods, while Cladocera biomass was considerably lower in Homer Lake. Copepoda and Rotifera biomass increased from the pre- to post-manipulation period in all three reservoirs (Figure 2.4). Total nearshore zooplankton density (all taxa combined) was also unaffected by the CWH addition (Table 2.5; Lincoln Trail Lake $F_{1,12} = 0.25$, $P = 0.63$, Homer Lake $F_{1,12} = 0.71$, $P = 0.42$). On average, nearshore zooplankton abundances were greater than offshore abundances due to higher abundances of Rotifera (Figure 2.5).

The CWH addition in Walnut Point Lake did not affect benthic macroinvertebrate total biomass when compared to each reference system (Table 2.6; Lincoln Trail Lake $F_{1,12} = 2.03$, $P = 0.18$; Homer Lake $P = 0.63$). Mean benthic macroinvertebrate total biomass increased over time in the treatment and reference reservoirs, with the greatest changes in Walnut Point Lake (2429 mg/m^2) and Lincoln Trail Lake (2538 mg/m^2; Figure 2.6). The interaction effect was not statistically significant for taxa-specific biomass of Diptera, Coleoptera, Ephemeroptera, Gastropoda, Hemiptera, Odonata, Ostracoda, Pelecypoda, and Trichoptera (Table 2.6). Dipterans (primarily Chironomidae and Ceratopogonidae) were the most abundant taxa collected in Walnut Point Lake (70.9%), Lincoln Trail Lake (56.2%), and Homer Lake (40.3%) of the total organisms collected during 2014-2021 (Figure 2.7). Dipteran mean biomass increased between study periods across the three reservoirs, but the largest increase was found in Walnut Point Lake, where mean biomass increased 1933 mg/m^2 between the pre- and post-manipulation periods. Amphipoda biomass was the only taxon-specific response to have a significant interaction effect but was only supported by the Lincoln Trail Lake reference comparison (Lincoln Trail Lake $F_{1,12} = 25.33$, $P = 0.0003$; Homer Lake $F_{1,12} = 2.15$, $P = 0.17$). The significant interaction effect was likely driven by a large increase in Amphipoda mean biomass in Lincoln Trail Lake during the post-period (Figure 2.8). Macroinvertebrate assemblages on wood substrate did not differ among reservoirs (Figure 2.9; $R = 0.03$, $P = 0.11$). Dipterans were the most common taxon collected on wood substrate in Walnut Point Lake, while Coleopterans were the most abundant on wood substrate in Lincoln Trail Lake, and Amphipoda were the most abundant on woody substrate in Homer Lake.

Largemouth bass comprised 22.5%, 17.5%, and 14.9% of the total catch from the electrofishing surveys in Walnut Point Lake, Lincoln Trail Lake, and Homer Lake, respectively. Gizzard shad made up 22.4% of the total catch from Homer Lake. Bluegill were the most common fish species collected during the fyke net surveys in Walnut Point Lake (54.8%), Lincoln Trail Lake (46.6%), and Homer Lake (45.5%). The addition of CWH in Walnut Point Lake did not affect the relative abundance of largemouth bass (Table 2.7; Lincoln Trail Lake $F_{1,12} = 0.11$, $P = 0.75$; Homer Lake $F_{1,12} = 0.08$, $P = 0.79$) and bluegill (Table 2.7; Lincoln Trail Lake $F_{1,12} = 1.47$, $P = 0.25$; Homer Lake $F_{1,12} = 0.76$, $P = 0.40$). Largemouth bass CPUE decreased consistently between study periods among the reservoirs. Largemouth bass CPUE in Walnut Point Lake decreased from 75 ± 7 fish/h during the pre-manipulation period to 58 ± 13 fish/h during the post-manipulation period, Lincoln Trail Lake decreased from 84 ± 16 fish/h to 58 ± 16 fish/h, and Homer Lake decreased from 64 ± 13 fish/h to 44 ± 11 fish/h (Figure 2.10). Overall, catch rates of Bluegill were low and showed little change between study periods in Walnut Point Lake and Lincoln Trail Lake. Bluegill CPUE in Homer Lake experienced the largest change with a decrease between study periods from 22 ± 8 fish/net-night to 9 ± 2 fish/net-night (Figure 2.10).

The size structures of the largemouth bass and bluegill populations were positively influenced by the CWH addition to Walnut Point Lake (Table 2.7; Largemouth Bass: Lincoln Trail Lake $F_{1,12} = 17.50$, $P = 0.001$; Homer Lake $F_{1,12} = 8.17$, $P = 0.01$; Bluegill: Lincoln Trail

Lake $F_{1,12} = 4.77$, $P = 0.0495$; Homer Lake $F_{1,12} = 7.34$, $P = 0.02$). Largemouth bass PSD decreased between study periods in both reference systems while increasing more than two-fold in Walnut Point Lake from 26 ± 2 to 54 ± 3 following the CWH addition (Figure 2.11). Bluegill PSD in Walnut Point Lake increased between the pre- and post-manipulation periods from 38 ± 6 to 77 ± 4 and increased in Homer Lake from 37 ± 4 to 45 ± 7. Meanwhile, Lincoln Trial Lake showed the opposite trend with bluegill PSD decreasing from 46 ± 13 to 38 ± 15 between study periods (Figure 2.11). Bluegill length-frequency distributions differed between the pre- and post-manipulation periods in Walnut Point Lake ($D = 0.51$, $P = < 0.0001$), Lincoln Trail Lake ($D = 0.44$, $P = < 0.0001$), and Homer Lake ($D = 0.08$, $P = 0.006$). There was a higher proportion of large fish (> 140 mm) and a lower proportion of small fish (< 120 mm) in Walnut Point Lake during the post-manipulation period. Length-frequency distributions of largemouth bass only changed between study periods for the treatment reservoir ($D = 0.18$, $P = 0.0005$), with a higher proportion of large fish (> 280 mm) following the habitat addition (Figure 2.12).

Despite increased reproductive output of *Lepomis* spp. in Walnut Point Lake following the CWH addition, there was not a statistically significant effect of the CWH treatment (Table 2.8; Lincoln Trail Lake $F_{1,12} = 1.51$, $P = 0.24$; Homer Lake $F_{1,12} = 3.06$, $P = 0.11$). Mean density of larval *Lepomis* consistently increased in Walnut Point Lake from 2019-2021 (Figure 2.13) and was roughly three times higher during the post-manipulation period (151 ± 27 N/m^3) compared to the pre-manipulation period (47 ± 15 N/m^3). Larval *Lepomis* density in Lincoln Trail slightly increased from 74 ± 29 N/m^3 to 89 ± 16 N/m^3 between study periods, while Homer Lake showed a decrease in larval *Lepomis* density from 99 ± 72 N/m^3 to 55 ± 44 N/m^3 (Figure 2.14).

Discussion

Habitat enhancements are widely used for freshwater and marine fisheries management, but their ecosystem effects and whether they increase fish production is still not well known. The lack of knowledge on these questions is in part due to the rarity of ecosystem-scale habitat enhancements and the difficulty of studying the effects of lake-scale manipulations on multiple trophic levels. The whole-lake CWH addition to Walnut Point Lake expands what is known about lake-scale habitat manipulations by quantifying responses within the context of a eutrophic reservoir. Eutrophic reservoirs have poor water clarity from high levels of primary production compared to natural lakes which can influence the differences in the strength of responses to habitat enhancement between ecosystem types (Sass et al. 2022). For example, turbidity decreases predator foraging efficiency (Shoup and Wahl 2009; Ortega et al. 2020), but the aggregation effect of prey to CWH can potentially increase predator-prey encounter rates and therefore increase predator foraging efficiency in turbid ecosystems. However, contrary to my prediction of a bottom-up increase in the production of prey resources, this hypothesis was not supported in my study.

Offshore zooplankton density and biomass of Walnut Point Lake appeared to be unaffected by the CWH addition. These lower trophic level organisms are often overlooked during habitat enhancements despite their ecological importance for influencing fish stocks and recruitment (Lomartire et al. 2021). Little is known about whether habitat additions affect zooplankton abundance, but a recent study by Porreca et al. (2022) also observed no change in zooplankton abundance in reservoir coves with and without synthetic offshore habitat structures. Detecting changes in zooplankton abundance can be challenging due to their typically patchy, spatially heterogeneous distributions (Cryer and Townsend 1988; Barnett et al. 2007).

Zooplankton patchiness is often driven by predator avoidance, reproduction, food availability, and wind and water movement (Folt and Burns 1999; Williamson et al. 2011; Detmer 2019; Cyr and Sprules 2022). Due to low water clarity and the large, anoxic hypolimnion throughout the summer months in Walnut Point Lake (Gardner 1981; Miner and Stein 1993; Doubek et al. 2018), diel horizontal migration (DHM) may be used by zooplankton in these systems to avoid predation by seeking refuge in the littoral zone during the day (Burks et al. 2001; Burks et al. 2002; Wojtal et al. 2003). A previous investigation found that zooplankton biomass was greater in nearshore than offshore areas in Walnut Point Lake, Lincoln Trail Lake, and Homer Lake, supporting the possibility of zooplankton DHM in these reservoirs (Detmer et al. 2019). Even though zooplankton density was also found to be higher in nearshore than offshore areas in my study, it was not attributed to the CWH addition. Zooplankton abundance is positively correlated with food availability (i.e., algal chlorophyll as an index of phytoplankton abundance) (Canfield and Jones 1996), but because Walnut Point Lake is a highly eutrophic reservoir, food availability may not have been limiting, resulting in relatively stable zooplankton populations.

The CWH addition in Walnut Point Lake also did not affect the biomass of benthic macroinvertebrates collected from sediments. The significant interaction of Amphipoda mean biomass with Lincoln Trail Lake was likely unrelated to the CWH addition in Walnut Point Lake unless the CWH inhibited a potential amphipod biomass increase. Quantitative macroinvertebrate data from woody structures were not available during the pre-habitat manipulation period and so could not be addressed in a BACI analysis. The abundance of aquatic invertebrates can be greater on CWH than adjacent sediment, but since sediment covers a larger area within a given water body, the sediment habitat provides greater overall invertebrate production at the scale of an entire lake (Smokorowski et al. 2006). The amount of littoral CWH was more than 12 times greater in Walnut Point Lake compared to Lincoln Trail Lake and Homer Lake, which would presumably result in a net gain of total macroinvertebrate production in Walnut Point Lake. Furthermore, macroinvertebrate production may increase over time as the CWH decays due to greater surface complexity (Smokorowski et al. 2006; Czarnecka et al. 2014).

Comparable to the results of a whole-lake CWH addition to a natural, oligotrophic lake in Wisconsin (Sass et al. 2012), bluegill and largemouth bass relative abundances were not affected by the CWH addition. In contrast, the size structure of the bluegill and largemouth bass populations increased in Walnut Point Lake due to the CWH addition. High abundances of CWH in the littoral zone have been shown to alter the foraging behavior of largemouth bass from actively searching to sit-and-wait predators (Ahrenstorff et al. 2009). A habitat manipulation experiment conducted by Ahrenstorff et al. (2009) in Wisconsin lakes found that the addition of CWH caused largemouth bass to spend more time in the littoral zone, have smaller home ranges, be less selective predators, and have higher consumption rates. By using this strategy, largemouth bass can allocate more energy to growth and reproduction instead of expending energy actively searching for prey. Largemouth bass select nesting sites near CWH (Lawson et al. 2011; Weis and Sass 2011); however, reproductive output was not measured for largemouth bass because their larvae are only effectively sampled via snorkel surveys (Siepker et al. 2009; Parkos et al. 2011). Nonetheless, the increased size structure of the largemouth bass population could benefit recruitment potential. Larger adult largemouth bass spawn earlier in the season which translates to their offspring having an earlier switch to piscivory, faster growth, and successful recruitment when prey is not limiting (Miranda and Muncy 1987; Goodgame and Miranda 1993; Phillips et al. 1995; Allen and Tugend 2002; Aday et al. 2009; Parkos and Wahl

2010; Parkos et al. 2011). Additionally, largemouth bass may have experienced a dietary shift to more energetically favorable prey (i.e., bluegill) or increased foraging efficiency due to the aggregation effect of CWH. On the other hand, since bluegill PSD increased in Walnut Point Lake, I also expected *Lepomis* reproductive output to increase due to the positive relationship between fecundity and body length (Roff 1983). Following the CWH addition, larval *Lepomis* density began peaking in June and continued through August, signaling a response of earlier and prolonged spawning throughout the summer. Even though larval *Lepomis* density appeared to be greater after the CWH addition, small length classes of bluegill (40-120 mm) were less abundant in the population indicating either lower recruitment, faster growth to longer length classes by the end of the growing season, or high predation mortality of juvenile bluegill by largemouth bass (Santucci and Wahl 2003).

Central Illinois has a longer growing season than northern Wisconsin which may contribute to the contrasting effects of CWH addition between the two whole-lake studies (Sass et al. 2012; Sass et al. 2022). The length of time it takes bluegill and largemouth bass to mature varies greatly depending on a suite of environmental conditions and biotic processes. Bluegill typically reach sexual maturity at age 3 or 4 in Illinois reservoirs (Hoxmeier et al. 2009; Oplinger et al. 2011), while largemouth bass reach sexual maturity between ages 2 to 4 (Illinois Department of Natural Resources). This lag between generations limits the amount of newly measurable production during short field experiments (< 4 years). It may take longer than 4 years to detect responses associated with a habitat addition, especially at higher latitudes. Large-scale, long-term studies that test for the effects of CWH manipulations, such as the on-going 20-year study conducted by Sass et al. (2019), are needed to provide accurate guidance for the management of lakes and reservoirs that lack structural fish habitat. Furthermore, the type of water body (reservoir vs. natural lake) and trophic state (eutrophic vs. oligotrophic) likely have a strong influence on the outcome of habitat manipulations and are important factors to consider prior to habitat enhancement (Sass et al. 2022).

Coarse woody habitat is an important feature for aquatic biota, but it is often limiting in aging reservoirs making habitat additions a favorable management practice. Since CWH is known to attract fishes, management agencies rely on CWH and other artificial habitat additions to improve recreational angling without fully knowing the consequences and effects that these habitat additions might have on an entire ecosystem. Fish populations and macroinvertebrates have been found to benefit from CWH additions by providing a surface area for colonization, refuge, foraging opportunities, and spawning substrate (Pardue 1973; Walters et al. 1991; Johnson et al. 1988; Lynch and Johnson 1989; Newbrey et al. 2005; Sass et al. 2006a; Sass et al. 2006*b*; Lawson et al. 2011; Weis and Sass 2011; Casartelli and Ferragut 2018). In my study, prey resource responses were consistent between the treatment and reference reservoirs indicating that other environmental variables had a stronger influence on zooplankton and macroinvertebrate abundances rather than the whole-lake habitat manipulation. The lack of prey responses may be attributed to trophic state, increased production balanced by increased predation, or low predation mortality (Porreca et al. 2022; Sass et al. 2022). My evaluation of the whole-lake CWH addition in Walnut Point Lake demonstrates that fish population responses to habitat enhancements are dynamic and influenced by the environmental context of the receiving system (Sass et al. 2022). Characteristics that influence ecosystem productivity such as nutrient loads, pre-manipulation habitat availability, and the receiving system’s fish assemblage (e.g., the presence of gizzard shad) are important considerations that likely dictate the amount and distribution (i.e., the scale) of structure that should be added to supplement reservoir habitat and the timescale that managers may expect to observe responses. Further assessment of whole-lake habitat additions are needed to continue building on current knowledge to understand the ecosystem effects of reservoir habitat enhancement.

Tables and Figures

Table 2.1 Morphological features, mean Secchi depth, and submerged log density of Walnut Point Lake, Lincoln Trail Lake, and Homer Lake, Illinois. Mean Secchi depth was calculated from post-manipulation data during June-September, 2018-2021, and mean chlorophyll-*a* was calculated during June-September 2020-2021. Pre-period log counts in the littoral zone were estimated using side-scan sonar in August 2016. Log counts were divided by shoreline length to obtain the tree density for each reservoir.

Characteristic	**Walnut Point Lake**	**Lincoln Trail Lake**	**Homer Lake**
Area (ha)	21	55	33
Shoreline length (km)	9	8.7	8.5
Mean depth (m)	3.8	4.9	2.5
Maximum depth (m)	9.8	10.7	7.3
Mean Secchi depth (m)	0.95	1.38	0.66
Mean Chlorophyll-*a* (µg/L)	59.1	32.1	45.4
Pre-period log density (log/km)	14.4	14.9	6.6
Post-period log density (log/km)	166.7	14.9	6.6

Table 2.2 Fish species present (denoted with an X) in Walnut Point Lake, Lincoln Trail Lake, and Homer Lake, Illinois based on electrofishing and fyke netting catch data during 2014-2021.

