

POTENTIAL INFLUENCES OF CLIMATE CHANGE AND TOURNAMENT ANGLING ON
LAKE ECOSYSTEMS WITH A FOCUS ON LARGEMOUTH BASS

BY

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THESIS

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ABSTRACT

Aquatic ecosystems and their inhabitants face a long list of threats to their well-being, and the effects of current stressors as well as those that may occur in the future must be assessed for their impact on these systems. Tournament angling an anthropogenic stressor that has the potential to negatively influence populations of popular sportfish, as fish are often removed from nesting grounds during the spawning season. While angled individuals often have limited reproductive success, the impact that these tournaments have on population-level recruitment and juvenile size structure is unclear. Using a replicated pond experiment with representative fish communities common in the Midwestern U.S., I gained insights into how competitive angling practices may affect largemouth bass (*Micropterus salmoides*), a common target of many fishing tournaments.

I also examined the potential effects of a warming climate on lake ecosystems of the Midwest. While the causes of global warming are debatable, there is significant evidence that suggests a warmer climate in the immediate future. Using power plant lakes across the central Midwestern U.S. as proxies for lake systems that may result from climate change, I compared a host of biotic and abiotic variables from these treatment lakes and control lakes of similar size and location, but lacking the artificially warm thermal regime. I found several differences between the two types of systems, including zooplankton concentration and community composition, fish growth, and fish spawning times. These differences lead me to conclude that regional lakes may change substantially in food web dynamics and ecosystem function in response to warmer climates. To determine potential impacts of warmer temperatures on fish health and thermal tolerance, I assessed tolerance of warmer temperatures of fish from both types of lakes using multiple methods. I found little difference in temperature tolerance between

largemouth bass from the different systems. I conclude that eurythermal species such as largemouth bass are able to tolerate a wide range of temperatures, and that similar species will likely be the most able to adapt and thrive in a changing climate.

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CHAPTER 1. POPULATION LEVEL CONSEQUENCES OF COMPETITIVE FISHING ON LARGEMOUTH BASS RECRUITMENT

ABSTRACT

Disturbances to spawning fish are known to affect reproduction among many species, and may have significant impacts on recruitment. Catch-and-release angling can cause such disturbances among popular sportfish, and the recent popularity of competitive angling could be even more problematic. Largemouth bass (*Micropterus salmoides*) are a common target of such tournament events, and practices associated with these tournaments have been shown to limit reproductive success among angled individuals. However, the impact of competitive fishing on population-level recruitment and size-structure is unclear. In this study, I examined the effects of simulated angling tournaments on experimental populations of largemouth bass in replicated ponds. Over two years, I subjected treatment ponds to simulated tournament angling procedures, while control ponds were left undisturbed. I monitored nest success, size structure of young-of-year bass, and overall recruitment to the first fall in all ponds, as well as measured a host of environmental variables that could potentially influence characteristics of the juvenile bass population. Although nest success was much greater in control ponds, the average number of recruits to the fall did not differ between treatments. I did find differences in the size structure of young individuals between treatment and control ponds, with larger fish present in the control ponds. Zooplankton densities were important for largemouth bass recruitment, and other abiotic variables explained some of the variation in size structure, independent of treatment. My study suggests that although high levels of tournament-style angling may negatively affect individual reproduction and recruitment other factors may be more important in driving population-level processes. Additional research is also needed on larger systems.

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INTRODUCTION

Disturbance to fish during spawning periods and the resulting effect on individual fitness and reproductive success has been well-documented in several fish species (Lowerre-Barbieri et al. 2003; Schreck et al. 2001). The ability of an individual fish to rear viable offspring can be influenced by a number of natural and anthropogenic factors, including weather (Checkley et al. 1988), macrohabitat and microhabitat conditions (Able and Hagan 2003; Wu et al. 2003; Kjesbu et al. 1998), chemical toxicants (Sohoni et al. 2001; Neilson et al. 1984), characteristics of the parental adults (Parkos et al. 2011; Steinhart and Lunn 2011; Marteinsdottir and Steinarsson 1998), spawning site degradation (Winfield 2004), and even standard fisheries sampling practices (Siepker et al. 2006). Commercial fishing pressure also has obvious effects on population-level reproduction due to the removal of a portion of the potential parental stock. Angling can also contribute to decreased reproductive success through a variety of mechanisms, including direct mortality and harvest, delayed mortality (Dedual 1996), decreased ability and motivation to protect offspring (Suski et al. 2003a; Cooke et al. 2000; Kieffer et al. 1995), and reduction in broods by nest predators (Steinhart et al. 2004; Olson et al. 1995).

During the last 30 years, competitive angling tournaments have developed widespread prominence, and have the potential to affect fish populations more than other forms of angling, especially when tournament catch rates exceed harvest rates (Allen et al. 2004). These tournaments vary widely in size, frequency, and distribution, and the extent to which these affect targeted fish has been a topic of considerable interest. The majority of research has focused on the black basses (*Micropterus* spp.) since they represent the most important gamefish sought in competitive angling events (Siepker et al. 2007; Schramm et al. 1991). Tournament-induced mortality in bass has been observed at varying rates (Driscoll et al. 2007; Edwards et al. 2004; Wilde 1998), and is caused in part by adverse livewell conditions (Suski et al. 2007; Suski et al. 2005). Direct mortality has an obvious negative effect on individual reproductive success, but non-lethal effects of tournament conditions have also been linked to reduced reproductive success (Siepker et al. 2009; Hanson et al. 2008).

The extent to which reduced reproductive output of some individuals has on population-level recruitment is still relatively unknown, and there is an explicit need to quantify the effects of competitive fishing events for black basses at the population level (Cooke and Schramm 2007; Siepker et al. 2007; Suski et al. 2006; Quinn 2002; Philipp et al. 1997). Because of logistical limitations, most research in this area is limited to tournament angling effects at the individual level. Egg-guarding males subjected to simulated tournament components, including time away from the nest and distance released from the nest, demonstrate increased abandonment (Siepker et al. 2009), which is often triggered by a reduction in brood size by nest predators (Steinhart et al. 2004; Suski et al. 2003a). Bass subjected to a typical tournament treatment have been shown to abandon over 90% of nests (Diana et al. 2012a). There is also evidence that the stress induced in angled bass subjected to tournament stressors affects reproduction, including timing of

spawning and quality of progeny (Ostrand et al. 2004). Reproductive success is also negatively correlated with physiological disturbances resulting from tournament stress (Suski et al. 2003b).

Although studies exist implicating tournament angling on individual spawning success, there is little documented evidence of angling having definitive population-level effects. There is skepticism among scientists and managers alike that largemouth bass populations are at risk from tournament pressure (Schramm and Hunt 2007). Given the success of largemouth bass throughout most of its range regardless of fishing pressure this is likely true in most systems. However, in systems where variables such as suitable spawning habitat or prey availability constrain largemouth bass populations (Parkos and Wahl 2010), the possibility of another limiting factor should not be ignored.

Modeling has shown that the detrimental effects of tournament angling at the individual level may affect recruitment of black bass populations (Ridgway and Shuter 1997). However, compensatory mechanisms may contribute, at least in part, to overall recruitment. Competition for prey (Post et al. 1999), refuge from predators (Holbrook and Schmitt 2002), and cannibalism (Post 2003; Pine et al. 2000) are important density-dependent factors that determine juvenile survival in other fish species. If these or other mechanisms are present in largemouth bass populations, then the lack of reproductive success of some individuals may result in increased success of others. These relationships could negate the effects of angling, provided that some proportion of spawning bass are able to reproduce unhindered. Evidence that bass recruitment is independent of spawning stock densities (Allen et al. 2011; Garvey et al. 2002) furthers the argument that there may not be a relationship between the number of successful nests and number of recruits.