Family and Species	**Walnut Point Lake**	**Lincoln Trail Lake**	**Homer Lake**
Centrarchidae			
Lepomis macrochirus, **bluegill**	X	X	X
Lepomis microlophus, **redear sunfish**	X	X	X
Lepomis cyanellus, **green sunfish**	X	X	X
Lepomis gulosus, **warmouth**		X	
Pomoxis nigromaculatus, **black crappie**	X	X	X
Pomoxis annularis, **white crappie**		X	X
Micropterus salmoides, **largemouth bass**	X	X	X
Ictaluridae			
Ictalurus punctatus, **channel catfish**	X	X	X
Pylodictis olivaris, **flathead catfish**	X		
Ameiurus natalis, **yellow bullhead**		X	X
Ameiurus melas, **black bullhead**			X
Cyprinidae			
Cyprinus carpio, **common carp**	X	X	X
Ctenopharyngodon idella, **grass carp**	X		
Notemigonus crysoleucas, **golden shiner**			X
Percidae			
Percina caprodes, **logperch**	X		
Sander canadensis x vitreus, **saugeye**			X
Esocidae			
Esox Lucius, **northern pike**			X
Clupeidae			
Dorosoma cepedianum, **gizzard shad**			X
Fundulidae			
Fundulus notatus, **blackstripe topminnow**		X	X
Moronidae			
Morone mississippiensis, **yellow bass**			X
Poeciliidae			
Gambusia affinis, **mosquitofish**	X	X	

Table 2.3 Statistical results (F-values and P-values) and transformations from two-way ANOVA for offshore zooplankton density.

Variable	df	*F*-value	*P*	Transformation
Homer Lake				
Total (All Taxa Combined)				ln(x)
Lake Type	1	1.37	0.27	
Before/After	1	11.62	0.005	
Trt × BA	1	0.04	0.84	
Chaoborus larvae				ln(x)
Lake Type	1	62.85	4.12e-06	
Before/After	1	0.21	0.66	
Trt × BA	1	2.05	0.18	
Cladocera				ln(x)
Lake Type	1	23.68	0.0004	
Before/After	1	13.96	0.003	
Trt × BA	1	4.00	0.07	
Copepoda				ln(x)
Lake Type	1	0.38	0.55	
Before/After	1	5.36	0.04	
Trt × BA	1	1.64	0.22	
Copepoda nauplii				ln(x)
Lake Type	1	0.01	0.91	
Before/After	1	5.98	0.03	
Trt × BA	1	2.36	0.15	
Rotifera				ln(x)
Lake Type	1	0.98	0.34	
Before/After	1	10.81	0.006	
Trt × BA	1	0.03	0.87	
Lincoln Trail Lake				
Total (All Taxa Combined)				ln(x)
Lake Type	1	6.33	0.03	
Before/After	1	7.90	0.02	
Trt × BA	1	0.21	0.65	
Chaoborus larvae				ln(x)
Lake Type	1	29.22	0.0002	
Before/After	1	6.10	0.03	
Trt × BA	1	0.004	0.95	
Cladocera				ln(x)
Lake Type	1	13.66	0.003	

Table 2.3 (cont.)

Before/After	1	3.07	0.11	
Trt × BA	1	0.07	0.79	
Copepoda				ln(x)
Lake Type	1	3.15	0.10	
Before/After	1	6.12	0.03	
Trt × BA	1	1.66	0.22	
Copepoda nauplii				ln(x)
Lake Type	1	17.87	0.001	
Before/After	1	4.03	0.07	
Trt × BA	1	0.95	0.35	
Rotifera				ln(x)
Lake Type	1	3.55	0.08	
Before/After	1	6.91	0.02	
Trt × BA	1	0.52	0.48	

Table 2.4 Statistical results (F-values and P-values) and transformations from two-way ANOVA for offshore zooplankton biomass.

Variable	**df**	***F*-value**	***P***	**Transformation**
Homer Lake				
Total (All Taxa Combined)				ln(x)
Lake Type	1	5.51	0.04	
Before/After	1	4.23	0.07	
Trt × BA	1	0.12	0.73	
Cladocera				ln(x)
Lake Type	1	23.49	0.0007	
Before/After	1	2.93	0.12	
Trt × BA	1	0.46	0.51	
Copepoda				ln(x)
Lake Type	1	0.0085	0.93	
Before/After	1	4.65	0.06	
Trt × BA	1	0.0002	0.99	
Rotifera				ln(x)
Lake Type	1	0.92	0.36	
Before/After	1	2.31	0.16	
Trt × BA	1	0.43	0.53	
Lincoln Trail Lake				
Total (All Taxa Combined)				ln(x)
Lake Type	1	3.65	0.08	
Before/After	1	6.27	0.03	
Trt × BA	1	0.12	0.73	
Cladocera				ln(x)
Lake Type	1	0.23	0.64	
Before/After	1	2.86	0.12	
Trt × BA	1	0.05	0.83	
Copepoda				ln(x)
Lake Type	1	3.19	0.10	
Before/After	1	7.61	0.02	
Trt × BA	1	0.006	0.94	
Rotifera				ln(x)
Lake Type	1	4.95	0.05	
Before/After	1	5.53	0.04	
Trt × BA	1	0.37	0.55	

Table 2.5 Statistical results (F-values and P-values) and transformations from two-way ANOVA for nearshore zooplankton density.

Variable	df	*F*-value	*P*	Transformation
Homer Lake				
Total (All Taxa Combined)				None
Lake Type	1	0.13	0.72	
Before/After	1	1.69	0.22	
Trt × BA	1	0.71	0.42	
Lincoln Trail Lake				
Total (All Taxa Combined)				ln(x)
Lake Type	1	0.78	0.39	
Before/After	1	2.29	0.16	
Trt × BA	1	0.25	0.63	

Table 2.6 Statistical results (F-values and P-values) and transformations from two-way ANOVA and Wilcoxon signed rank tests for benthic macroinvertebrate biomass.

Variable	df	*F*-value	*P*	Transformation
Homer Lake				
Total (All Taxa Combined)				Nonparametric Test
Lake Differences BA	-	-	0.63	
Amphipoda				None
Lake Type	1	7.66	0.02	
Before/After	1	4.53	0.05	
Trt × BA	1	2.15	0.17	
Coleoptera				ln(x+1)
Lake Type	1	13.60	0.003	
Before/After	1	4.71	0.05	
Trt × BA	1	0.95	0.35	
Diptera				Nonparametric Test
Lake Differences BA	-	-	0.63	
Ephemeroptera				Nonparametric Test
Lake Differences BA	-	-	0.63	
Gastropoda				None
Lake Type	1	10.46	0.007	
Before/After	1	0.69	0.42	
Trt × BA	1	1.30	0.28	
Hemiptera				ln(x+1)
Lake Type	1	2.50	0.14	
Before/After	1	0.01	0.92	
Trt × BA	1	1.69	0.22	
Odonata				None
Lake Type	1	3.50	0.09	
Before/After	1	0.69	0.42	
Trt × BA	1	0.36	0.56	
Ostracoda				ln(x+1)
Lake Type	1	2.19	0.16	
Before/After	1	3.61	0.08	
Trt × BA	1	2.28	0.16	
Pelecypoda				ln(x)
Lake Type	1	0.01	0.91	
Before/After	1	0.06	0.82	
Trt × BA	1	0.02	0.90	
Trichoptera				$\sqrt{x}$
Lake Type	1	3.63	0.08	
Before/After	1	0.33	0.58	
Trt × BA	1	0.09	0.77	
Lincoln Trail				
Total (All Taxa Combined)				ln(x)
Lake Type	1	3.33	0.09	
Before/After	1	20.52	0.0007	
Trt × BA	1	2.03	0.18	

Table 2.6 (cont.)

Amphipoda				None
Lake Type	1	35.71	6.45e-05	
Before/After	1	32.95	9.31e-05	
Trt × BA	1	25.33	0.0003	
Coleoptera				ln(x)
Lake Type	1	2.72	0.12	
Before/After	1	6.96	0.02	
Trt × BA	1	1.38	0.26	
Diptera				ln(x)
Lake Type	1	12.12	0.005	
Before/After	1	21.89	0.0005	
Trt × BA	1	2.82	0.12	
Ephemeroptera				ln(x)
Lake Type	1	7.59	0.02	
Before/After	1	0.35	0.56	
Trt × BA	1	0.03	0.86	
Gastropoda				None
Lake Type	1	0.0003	0.99	
Before/After	1	6.30	0.03	
Trt × BA	1	1.67	0.22	
Hemiptera				ln(x+1)
Lake Type	1	0.03	0.86	
Before/After	1	0.74	0.41	
Trt × BA	1	0.80	0.39	
Odonata				None
Lake Type	1	1.09	0.32	
Before/After	1	2.87	0.12	
Trt × BA	1	0.43	0.52	
Ostracoda				ln(x+1)
Lake Type	1	3.90	0.07	
Before/After	1	5.38	0.04	
Trt × BA	1	1.20	0.29	
Pelecypoda				ln(x)
Lake Type	1	0.56	0.47	
Before/After	1	1.05	0.33	
Trt × BA	1	0.34	0.57	
Trichoptera				$\sqrt{x}$
Lake Type	1	1.08	0.32	
Before/After	1	0.64	0.44	
Trt × BA	1	0.002	0.97	

Table 2.7 Statistical results (F-values and P-values) and transformations from two-way ANOVA for bluegill and largemouth bass relative abundance and proportional size distribution.

Variable	df	*F*-value	*P*	Transformation
Fish Relative Abundance (CPUE)				
Homer Lake				
Bluegill				ln(x)
Lake Type	1	7.81	0.02	
Before/After	1	4.28	0.06	
Trt × BA	1	0.76	0.40	
Largemouth Bass				None
Lake Type	1	1.26	0.28	
Before/After	1	2.64	0.13	
Trt × BA	1	0.03	0.87	
Lincoln Trail Lake				
Bluegill				ln(x)
Lake Type	1	0.73	0.41	
Before/After	1	0.05	0.83	
Trt × BA	1	1.47	0.25	
Largemouth Bass				None
Lake Type	1	0.11	0.75	
Before/After	1	2.39	0.15	
Trt × BA	1	0.11	0.75	
Fish Proportional Size Distribution (PSD)				
Homer Lake				
Bluegill				None
Lake Type	1	9.01	0.01	
Before/After	1	17.33	0.001	
Trt × BA	1	7.34	0.02	
Largemouth Bass				$x^{2.5}$
Lake Type	1	2.87	0.12	
Before/After	1	0.15	0.70	
Trt × BA	1	8.17	0.01	
Lincoln Trail Lake				
Bluegill				None
Lake Type	1	2.29	0.16	
Before/After	1	2.10	0.17	
Trt × BA	1	4.77	0.05	
Largemouth Bass				None
Lake Type	1	23.38	0.0004	
Before/After	1	4.19	0.06	
Trt × BA	1	17.5	0.001	

Table 2.8 Statistical results (F-values and P-values) and transformations from two-way ANOVA for larval *Lepomis* density.

Variable	df	*F*-value	*P*	Transformation
Homer Lake				
Lepomis				ln(x)
Lake Type	1	2.74	0.12	
Before/After	1	0.14	0.71	
Trt × BA	1	3.06	0.11	
Lincoln Trail Lake				
Lepomis				ln(x)
Lake Type	1	0.12	0.73	
Before/After	1	6.84	0.02	
Trt × BA	1	1.51	0.24	

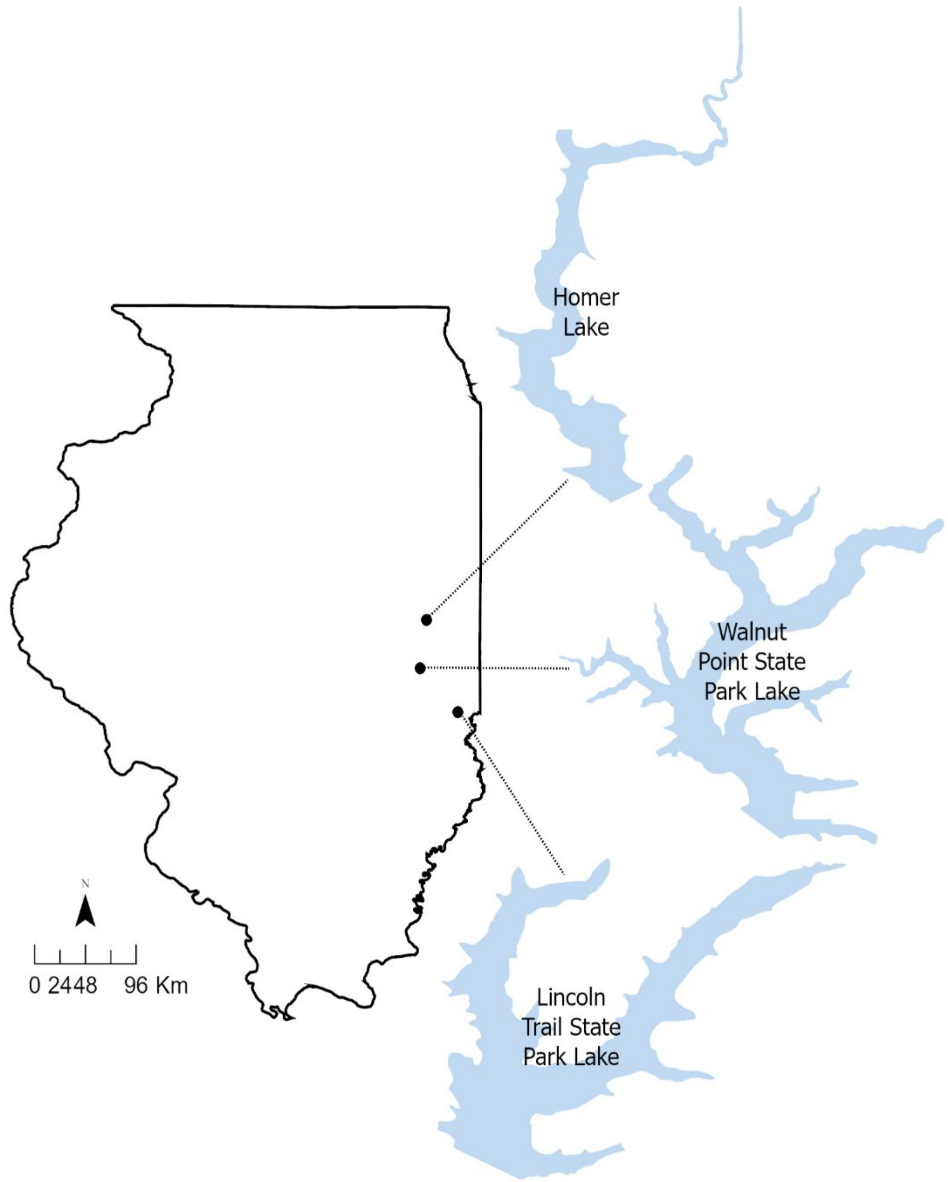


Figure 2.1 Locations of Walnut Point Lake, the treatment reservoir, and the two reference systems, Lincoln Trail and Homer Lake, in East Central Illinois.

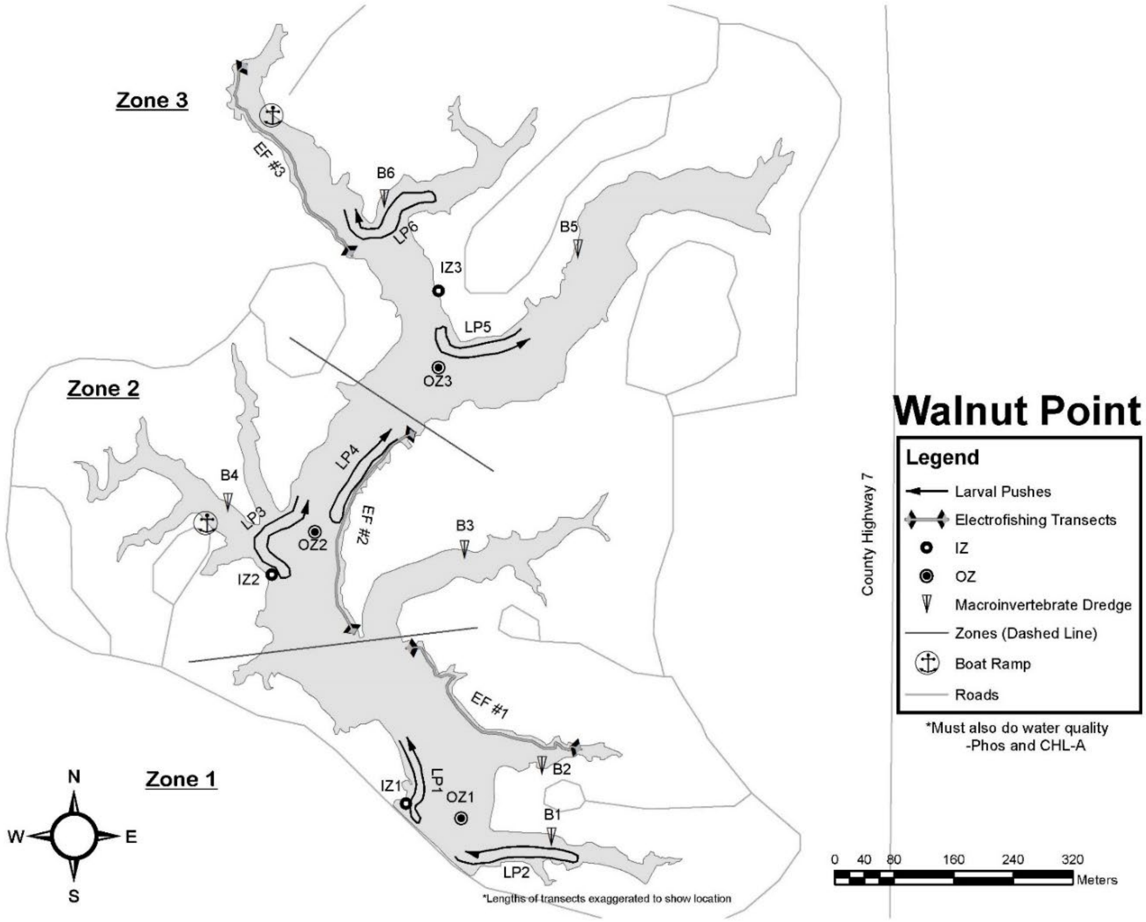


Figure 2.2 Sampling map of Walnut Point Lake, Illinois. OZ represents the offshore and IZ represents the nearshore zooplankton collection sites.

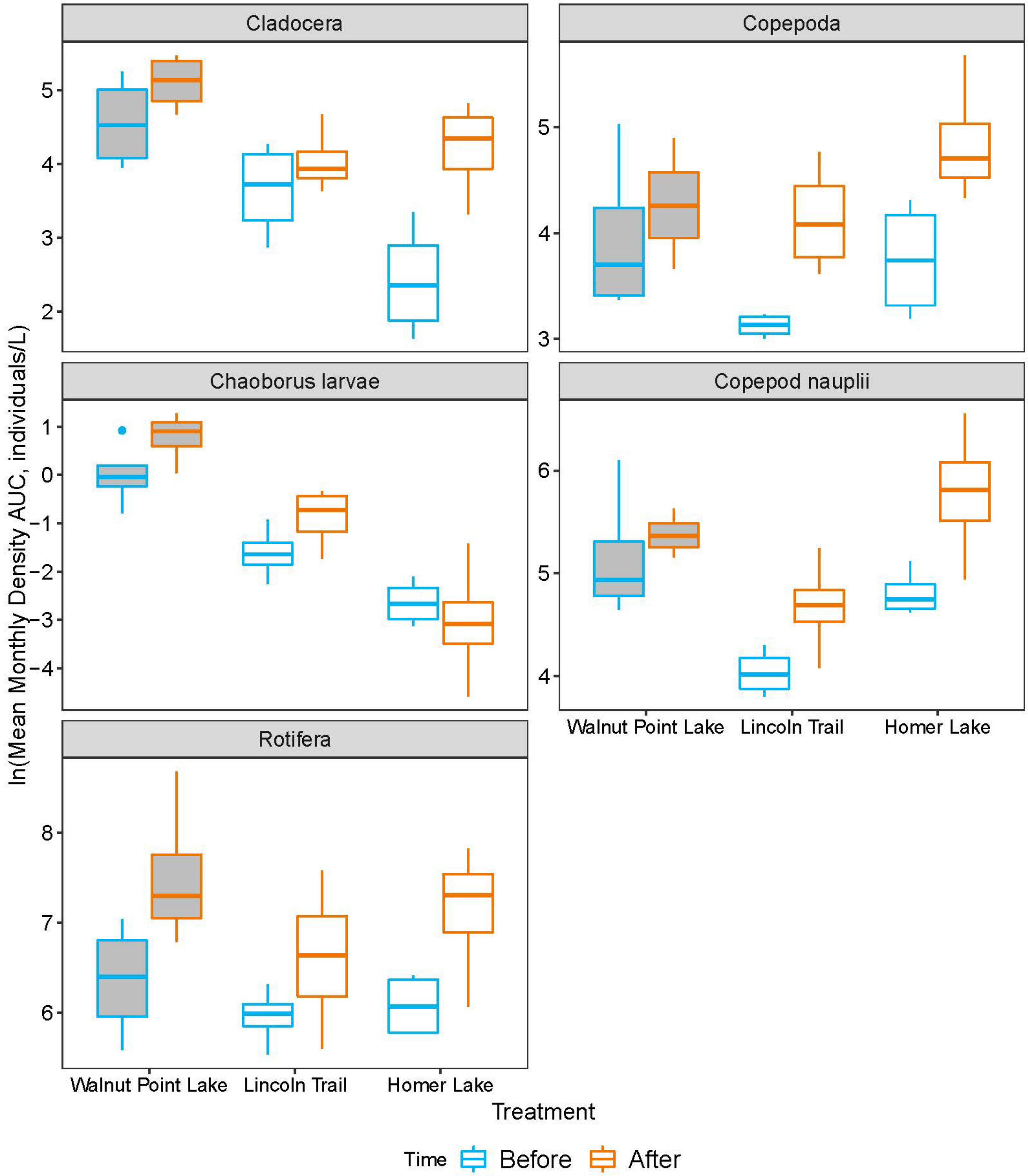


Figure 2.3 Natural log transformed area under the curve (AUC) from mean monthly density (individuals/L) of Cladocera, *Chaoborus* larvae, Copepoda, copepod nauplii, and Rotifera zooplankton from Walnut Point Lake (treatment, grey shaded boxplots) and the reference reservoirs (Lincoln Trail and Homer Lake, open boxplots) before (in blue) and after (in orange) the addition of CWH to Walnut Point Lake.

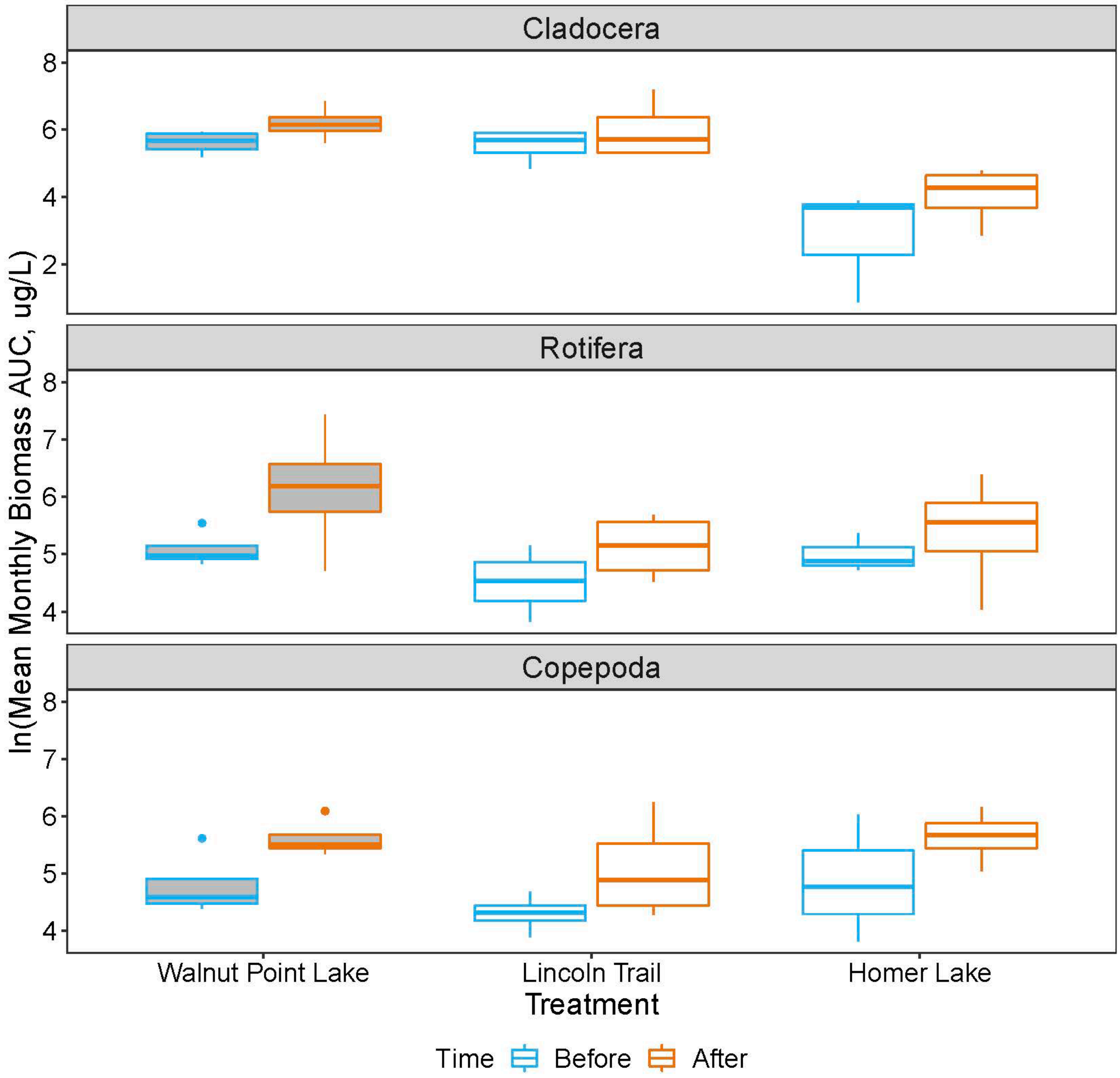


Figure 2.4 Natural log transformed area under the curve (AUC) from mean monthly biomass (ug/L) of Cladocera, Rotifera, and Copepoda zooplankton from Walnut Point Lake (treatment, shaded boxplots) and two reference reservoirs (Lincoln Trail and Homer Lake, open boxplots) before (in blue) and after (in orange) the addition of CWH to Walnut Point Lake.

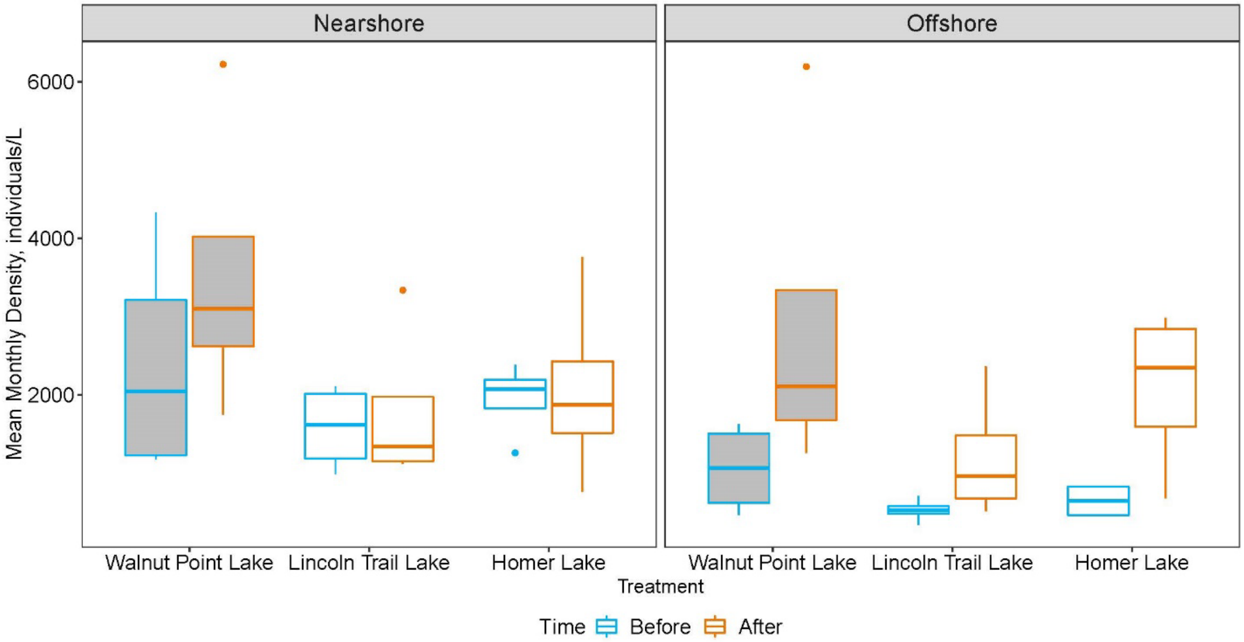


Figure 2.5 Area under the curve (AUC) from mean monthly density (individuals/L) of total nearshore zooplankton from Walnut Point Lake (treatment, shaded boxplots) and two reference reservoirs (Lincoln Trail and Homer Lake, open boxplots) before (in blue) and after (in orange) the addition of CWH to Walnut Point Lake.

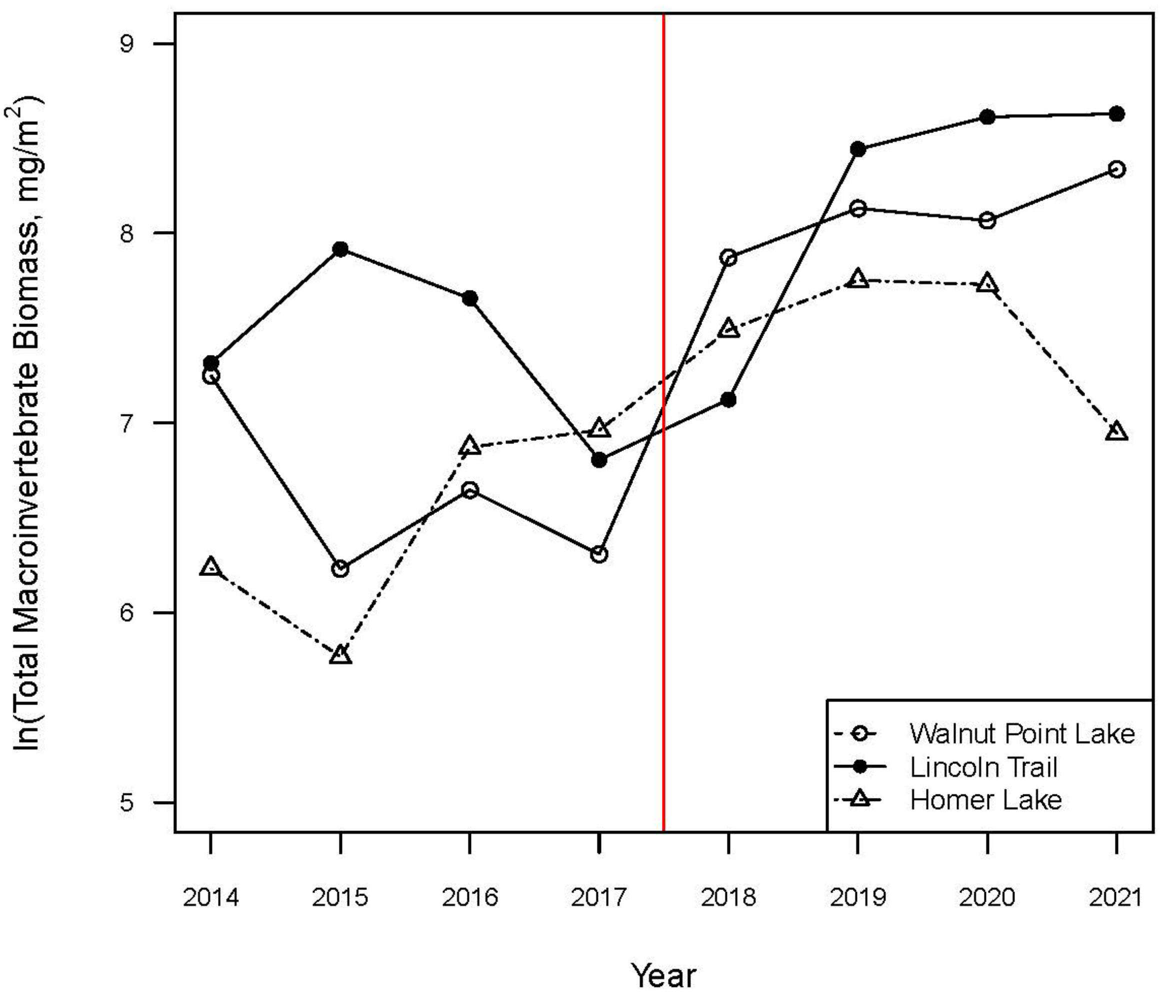


Figure 2.6 Natural log transformed mean total macroinvertebrate biomass (mg/m^2) of Walnut Point Lake (treatment, solid line and filled circles), Lincoln Trail Lake (reference, dashed line and open circles), and Homer Lake (reference, dotted line and open triangles) during 2014-2021. The red vertical line indicates when the habitat addition occurred in Walnut Point Lake (January 2018).