Previous research has simulated some aspects of tournaments to the point that they are no longer representative of actual tournament scenarios. In many instances, individual fish or nests are targeted for an extended period of time, or nests are randomly assigned for brood manipulation regardless of actions by the guarding male. Vulnerability to angling is quite variable among individual fish (Philipp et al. 2009; Cooke et al. 2007; Garrett 2002), and selecting treatment fish independent of methods employed by actual tournament anglers may misrepresent effects on fish populations. It is currently unknown if fish displaying high or low vulnerability to angling tend to contribute more or less to population recruitment, but it is plausible that such a link exists (Parkos et al. 2011). Likewise, it is unclear whether vulnerability to angling could be correlated with willingness to abandon nests after being angled, although metabolic rates and ability to defend a nest have been shown to positively covary with angling vulnerability (Nannini et al. 2011; Cooke et al. 2007). Because susceptible fish may be more important to population recruitment due to increased parental care activity and greater number of eggs (Suski and Philipp 2004), randomly removing fish may under-represent actual tournament effects. Variable nest defense and differences in vulnerability at different nest stages are also ignored when fish are removed randomly, and this practice is inconsistent with actual angling practices (Ridgway 1988). Thus, studies using manual removal of eggs and other methods that ignore individual differences among largemouth bass have limited inference in terms of population-level effects of tournament angling.

Because of the limitations of previous studies and lack of research focused on population-level effects of competitive fishing, I designed a replicated pond experiment with identical largemouth bass populations. I used a high level of tournament-style angling as the treatment, and determined the effect that this had as compared to unfished ponds. I sought to quantify the

effect that competitive angling events may have on bass populations in terms of numbers of young-of-year surviving to the fall, the size structure of juvenile fish, hatch dates of nests, and brood sizes. I also measured a number of environmental variables to assess their influence on young-of-year bass and for use as covariates in subsequent analyses.

METHODS

Experimental design

Eight, 0.4 ha ponds at the Sam Parr Biological Station in Marion County, Illinois were used for the experiment. The drainable, rectangular ponds (average depth = 1 m) were stocked in early spring of 2010 and 2011 with populations of wild-caught adult largemouth bass and adult bluegill (*Lepomis macrochirus*) obtained by electrofishing nearby lakes. Ten female and 12 male adult bass (280 - 430 mm) were stocked into each pond. Densities were based on largemouth bass population estimates from four representative Illinois reservoirs (Diana and Wahl 2009). Sex for each fish was determined using a 1 mm diameter straw to probe the urogenital opening (Benz and Jacobs 1986). Bluegill densities from spring seine hauls from 17 Illinois lakes between 2007 and 2009 were averaged to determine a representative density for each pond. As a result, 2,200 age-1 bluegill were stocked in each pond to simulate a typical lake ecosystem in the Midwestern U.S., and to serve as nest predators and resource competitors (Olson et al. 1995). An additional 15 adult male and 15 adult female bluegill were also stocked into each pond to produce juvenile bluegill to serve as prey for young largemouth bass as their diet shifts to piscivory, which generally occurs within the first few months after hatching (Olson 1996; Olson et al. 1995).

Tournament angling treatment

Each year, four ponds were randomly assigned to receive a tournament angling treatment, whereas the other four served as unfished controls. Treatment ponds received a simulated tournament twice a week throughout the duration of the spawning season, which typically encompasses April and May in the study region. Tournaments began when adult bass were first observed staging and nest-building (March 31 in 2010, April 8 in 2011), and continued until all nesting activities had ceased (May 13 in 2010, May 18 in 2011). I chose to begin simulated tournaments before males were observed directly guarding nests so that the prespawn period for females, during which disturbances have been shown to reduce reproductive output (Ostrand et al. 2004), was included in the treatment period.