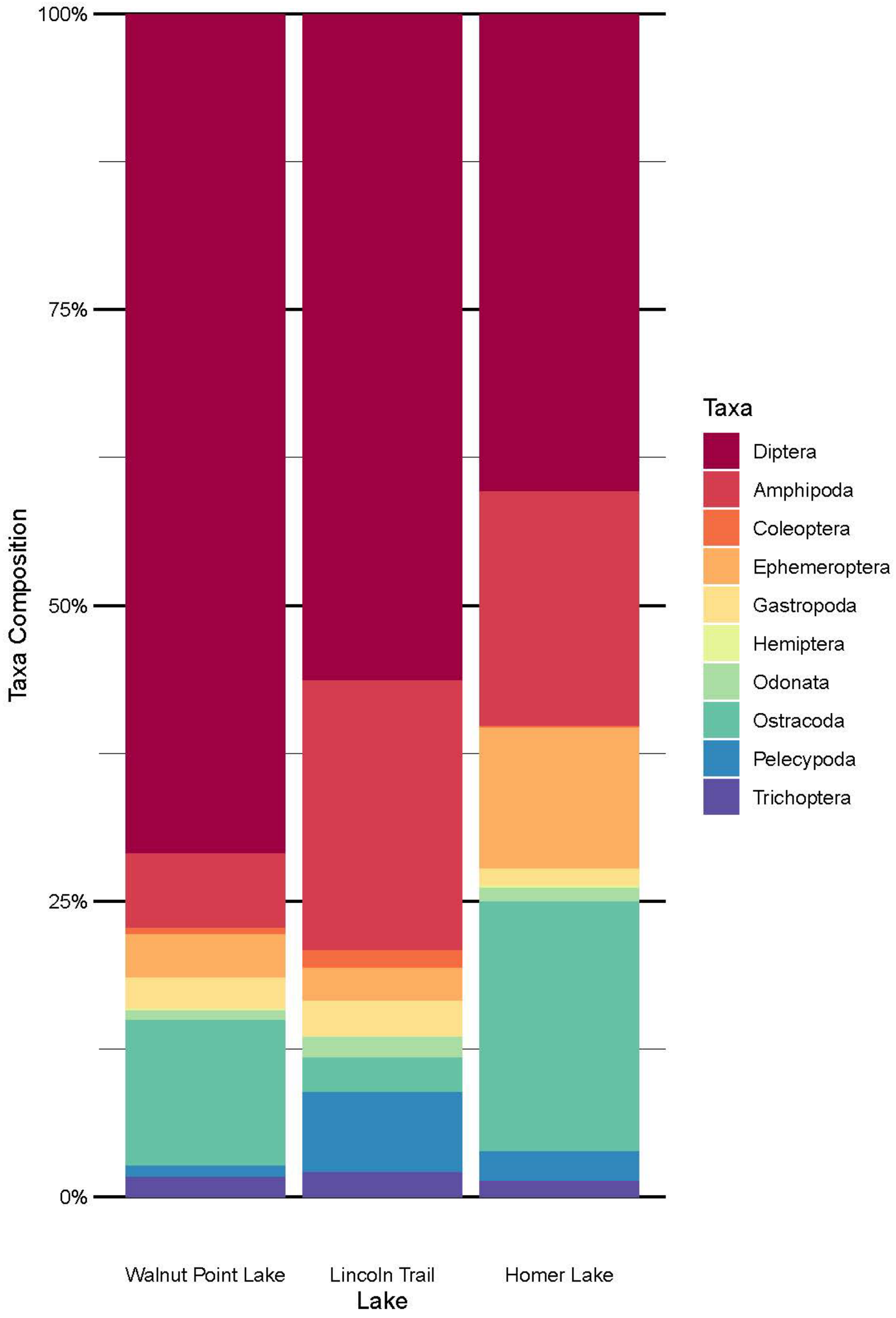


Figure 2.7 Benthic macroinvertebrate taxonomic composition of Walnut Point Lake, Lincoln Trail, and Homer Lake pooled from stovepipe and petite Ponar dredge samples collected during the eight-year study period.

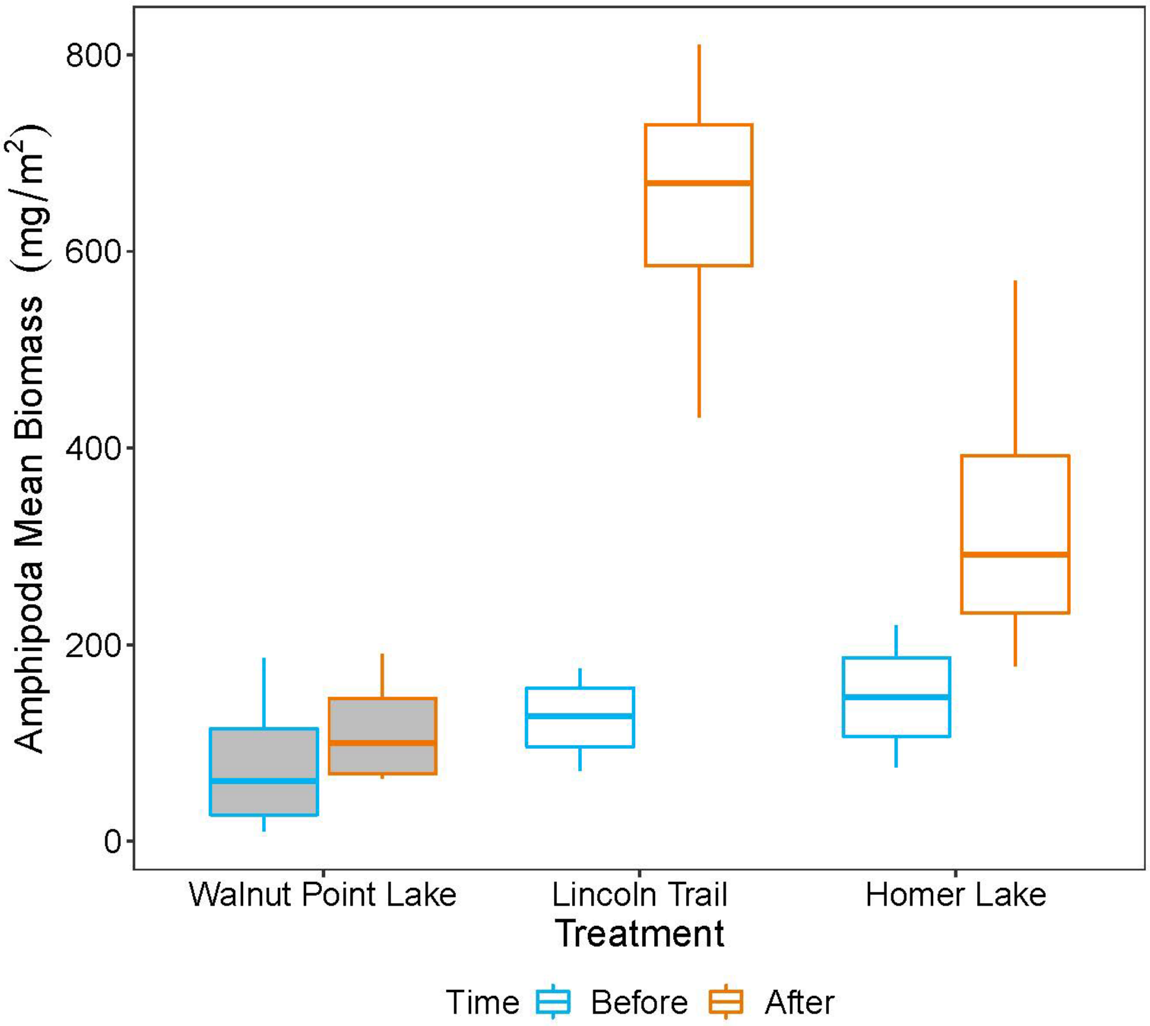


Figure 2.8 Amphipoda mean biomass (mg/m^2) from Walnut Point Lake (treatment, shaded boxplots) and the reference reservoirs (Lincoln Trail and Homer Lake, open boxplots) before and after the CWH addition to Walnut Point Lake.

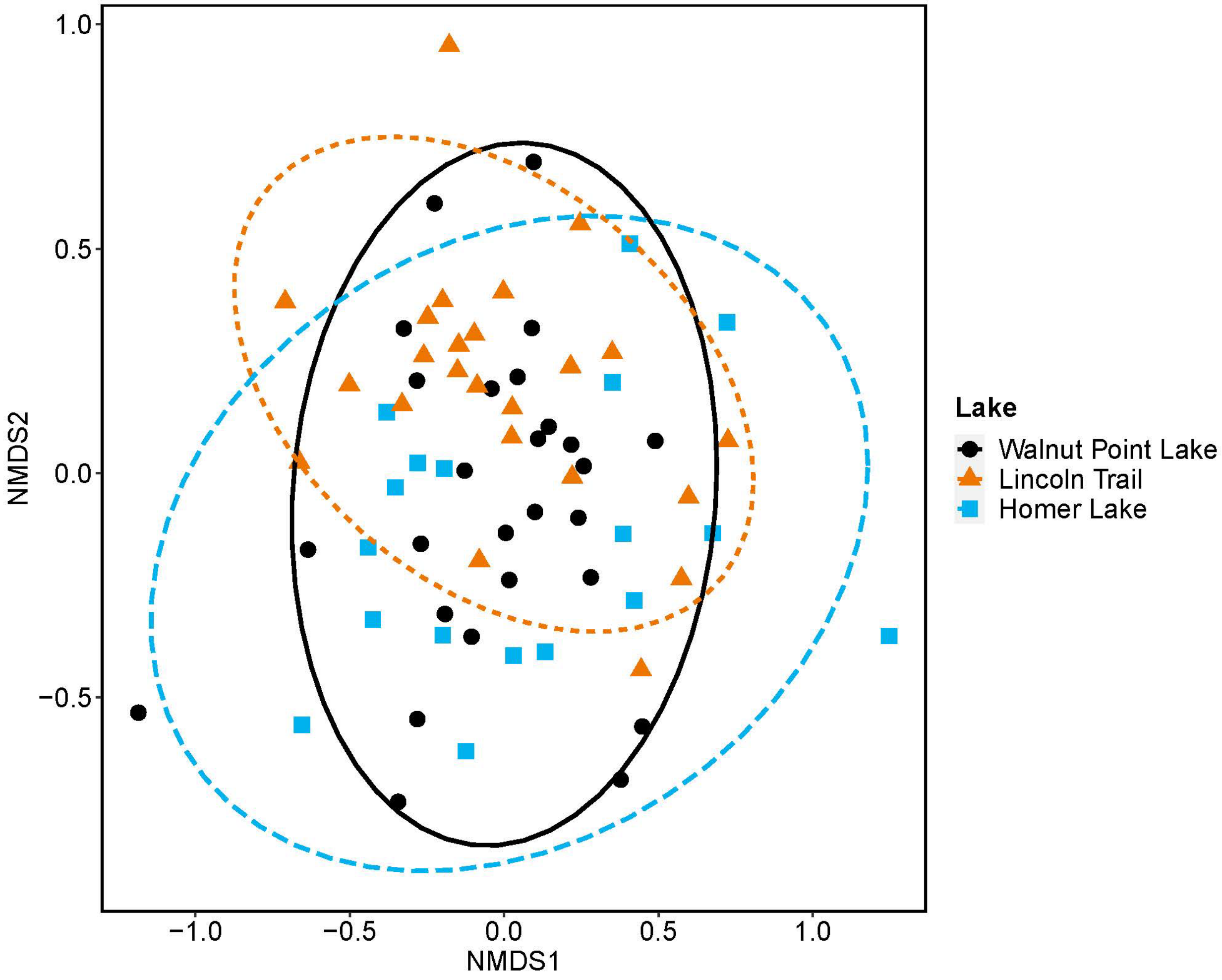


Figure 2.9 Non-metric multidimensional scaling plot of macroinvertebrate assemblage structure based on D-net sweeps from CWH during 2018-2021 in Walnut Point Lake (black circles), Lincoln Trail Lake (orange triangles), and Homer Lake (blue squares). Ellipses indicate a 95% confidence limit.

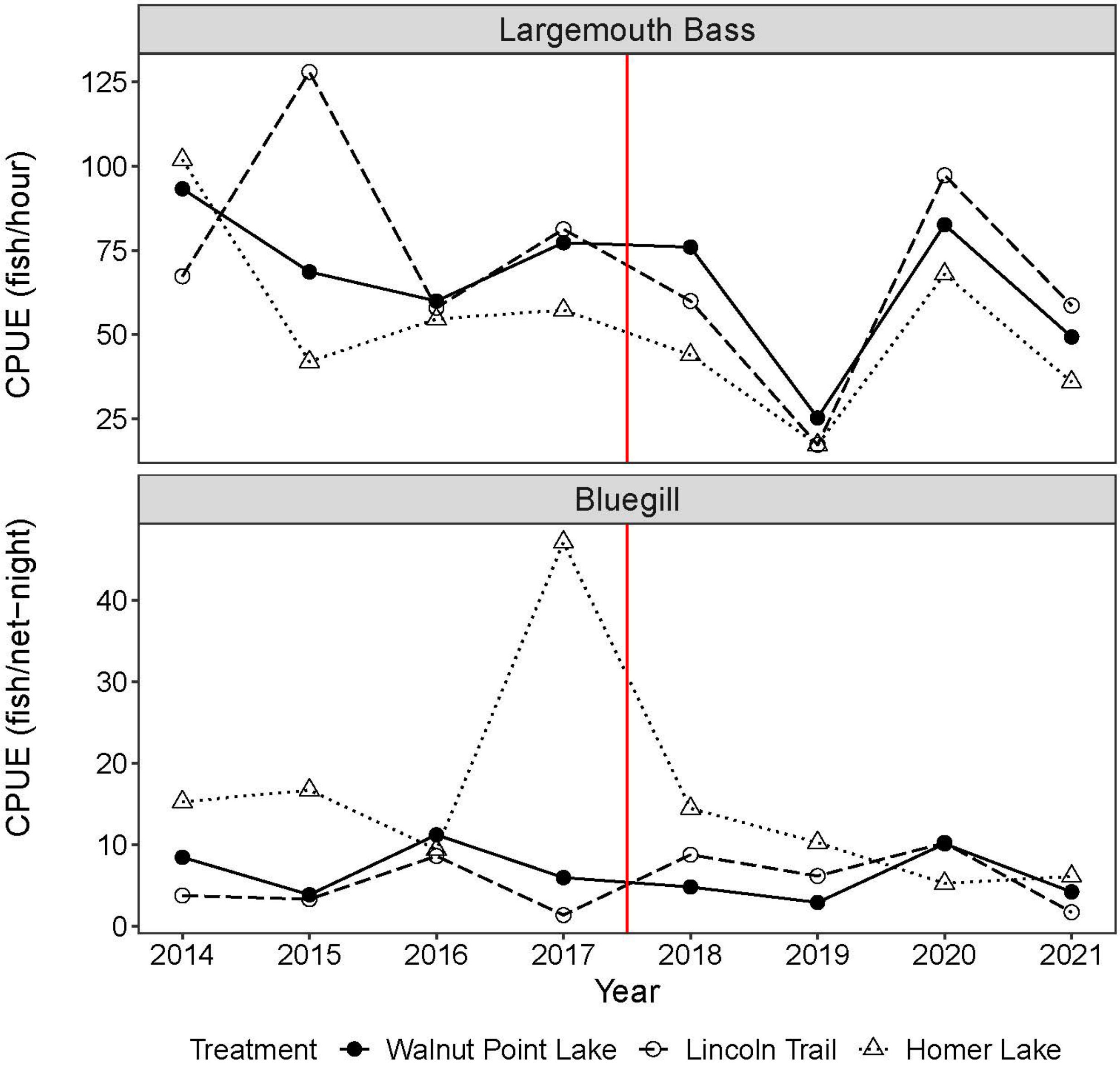


Figure 2.10 Catch per unit effort of largemouth bass (fish/hour) collected during electrofishing surveys and bluegill (fish/net-night) collected during fyke netting surveys from Walnut Point Lake (treatment, solid line and filled circles), Lincoln Trail (reference, dashed line and open circles), and Homer Lake (reference, dotted line and open triangles) throughout the eight-year study period during 2014-2021. The red vertical line indicates when CWH was added to Walnut Point Lake (January 2018).

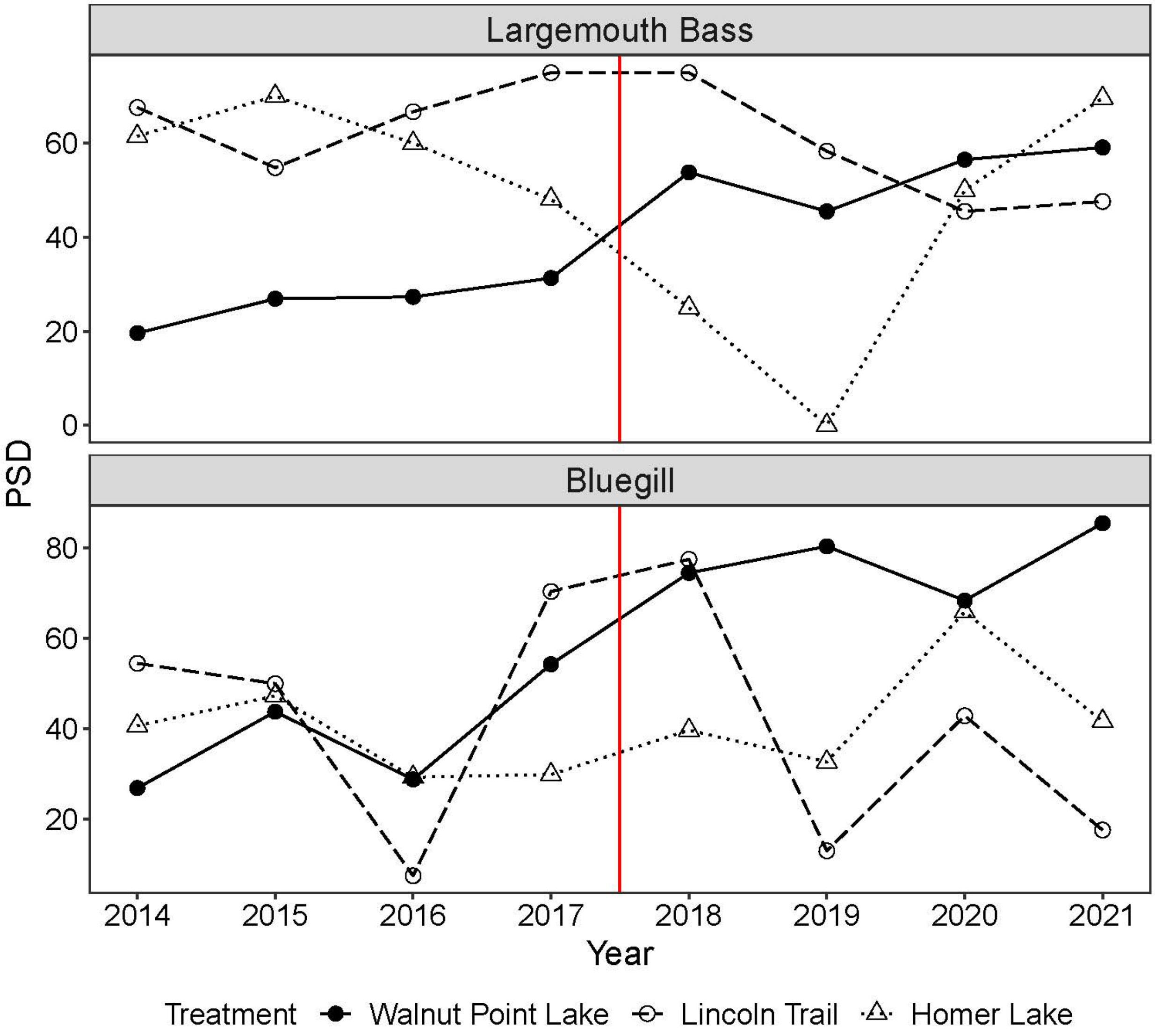


Figure 2.11 Proportional size distribution (PSD) of largemouth bass collected during electrofishing surveys and bluegill (fish/net-night) collected during fyke netting surveys from Walnut Point Lake (treatment, solid line and filled circles), Lincoln Trail (reference, dashed line and open circles), and Homer Lake (reference, dotted line and open triangles) throughout the eight-year study period during 2014-2021. The red vertical line indicates when CWH was added to Walnut Point Lake (January 2018).

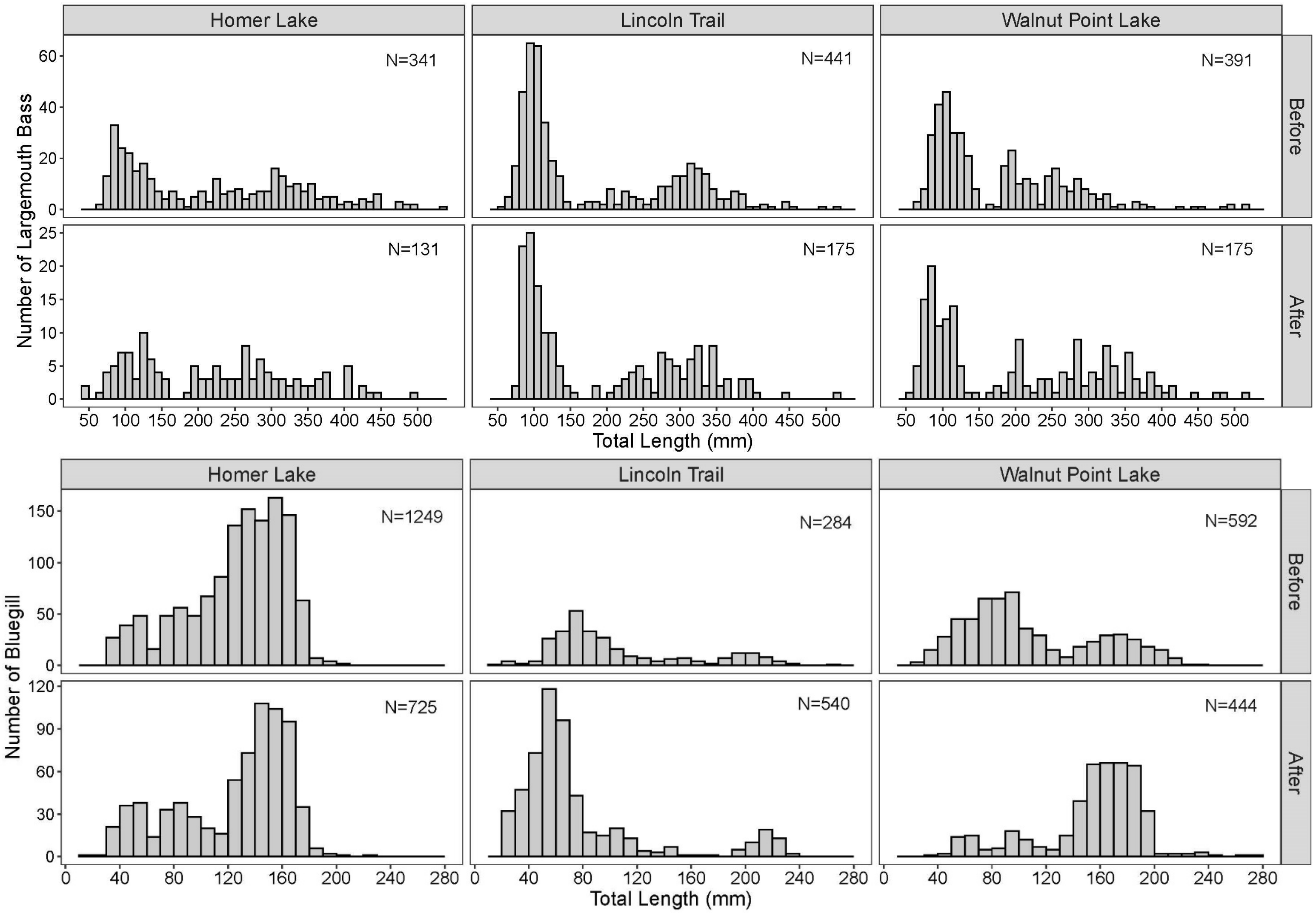


Figure 2.12 Length-frequency distributions for largemouth bass (top) and bluegill (bottom) from Homer Lake, Lincoln Trail Lake, and Walnut Point Lake. "Before" represents data pooled during 2014-2017, prior to the addition of CWH to Walnut Point Lake, and "after" represents data pooled during 2018-2021, the post-addition monitoring period.

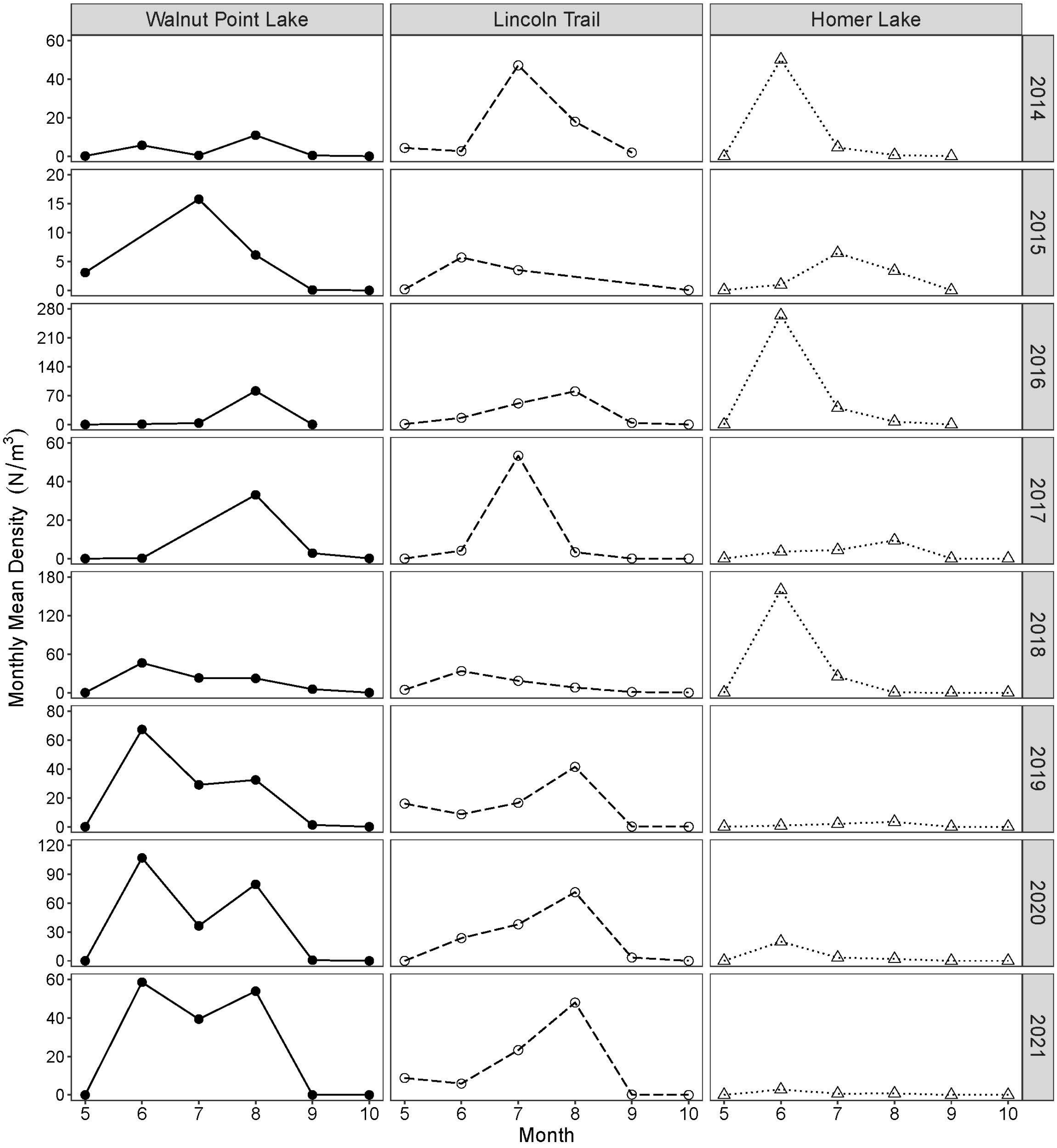


Figure 2.13 Monthly mean density of larval *Lepomis* (N/m^3) in Walnut Point Lake, Lincoln Trail Lake, and Homer Lake during 2014-2021. CWH was added to Walnut Point Lake in January 2018.

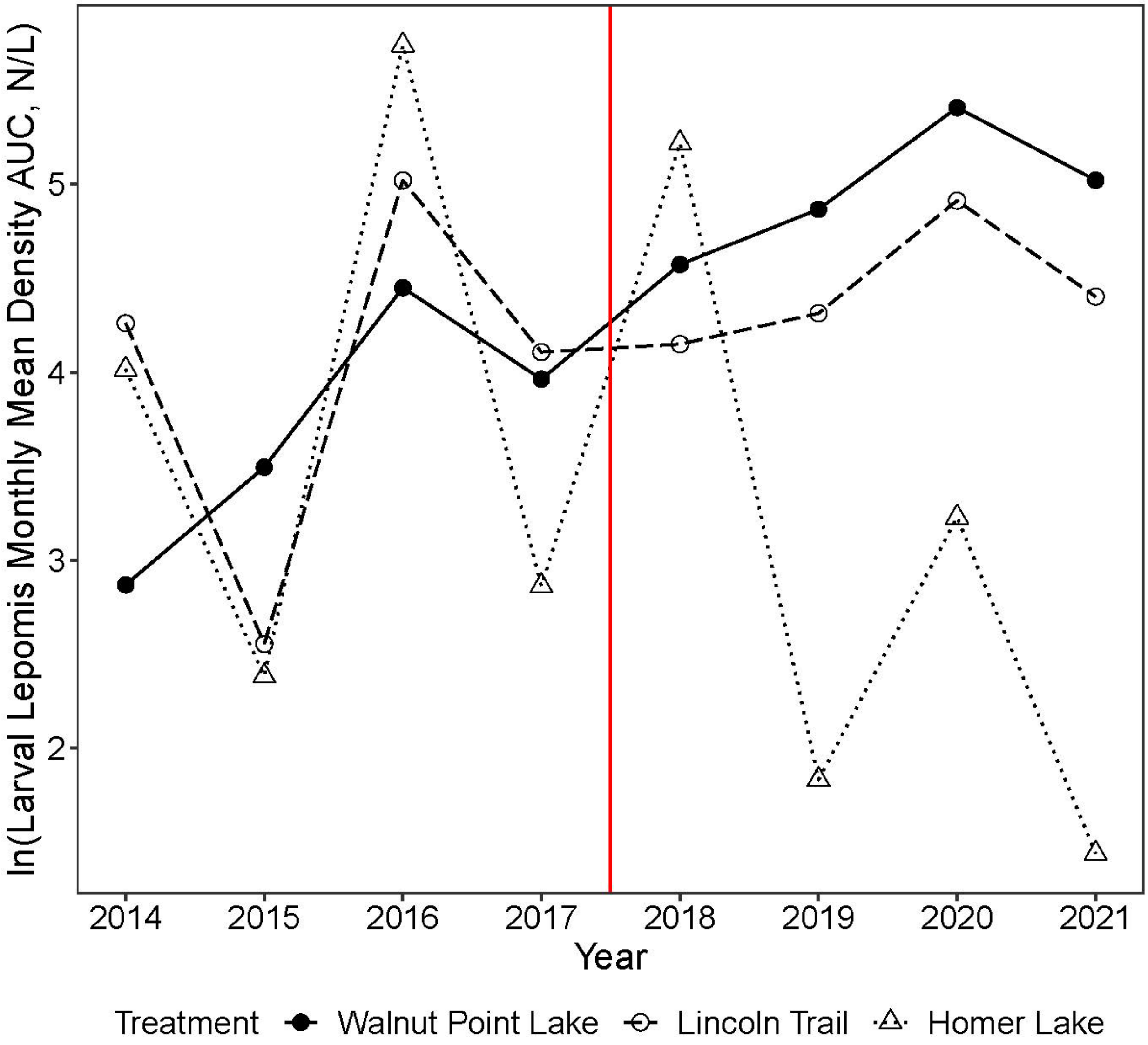


Figure 2.14 Larval *Lepomis* area under the curve (AUC) from monthly mean density (individuals/m^3) in Walnut Point Lake (treatment, solid line and filled circles), Lincoln Trail (reference, dashed line and open circles), and Homer Lake (reference, dotted line and open triangles) during the eight-year study period, with the red vertical line indicating when CWH was added to Walnut Point Lake (January 2018).

CHAPTER 3: PATTERNS OF FISH OCCUPANCY AND CATCH RATES AT OFFSHORE SYNTHETIC HABITAT STRUCTURES IN A LARGE RESERVOIR

Introduction

Restoring degraded fish habitat in aging reservoirs has become a major objective for anglers, stakeholder groups, and management agencies (Miranda et al. 2010). This objective is increasingly addressed through habitat enhancement efforts that supplement lost natural structures such as coarse woody habitat (CWH) with artificial habitat structures (Tugend et al. 2002). Artificial habitat structures range in materials from evergreen and hardwood trees to synthetic structures composed of plastics (Bolding et al. 2004). The longevity and cost of artificial habitat structures are frequently the deciding factors for use by fisheries managers (Baumann et al. 2016). Brush piles, evergreen trees, and other CWH additions are inexpensive compared to commercial fish attractors but degrade and lose complexity rapidly and may be locally unavailable (Tugend et al. 2002; Daugherty et al. 2014; Baumann et al. 2016). Thus, adding CWH may only provide short-term benefits to a fishery before needing to be replaced. As a result, many organizations and agencies design and build their own artificial habitat structures from polyethylene or PVC pipe, which are relatively inexpensive to construct and can last 100s of years or more (Baumann et al. 2016; Driscoll et al. 2020).

Plastic structures are assumed to function similarly to habitats composed of natural materials by providing refuge for juvenile fish, spawning habitat, and foraging opportunities for adult fishes (Bassett 1994; Tugend et al. 2002). Comparisons have been made between different plastic designs (Rogers and Bergersen 1999) and between woody and plastic structures (Rold et al. 1996; Magnelia et al. 2008; Baumann et al. 2016) to determine which material type and design is the most effective at concentrating fish. However, the long-term (i.e., multiple years) effectiveness of plastic habitat structures in meeting management objectives has not been assessed despite their physical longevity and widespread adoption where legal.

In large reservoirs, the ability of artificial structures to achieve management objectives over time may depend on seasonal changes in fish distribution (Moring and Nicholson 1994; Daugherty et al. 2014) and local (i.e., at the scale of the structure; Walters et al. 1991; Allen et al. 2014) and longitudinal physical and chemical conditions (Daugherty et al. 2014; Sass et al. 2022). During spring/early summer spawning, centrarchids use inshore areas and move to offshore areas during peak summer and winter temperatures to seek thermal refuge (Markham et al. 1991; Guy et al. 1992; Suski and Ridgway 2009). Abiotic factors, such as water temperature and dissolved oxygen, likely have a great influence on use of artificial habitats by fishes because if temperature and dissolved oxygen requirements are not met, then artificial structures will likely be devoid of fish. Centrarchids have been shown to avoid artificial structures when water temperatures are < 10-12 °C (Moring and Nicholson 1994; Daugherty et al. 2014). In the summer during thermal stratification, fish are vertically distributed above the oxycline where optimal dissolved oxygen levels are present, making deployment depth of structures an important consideration (Bohnsack et al. 1991; Walters et al. 1991; Allen et al. 2014). Stratification is most prominent at the downstream end of large reservoirs because of greater depth compared to the upstream end where reservoirs are typically shallower, more turbid, and have more complex, structural fish habitat (Thornton et al. 1990; Miranda and Bettoli 2010; Sass et al. 2022). This longitudinal gradient of physical and biological conditions within reservoirs likely has a pronounced effect on the effectiveness of artificial habitat additions. The variability of environmental conditions is important to consider given the longevity of synthetic habitat structures.

The longevity of plastic fish habitats provides an opportunity to test for patterns of colonization and succession of freshwater fish communities, and thus offers insight into the long-term performance of these structures. Bohnsack and Sutherland (1985) asserted that fish communities took between one and five years to reach equilibrium; however, colonization of artificial structures is typically only studied for between four to 24 months (Moring and Nicholson 1994; Rold et al. 1996; Magnelia et al. 2008; Smith et al. 2022). Compared to successional patterns observed near artificial structures in regions with high fish diversity and mild seasonal changes in temperature (e.g., tropical regions; Santos et al. 2011), reservoirs in temperate regions may have stronger seasonal variation in fish composition near structures than long-term successional trends. However, this prediction has not been directly tested in temperate freshwater ecosystems because species turnover on artificial structures has not been studied over appropriate temporal scales. Furthermore, given that one of the motivations for using structures constructed of synthetic materials is their longevity, verification of their efficacy in concentrating fisheries-targeted species years after deployment is warranted.

I tested whether fish use (i.e., occupancy, catch per unit effort) of synthetic structures changed based on dissolved oxygen concentrations, the size of the habitat patch, structure location, and structure time at large within a large reservoir. I also examined fish assemblages associated with the synthetic structures by sampling event to test for seasonal changes and by structure age (time since deployment) to test for successional changes. I hypothesized that fish use would be more influenced by dissolved oxygen, habitat patch size, and structure location than structure age due to the structural integrity of synthetic materials. These factors have been shown to affect the ability of artificial habitats to attract fish (Bolding et al. 2004; Allen et al. 2014; Daugherty et al. 2014) but have not been directly evaluated regarding the longitudinal ecological gradient within a large reservoir.

Methods

Study Site

Lake Shelbyville is a 4,500-ha eutrophic reservoir (Shelby and Moultrie Counties, IL) constructed in 1970 by impounding the Kaskaskia River. It is managed by the US Army Corps of Engineers, St. Louis District for flood control, but also serves as an area for recreational opportunities and wildlife management. Water levels in Lake Shelbyville vary seasonally and have a targeted summer pool of 182.79 m and winter pool of 181.05 m although more extreme fluctuations are common. The mean depth is 5.8 m but reaches 18 m near the dam. Lake Shelbyville has 193 km of irregular shoreline with steep sloping banks caused by erosive processes such as water level fluctuations and wind/wave action. There is minimal structurally complex habitat because most of the standing timber has decayed in the last fifty years and siltation and turbidity hinder establishment of aquatic vegetation in the littoral zone. Common sportfish species include bluegill (*Lepomis macrochirus*), largemouth bass (*Micropterus salmoides*), black crappie (*Pomoxis nigromaculatus*), white crappie (*Pomoxis annularis*), white bass (*Morone chrysops*), yellow bass (*Morone mississippiensis*), walleye (*Sander vitreus*), sauger (*Sander canadensis*), muskellunge (*Esox masquinongy*), channel catfish (*Ictalurus punctatus*), and flathead catfish (*Pylodictis olivaris*). Gizzard shad (*Dorosoma cepedianum*) and freshwater drum (*Aplodinotus grunniens*) are also abundant fish species found in Lake Shelbyville (Illinois Natural History Survey unpublished data).

Artificial Structure Design

The US Army Corps of Engineers and the Illinois Department of Natural Resources began deploying artificial habitat structures into Lake Shelbyville in December 2016, with the goal of improving the fishery by supplementing fish habitat. There are currently over 1,100 synthetic cube structures throughout Lake Shelbyville. The synthetic habitat structures consist of two different designs, the Georgia cube which has been widely adopted throughout the United States and the Shelbyville cube. The Shelbyville cube is a modified version of the Georgia cube designed for improved largemouth bass attraction due to its taller profile (Rogers and Bergersen 1999). The Shelbyville cube is a plastic cube frame constructed from 3.81-cm PVC pipe and wrapped with about 28 m of 10.16-cm corrugated tubing. The Shelbyville cube dimensions are 1.14 m length by 1.14 m width by 1.52 m height, with six parallel and diagonal layers of corrugated tubing placed within the top interior of the frame to add complexity, while leaving an open space at the bottom (Figure 3.1). Each Shelbyville cube encompasses a volume of about 1.98 m^3. The Georgia cube is made from the same materials and encompasses a smaller volume of 1.18 m^3 with dimensions of 1.14 m length by 1.14 m width by 0.91 m height (Figure 3.2). The synthetic structures were deployed in clustered pairs and groups of the same design or a combination of both designs.

Fish Sampling

I selected 50 locations along the longitudinal ecological gradient of the reservoir (Figure 3.3) where two to six PVC cubes (patch size) were deployed from < 1 year to just under 5 years (structure age) and were at least 30-m from other added artificial structures (i.e., PVC cubes, stumps, rock piles, porcupine balls). In order to sample fish from these 50 cube locations, two separate boats were used, one to locate and identify the cubes using Garmin PanOptix LiveScope sonar and one to conduct deep-water AC boat electrofishing (Parkos et al. 2019; Porreca et al. 2022). Traditional boat electrofishing does not effectively sample fish from artificial structures at depth. Instead, a 240-V, three-phase AC generator and 3 booms with one dropper on each boom was used to target fish in deep water. The droppers were insulated with a cable that only exposed the electrode at a desired depth. The length of the exposed electrode was adjusted to account for differences in water temperature and conductivity, with a target of 7-8 amps during the sampling events (Porreca et al. 2022). The sonar boat was used to ensure that the electrofishing boat remained stationary directly over the structure during a 5-minute sampling period of continuous power. Each boat had a single dip-netter to collect any fish that emerged, while the sonar boat was used to capture fish out of reach of the electrofishing boat netter. All collected fish were identified to species and measured for total length (mm). The 50 cube locations were sampled three times (September 2021, November 2021, and March 2022), encompassing major seasonal changes in water temperature and dissolved oxygen. Temperature and dissolved oxygen was measured using a YSI sonde at the structure depth of each site during each survey.

Statistical Analysis

Non-parametric approaches were used to test for the effects of habitat patch (i.e., cube) age (time since deployment), size (number of cubes), and location (km from the dam) on the presence and numbers of fish. Fish presence/absence was modelled as a binomial response and catch per unit effort (CPUE; number of fish collected per 5-minutes of electrofishing sampling effort) was modelled with a negative binomial distribution to account for the over-dispersed count data. Tests were conducted as Type-III ANOVAs, with cube age binned into five age categories (0 = < 12 months, 1 = 12 – 23 months, 2 = 24 – 35 months, 3 = 36 – 47 months, 4 =

48 – 59 months) and distance from the dam natural log-transformed. Separate tests were conducted for each survey for each of the following occupancy and CPUE responses: all species combined, both *Pomoxis* species combined, and freshwater drum. Water temperature was not included as an explanatory factor and dissolved oxygen was only included as an explanatory variable in September models because environmental conditions such as temperature and dissolved oxygen at structure depth varied minimally within surveys, except for dissolved oxygen concentrations during September which ranged from 1.5 to 10.1 mg/L (Figure 3.4). Preliminary tests were conducted to verify that explanatory factors were not confounded. Cube location was only weakly correlated with patch size (Spearman's $r_s = +0.34$, $P = 0.02$, N = 50) and September dissolved oxygen (Spearman's $r_s = -0.35$, $P = 0.01$, N = 50), and structure age category did not differ in distance from the dam ($F_{4,45} = 2.29$, $P = 0.07$). Effects were considered significant at alpha = 0.05. All analyses were conducted with the generalized model procedure (GENMOD) in SAS version 9.4 statistical software. Additionally, to test whether seasonal or successional change occurred at PVC cubes, I used non-metric multidimensional scaling (NMDS) based on Bray-Curtis dissimilarity values that were cube root transformed to test whether if fish assemblage structure changed among surveys or between cube age categories. Assemblages were considered to be statistically different if there was no overlap in their 95% confidence intervals. NMDS plots were generated using the vegan package in RStudio software version 4.2.1.

Results

Environmental conditions varied among sampling events, with mean bottom temperature decreasing from September (24.6 ± 0.03 ºC) to November (13.5 ± 0.13 ºC) to March (5.8 ± 0.12

ºC), and mean bottom dissolved oxygen increasing from September (5.8 ± 0.28 mg/L) to November (7.3 ± 0.10 mg/L) to March (11.0 ± 0.08 mg/L). Mean structure depths changed relative to reservoir pool elevation and were shallowest during the September sampling event (5.43 m) and deepest during the November sampling event (6.89 m; Table 3.1).

A total of 421 fish comprising 15 species were collected from the PVC cube structures during the three sampling events. White crappie were the most common species collected throughout the study and comprised 56.2% of the total fish collected. Bluegill (14.8% of total) and freshwater drum (10.5% of total) comprised the majority of the remaining catch. Largemouth bass were rarely collected from the PVC cubes and only comprised 0.2% of the total fish collected (Table 3.2). Mean total length of all fish using the PVC cubes was 220.9 ± 5.8 mm with only 7.6% < 100 mm. Fish assemblages were similar among the three sampling events and among structure ages (Figure 3.5), and as a result, no further evaluations of assemblage structure were conducted. Two outlier sites contained only uncommon species (two yellow bass and one channel catfish in September and one channel catfish in November).

Overall, the percentage of cube structures occupied by fish was higher in March (70.0%) than in September (64.0%) and November (62.0%). Fish occupancy was not significantly influenced by any of the factors examined in the September and March surveys. In contrast, fish occupancy of cubes in November was influenced by structure age and location with occupancy highest at age-1 structures (89.0%) and percent occupancy higher in the lower half of the reservoir (80.0%; near to the dam) compared to the upper half of the reservoir (50.0%). Freshwater drum occupancy was not explained by structure age, patch size, or location, with *Pomoxis* the only specific fish group to be significantly affected by the tested factors (Table 3.3). Occupancy for *Pomoxis* was significantly influenced by dissolved oxygen in September and by structure age, patch size, and location in November and March. Age-1 structures had the highest occupancy of *Pomoxis* during the November (66.7%) and March (88.9%) surveys. Small habitat patches containing two cubes had the highest proportion occupied by *Pomoxis* in November (52.6%) and March (84.2%), with *Pomoxis* not present at intermediate sized habitat patches (4 cubes). *Pomoxis* occupied 70.0% (November) and 95% (March) of structures in the lower half of the reservoir (closest to the dam) compared to 20.0% (November) and 30% (March) in the upper half of the reservoir.

Mean CPUE of all fish at PVC cubes was 3.44 ± 0.69 fish per 5-min. sample in September, 1.50 ± 0.27 fish/sample in November, and 3.46 ± 0.60 fish/sample in March. Fish counts (i.e., CPUE) were significantly influenced by bottom dissolved oxygen in September, while location influenced fish counts in November and March (Table 3.4). September CPUE was positively related to bottom dissolved oxygen concentrations, such that 79% of fish were collected at PVC cubes with dissolved oxygen levels > 5.0 mg/L in September (Figure 3.6). Mean CPUE was higher at PVC cubes in the lower half of the reservoir (close to the dam) compared to the upper half of the reservoir for all sampling months (Figure 3.7). Catch per unit effort of *Pomoxis* was most supported by structure age and dissolved oxygen in September, patch size and location in November, and structure age, patch size, and location in March. Catch per unit effort of *Pomoxis* was highest at age-1 cubes (3.11 ± 1.29 fish/sample) and age-4 cubes (3.08 ± 1.84 fish/sample) in September and was highest at age-4 cubes (4.17 ± 1.47 fish/sample) in March. Additionally, *Pomoxis* CPUE was highest for the smallest habitat patches (two cubes) during all three sampling events (Table 3.5). Since *Pomoxis* comprised the majority of the fish using PVC cubes, spatial pattern of *Pomoxis* CPUE was similar to that of total fish, being highest at sites closer to the dam. Freshwater drum CPUE was not related to any of the tested factors during the three sampling months. Though distance from the dam did not significantly influence CPUE of freshwater drum, 90% of freshwater drum captured during this study were collected from PVC cubes located in the upper half of the reservoir.

Discussion

Overall, PVC cubes in Lake Shelbyville were effective at attracting cover-seeking centrarchids, specifically *Pomoxis* and *Lepomis* species, and fish use (i.e., occupancy and catch per unit effort) of the offshore PVC structures varied seasonally and spatially. More structures were occupied by higher relative abundances of fish in March when the reservoir was well-mixed and fish activity was likely to be low due to cold water temperatures (Suski and Ridgway 2009). After fall turnover (November and March), location influenced the relative abundance of fish at PVC structures, while dissolved oxygen concentrations influenced fish abundance during thermal stratification (September). Structure age, habitat patch size, and location affected *Pomoxis* occupancy and abundance in November and March. As expected, the oldest structures continued to concentrate fish, with spatio-temporal environmental conditions the most important factors affecting fish use of synthetic habitat structures in Lake Shelbyville.

Artificial habitat additions constructed from synthetic materials do not degrade rapidly like those constructed from natural materials such as evergreen trees and bush piles (Wilbur 1978; Walters 1991; Rogers and Bergersen 1999; Bolding et al. 2004; Daugherty et al. 2014; Baumann et al. 2016). The oldest PVC cubes in Lake Shelbyville were deployed about 5 years ago, and based on sonar imagery, remained intact with no signs of degradation. The ability of the PVC cubes to attract fish was maintained for several years (i.e., age-4 structures) and will likely persist for decades (Bolding et al. 2004; Baumann et al. 2016). PVC cubes that were deployed for less than one year held less fish on average than older structures during the September and March sampling events, even though fish attraction to newly added habitat is known to occur rapidly (Bohnsack and Sutherland 1985; Moring and Nicholson 1994). Also, age-0 structures were located in the upper half of the reservoir where catch rates were lower; therefore, fish use may be influenced by the location of these newly added structures rather than the time since deployment.

Fish use of PVC structures was affected by location within the reservoir during November and March. This pattern was driven by higher relative abundances of fish, mainly crappies and bluegill, using PVC cubes in the lower half of the reservoir despite these species being distributed at similar relative abundances in nearshore areas throughout the reservoir (Illinois Natural History Survey, unpublished data). Daugherty et al. (2014) also collected more bluegill and largemouth bass at added habitat in the lower portion of a Texas reservoir. Offshore PVC cubes did not effectively attract largemouth bass (Porreca et al. 2022), despite their observed use of synthetic structures in other large and small reservoirs (Rogers and Bergersen 1999; Driscoll et al. 2020). Largemouth bass may not use offshore structures if there is a lack of small prey fish present, as observed in this study, or low visibility at structure depth (Hambright 1991; Shoup and Wahl 2009). Increased turbidity has been shown to decrease predator foraging efficiency and reduce predator-prey encounter rates (Shoup and Wahl 2009; Ortega et al. 2020). Additionally, largemouth bass may prefer woody habitats found in the littoral zone (Magnelia et al. 2008; Allen et al. 2014; Daugherty et al. 2014). In general, natural habitat quality and quantity varies spatially in reservoirs, such that more complex habitat is available in upper reservoir regions (Daugherty et al. 2014; Sass et al. 2022), potentially diminishing the use of added synthetic habitats in those areas.

Water level fluctuations affect the amount of natural littoral habitat available for fish use in flood control reservoirs. Low water levels can expose littoral habitats and strand CWH reducing structural habitat complexity (Gaeta et al. 2014). In contrast, high water levels can flood terrestrial vegetation and provide additional complex habitats (Miranda 2017; Roy et al. 2021). Among the three sampling events in this study, water levels remained above normal summer pool and were highest during the November sampling event (+2.3 m). Added habitat structures may be used less often when there is more natural littoral habitat available (Rogers and Bergensen 1999; Wills et al. 2004). Structure depth was directly affected by water level fluctuations and has been shown to influence fish use of artificial habitats. For example, bluegill were more abundant in water depths of 3.0 m compared to 4.5 m in an Ohio reservoir (Walters et al. 1991). Bluegill in Lake Shelbyville used structures at a mean depth of 5.7 m, and overall, fish occupied structures at depths that ranged from 2.2 m to 9.4 m indicating that structure depth was not an important factor explaining fish use of PVC cubes.

Environmental constraints, as well as seasonal changes in fish movement and activity, are important temporal factors that can affect fish use of synthetic habitats (Markham et al. 1991; Walters et al. 1991; Suski and Ridgway 2009). In September, fish use of PVC cubes was most influenced by dissolved oxygen and less influenced by spatial factors such as structure age, patch size, and location, indicating the importance of structure placement above the oxycline. When stratification was still apparent, fish were collected from numerous structures with low dissolved oxygen concentrations (< 5.0 mg/L). Avoidance behaviors have been observed at lower oxygen concentrations (at or below hypoxic conditions; Whitmore et al. 1960; Coble 1982; Johnson and Lynch 1992), even though oxygen levels below 5.0 mg/L are known to be physiologically stressful for many fish species (Davis 1975). Contrary to previous studies that observed fishless littoral structures when surface water temperatures dropped below 10-12ºC (Moring and Nicholson 1994; Rold et al. 1996), fish occupancy and mean CPUE at the synthetic habitat structures in Lake Shelbyville were highest in March when the average bottom water temperature was 5.8ºC suggesting a potential increased use of offshore habitat structures during cold temperatures. Centrarchids are known to move to deeper water over winter and reduce their activity levels (Moring and Nicholson 1994; Suski and Ridgway 2009). Additionally, white crappie are morphologically adapted to open-water, pelagic environments (Porreca et al. 2020), making them more likely to be found further offshore at the PVC structures compared to other centrarchids.

My study showed that offshore PVC structures effectively attracted fish through time (< 5 years) as a result of the maintained structural integrity of plastic, and thus making the use of offshore synthetic habitat structures a favorable option in flood-control reservoirs with large water level fluctuations. The location of structure placement was found to be an important factor affecting fish use of the offshore, synthetic habitats. As a result, offshore structures may be most effective at attracting fish in areas where natural habitat is limiting, dissolved oxygen concentrations are high, and turbidity is low. Explicit consideration of habitat location within the broad spatial pattern of reservoir conditions may provide a foundation for improving the efficacy of artificial habitat additions in large, eutrophic reservoirs.

Tables and Figures

Table 3.1 Mean (± 1 SE) summary characteristics of the three sampling events at the 50 synthetic structure locations during September 2021, November 2021, and March 2022 in Lake Shelbyville, Illinois. Pool elevation represents the water level at the time of each survey.

Metric	September 2021	November 2021	March 2022
Pool Elevation (m)	183.6	185.1	183.7
Mean Structure Depth (m)	5.43 (0.15)	6.89 (0.15)	5.66 (0.14)
Mean Bottom Temperature (℃)	24.56 (0.03)	13.51 (0.13)	5.83 (0.12)
Mean Bottom Dissolved Oxygen (mg/L)	5.84 (0.28)	7.27 (0.10)	11.00 (0.08)
Mean CPUE (fish/5-min. sample)	3.44 (0.69)	1.50 (0.27)	3.46 (0.60)

Table 3.2 Total catch and percent composition of all fish species collected from the 50 PVC cube structures during three sampling events (September 2021, November 2021, and March 2022) in Lake Shelbyville, Illinois. Fish were sampled with AC boat electrofishing modified to incapacitate fish at the depth of structures.

Species	Number Collected	Composition
White Crappie, *Pomoxis annularis*	236	56.2%
Bluegill, *Lepomis macrochirus*	62	14.8%
Freshwater Drum, *Aplodinotus grunniens*	44	10.5%
Black Crappie, *Pomoxis nigromaculatus*	19	4.5%
Gizzard Shad, *Dorosoma cepedianum*	17	4.0%
Bigmouth Buffalo, *Ictiobus cyprinellus*	12	2.9%
Smallmouth Buffalo, *Ictiobus bubalus*	8	1.9%
Yellow Bass, *Morone mississippiensis*	5	1.2%
White Bass, *Morone chrysops*	4	1.0%
Common Carp, *Cyprinus carpio*	3	0.7%
Hybrid Sunfish	3	0.7%
Channel Catfish, *Ictalurus punctatus*	2	0.5%
Longear Sunfish, *Lepomis megalotis*	2	0.5%
River Carpsucker, *Carpiodes carpio*	2	0.5%
Largemouth Bass, *Micropterus salmoides*	1	0.2%

Table 3.3 Statistical summary (*P*-values) of ANOVA analyses testing for factors influencing occupancy of all species combined, *Pomoxis*, and freshwater drum at synthetic habitat structures in Lake Shelbyville, Illinois. “DO” = dissolved oxygen recorded at the structure. Bolded *P*-values are significant at alpha = 0.05.

OCCUPANCY	SURVEY MONTH	AGE	SIZE	LOCATION	DO
ALL FISH	September	0.12	0.10	0.57	0.12
	November	**0.02**	0.49	**0.02**	–
	March	0.08	0.19	0.06	–
POMOXIS	September	0.08	0.64	0.42	**0.05**
	November	**0.02**	**0.02**	**0.002**	–
	March	**0.0001**	**0.0001**	**0.0001**	–
FRESHWATER DRUM	September	0.77	0.55	0.63	0.99
	November	0.23	0.74	0.12	–
	March	–	–	–	–

Table 3.4 Statistical summary (*P*-values) of ANOVA analyses testing for factors influencing CPUE of all species combined, *Pomoxis*, and freshwater drum at synthetic habitat structures in Lake Shelbyville, Illinois. “DO” = dissolved oxygen recorded at the structure. Bolded *P*-values are significant at alpha = 0.05.

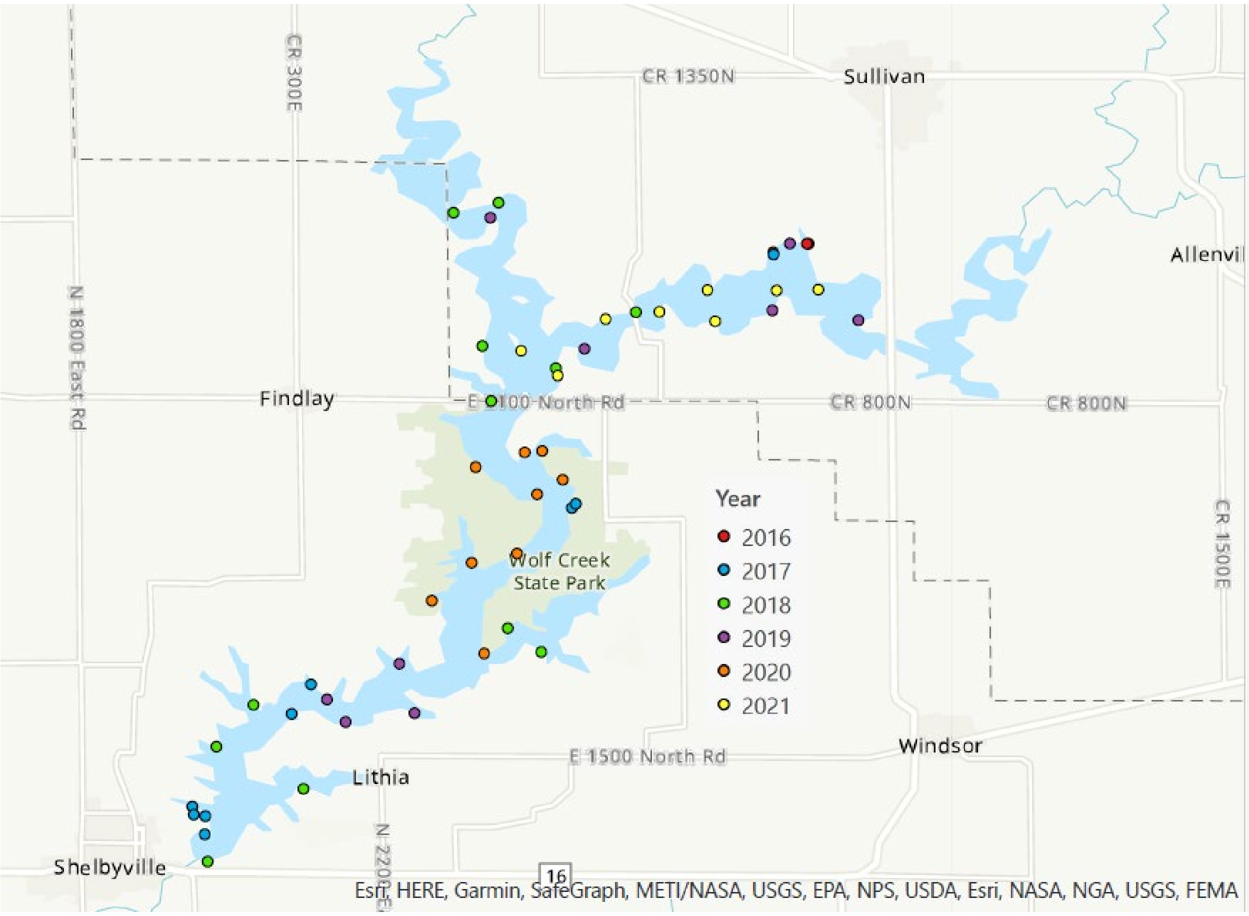
CPUE	SURVEY MONTH	AGE	SIZE	LOCATION	DO
ALL FISH	September	0.11	0.46	0.84	**0.008**
	November	0.06	0.23	**0.05**	–
	March	0.65	0.36	**0.04**	–
POMOXIS	September	**0.03**	0.43	0.60	**0.03**
	November	0.10	**0.04**	**0.01**	–
	March	**0.005**	**0.0009**	**0.007**	–
FRESHWATER DRUM	September	0.91	0.88	0.39	0.43
	November	0.22	0.94	0.24	–
	March	0.11	0.11	0.24	–

Table 3.5 Mean (± 1 SE) catch per unit effort of *Pomoxis* collected from PVC cubes of various age categories (time since deployment) and habitat patch sizes (number of cubes per site) in Lake Shelbyville, Illinois during three sampling events. Count refers to the number of sampling sites (grand total = 50) within each age category.

Structure Age	**Count**	**September 2021**	**November 2021**	**March 2022**
0	8	0.13 (0.13)	0.63 (0.50)	0.13 (0.13)
1	9	3.11 (1.29)	1.22 (0.62)	2.44 (0.75)
2	11	1.36 (0.65)	0.36 (0.20)	1.82 (0.90)
3	10	1.00 (0.60)	1.00 (0.37)	3.00 (1.29)
4	12	3.08 (1.84)	0.92 (0.42)	4.17 (1.47)
Patch Size	**Count**	**September 2021**	**November 2021**	**March 2022**
2	19	2.74 (1.20)	1.16 (0.30)	4.74 (1.07)
4	6	1.00 (0.82)	0.00 (0.00)	0.00 (0.00)
5	8	0.50 (0.38)	0.38 (0.26)	1.25 (0.75)
6	17	1.71 (0.76)	0.94 (0.40)	1.35 (0.49)

Figure 3.1 Shelbyville cube design.

Figure 3.2 Georgia cube design (short) next to Shelbyville cubes (tall).



Esri, HERE, Garmin, SafeGraph, METI/NASA, USGS, EPA, NPS, USDA, Esri, NASA, NGA, USGS, FEMA

Figure 3.3 Map of Lake Shelbyville, Illinois showing the locations of the 50 selected PVC cube structures and color coded based on the year of deployment. Cubes were sampled for fish September 2021, November 2021, and March 2022.

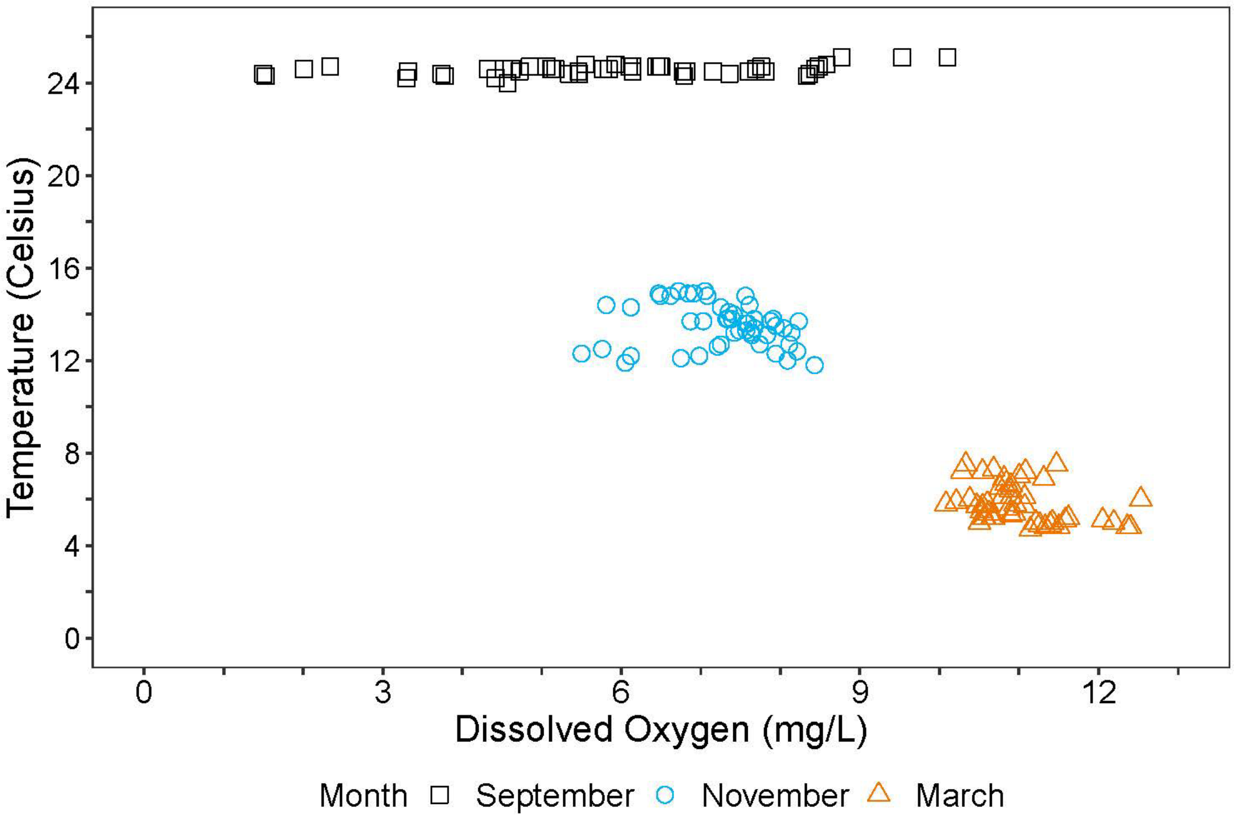


Figure 3.4 Dissolved oxygen concentration (mg/L) versus temperature (℃) for each sampling site during September (black squares), November (blue circles), and March (orange triangles) in Lake Shelbyville, Illinois.

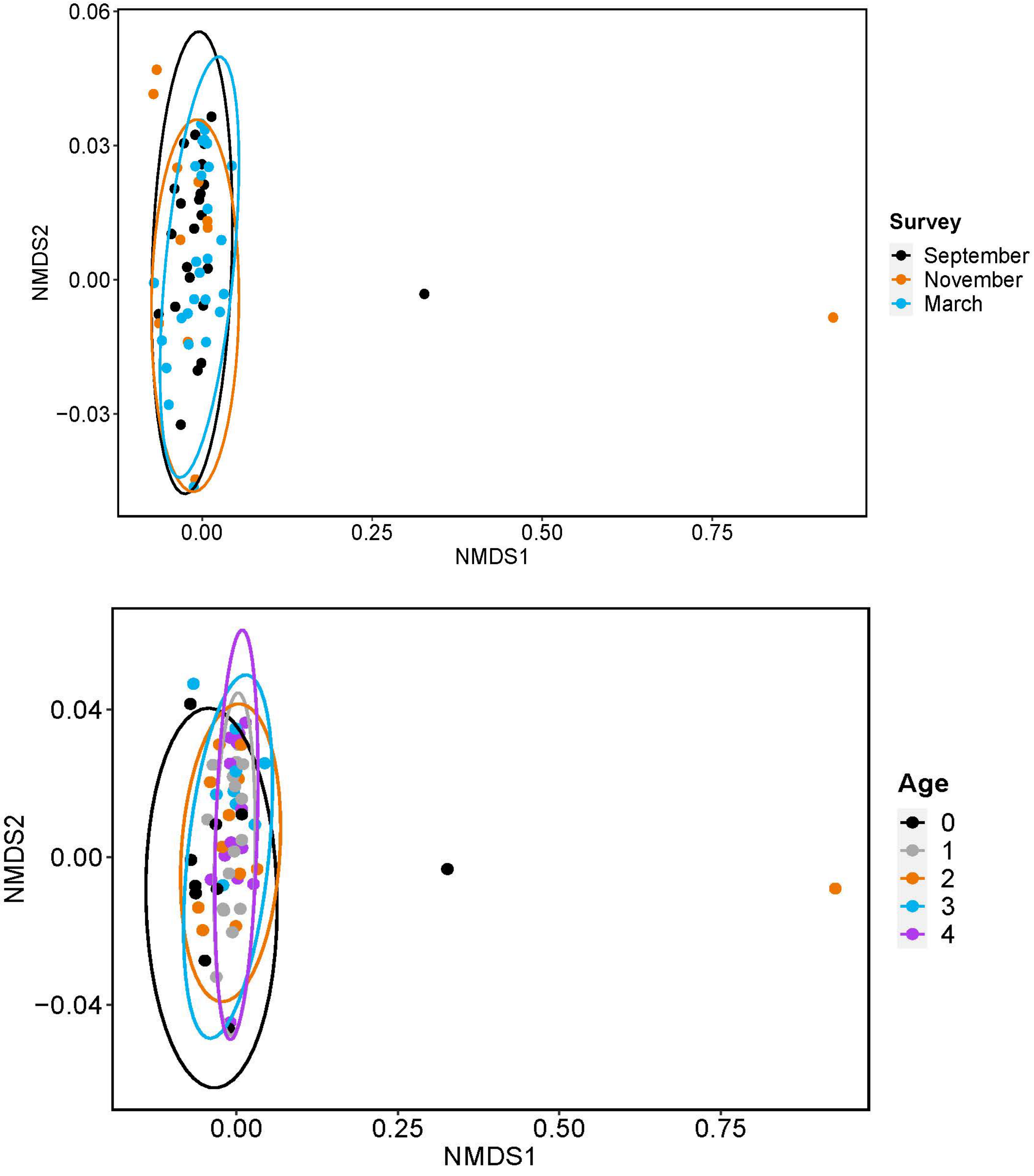


Figure 3.5 Non-metric multidimensional scaling plot of fish assemblages (A) during each sampling event in September 2021 (black), November 2021 (orange), and March 2022 (blue) and (B) among structure age class 0 (black), 1 (grey), 2 (orange), 3 (blue), 4 (purple) in Lake Shelbyville, Illinois. Ellipses indicate a 95% confidence limit.

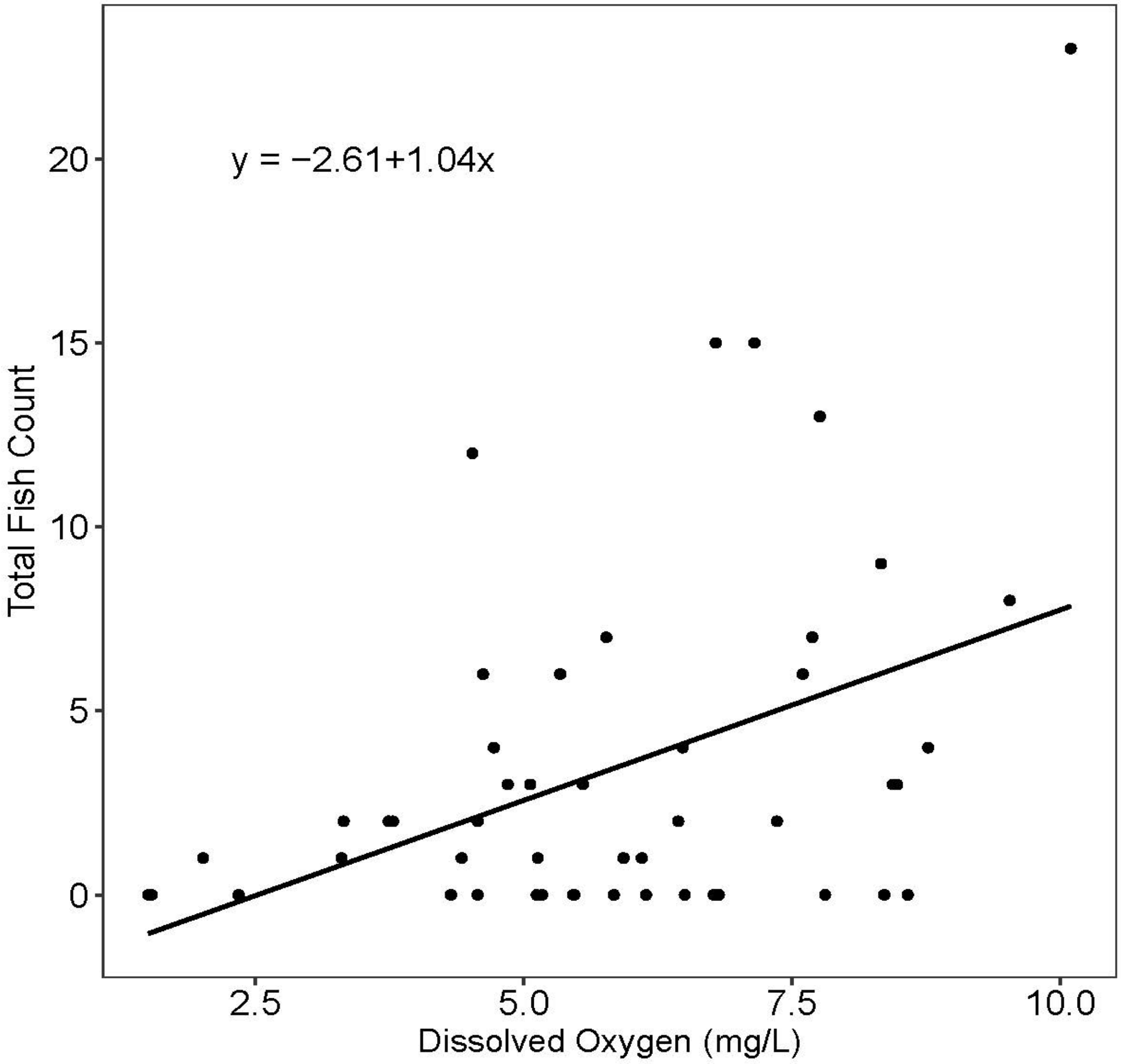


Figure 3.6 Dissolved oxygen concentration (mg/L) versus total fish count (CPUE) for each sampling site during September 2021 in Lake Shelbyville, Illinois.

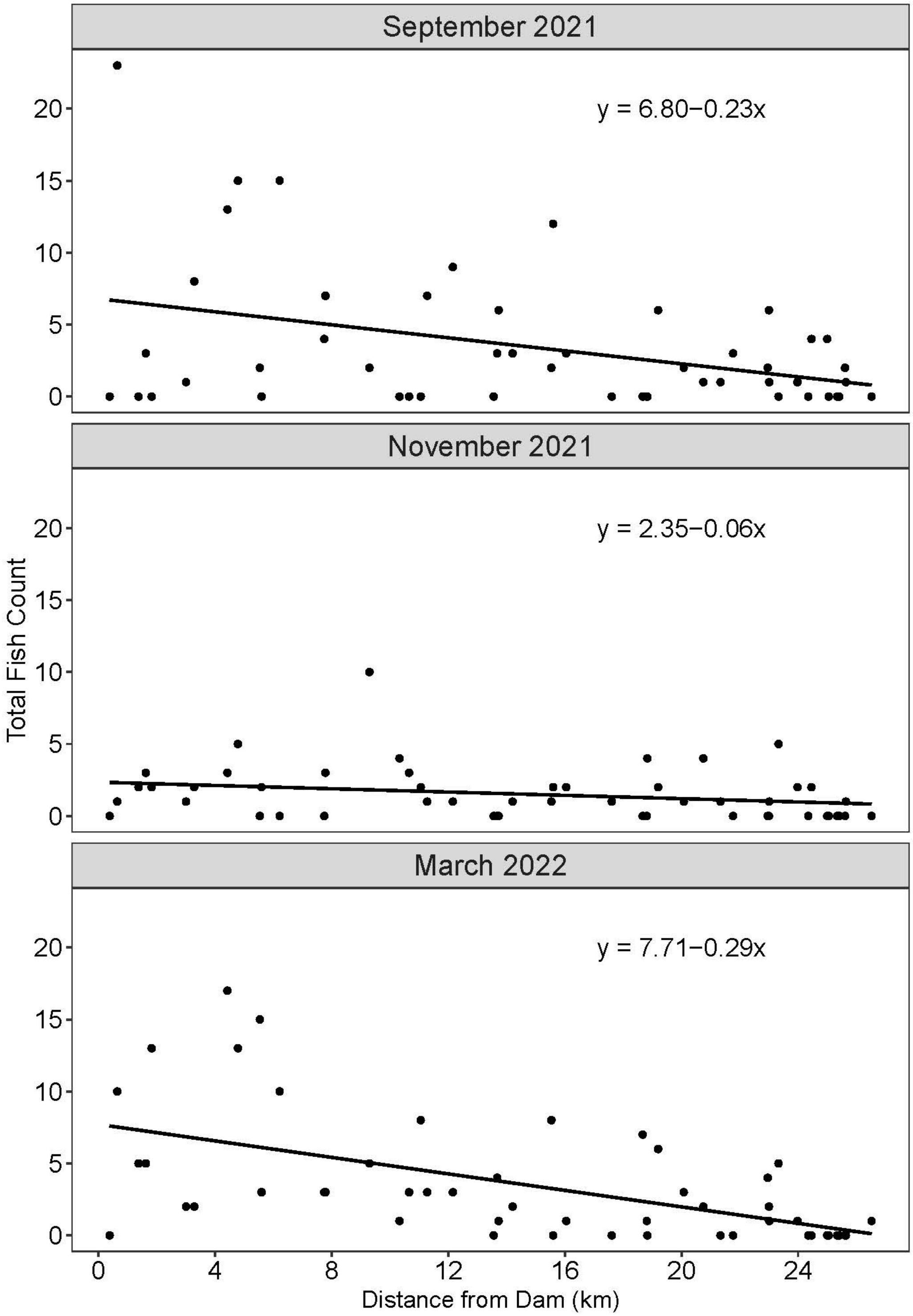


Figure 3.7 Total fish counts (CPUE) as a function of distance from the dam (km) for each sampling site during September 2021, November 2021, and March 2022 in Lake Shelbyville, Illinois.

CHAPTER 4: SUMMARY AND BROADER IMPLICATIONS

Illinois reservoirs have surpassed a mean age of 57 years old (National Inventory of Dams) and are undergoing progressive degradation of structural habitat that is critical to the life histories of many fishes (Sass 2009; Miranda et al. 2010; Lawson et al. 2011). The increasing need for habitat enhancement has anglers, stakeholder groups, and management agencies installing large-scale, artificial fish habitats without knowing the implications for reservoir ecosystems. Walnut Point Lake and Lake Shelbyville, two reservoirs that differ in surface area and water level stability, received different large-scale habitat additions to address the lack of structural fish habitat in each reservoir [i.e., coarse woody habitat (CWH) and aquatic macrophytes]. Trees were felled along the entire shoreline of Walnut Point Lake, a small reservoir with relatively stable water levels, to mitigate the adverse effects of eutrophication on fish populations. Lake Shelbyville, a large, flood-control reservoir that experiences shoreline erosion from substantial water level fluctuations and wind/wave action, had more than a thousand offshore synthetic habitat structures deployed over the last five years to improve the recreational value of the fishery and to maintain angling success. Although management objectives ultimately control what type of habitat additions are implemented, consideration of in-reservoir biotic and abiotic factors is also important as these factors influence the ability of artificial habitat structures to attract fish and their potential to increase fish production.

In Chapter 2, I found that the whole-lake CWH addition of Walnut Point Lake increased the size structure of the bluegill and largemouth bass populations yet had no effect on the relative abundance of these species and their prey resources. Furthermore, reproductive output of *Lepomis* (primarily bluegill and redear sunfish), indexed as larval *Lepomis* density, only weakly increased following the CWH addition. The aggregation effect of CWH in this turbid, eutrophic reservoir may have altered the foraging behavior and increased the foraging efficiency of bluegill and largemouth bass. Because of the increases in population size structure, I expected a stronger response from *Lepomis* reproductive output, but this may have been masked by high larval mortality. Ecologically, four years of post-manipulation monitoring is a relatively short time to test for changes to fish populations after a manipulation but may be considered a time constraint from a management perspective. Expanding the temporal scale of large-scale evaluations may reveal positive, neutral, or negative responses that went undetected in the short-term. My case-study of a small, highly eutrophic reservoir showed that large-scale habitat additions may enhance fish productivity through the increased availability of spawning habitat, dietary shifts, altered foraging behavior, and increased foraging efficiency due to the aggregation effect of CWH. My results indicate that trophic state (i.e., eutrophic vs. oligotrophic) and turbidity may be important factors affecting ecosystem responses to habitat additions. Predator-prey interactions are negatively influenced by turbidity in eutrophic systems, but the addition of CWH may alleviate the challenge of encountering prey in highly turbid reservoirs. Furthermore, oligotrophic lakes have lower productivity, higher water clarity, and shorter growing seasons by which less extensive habitat enhancements may elicit fish community responses compared to that of eutrophic reservoirs (Sass et al. 2022).

In Chapter 3, I found that fish aggregations at offshore synthetic PVC structures in Lake Shelbyville were dominated by white crappie and total fish occupancy and abundance varied seasonally. Fish relative abundance was influenced by dissolved oxygen concentrations at structure depth in September when the reservoir was thermally stratified and influenced by distance from the dam in November and March when fall and spring turnover resulted in more uniform temperature and dissolved oxygen conditions among sample sites. Higher relative abundances of fish were found at PVC structures in the lower region of the reservoir. As expected, due to the longevity of plastic, fish use of PVC structures was not strongly affected by structure age (time since deployment) and catch rates were highly variable among structure age classes. My study showed that the location of added habitat is likely an important driver of fish aggregation at synthetic PVC structures due to variation in environmental conditions (i.e., reservoir morphometry, flow velocity, turbidity, primary productivity, and zooplankton abundance) along the longitudinal ecological gradient of large reservoirs.

Most studies on fish responses to habitat enhancements focus on the influence of placement and physical characteristics (i.e., material type, complexity, depth, size, shape, and configuration) of artificial habitat structures at a localized scale. As a result, studies that address the effects of artificial habitat additions from an ecosystem perspective with attention to the attraction-production hypothesis or the influence of the longitudinal spatial heterogeneity in large reservoirs are limited (Sass et al. 2012; Daugherty et al. 2014; Miranda 2017; Sass et al. 2019). Large-scale habitat manipulations and accompanying assessments, such as those conducted in Walnut Point Lake and Lake Shelbyville, are challenging but understanding the effects at multiple spatial and temporal scales is vital for the guidance of future habitat enhancement programs in aging reservoirs.

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