An individual tournament consisted of two angler-hours per 0.4-ha pond, representing tournament pressure much greater than what is typically observed in Illinois (3-52 angler-hours / ha / year, Diana et al. 2012b). However, since my experimental ponds are composed entirely of littoral area and bass spawning habitat, as compared to the low percentage of suitable spawning habitat in most lakes, the actual amount of angling pressure on spawning fish is more similar between my treatment and what typically occurs in lakes. During each tournament, the pond was systematically fished so that the entire pond was covered by the anglers. Similar to previous studies examining catch and release angling, a white tube jig, a black plastic worm, and a gold surface lure were used in equal proportions (Philipp et al. 1997; Kieffer et al. 1995). Anglers with previous tournament experience were used for the angling, and they were instructed to catch as many fish as possible within the constraints detailed above. Anglers were encouraged to attempt to catch largemouth bass that were observed to be guarding nests, as they would

represent likely targets of actual tournament anglers and were expected to be the most susceptible to angling (Philipp et al. 1997).

Once caught, fish were subjected to a suite of simulated tournament conditions similar to those used by Hanson et al. (2008). Following capture, bass were initially held out of the water for two minutes for hook removal and measurement. Fish were then placed in separate 38 L insulated coolers with fresh pond water for four hours, during which time water was changed every hour to ensure proper aeration. After simulated livewell confinement, fish were again removed from water for three minutes to simulate tournament weigh-in. Each fish was weighed and measured at this time, and then released back into their respective pond.

Nest and Recruitment Monitoring

Active bass nests were monitored by snorkelers the day before and after each tournament so that nesting success and nest abandonment could be quantified. Date of appearance and location of nests in all ponds were recorded, and subsequent nest visits were used to determine hatch dates and nest abandonment. Each nest was also given an egg score from 1-4 to provide an estimate of its overall size (Kubacki 1992). Previous work has verified the correlation between egg scores and egg number estimates, with scores of 1 \approx 9,000 eggs, 2 \approx 13,000 eggs, 3 \approx 15,000 eggs, and a 4 \approx 29,000 eggs (Parkos et al. 2011). Nests were deemed to be abandoned when the parental male was absent from the nest for multiple observations prior to swim-up by the developing offspring.

In early July of each summer, after all spawning activities had ceased, 100 juvenile largemouth bass were removed from each pond via beach seine so that midsummer size structure could be determined. A group of these individuals (16-24) from each pond were also aged using

sagittal otoliths (Miller and Storck 1982) so that hatch dates of surviving individuals could be calculated. The early July sampling period was chosen so that the period of highest mortality of juveniles in the immediate weeks after hatching had passed, but before age estimates from sagittal otolith rings became less reliable (Miller and Storck 1982).

Ponds were drained in early October to quantify all juvenile bass surviving to the first fall, and at least 100 from each pond were weighed and measured. Although largemouth bass recruitment has been proposed to be determined as survival to age 1 after the first winter (Parkos and Wahl 2002; Ludsin and DeVries 1997), the abundance of post-winter largemouth bass recruits in Illinois lakes is generally determined by the number present in the previous fall (Parkos and Wahl 2010; Ostrand et al. 2005; Garvey et al. 2004; Fuhr et al. 2002), and post-winter abundance of juveniles is often correlated with abundance estimates from the preceding year (Jackson and Noble 2000).

Habitat Monitoring

Because experimental ponds can differ in habitat variables that may influence bass recruitment (Buck et al. 1970), several biotic and abiotic factors were sampled throughout the summer. Vegetation biomass was sampled monthly using a 50 cm diameter metal ring tossed at 10 random locations in each pond. All vegetation in each ring was then weighed and extrapolated to estimate total vegetation biomass for each pond. Zooplankton, benthic invertebrates, phytoplankton biomass, and total phosphorus concentration were also sampled monthly. Zooplankton were measured using a 7 cm diameter plastic tube (DeVries and Stein 1991) to take a 1 m deep integrated water sample from three random locations in each pond. The subsamples were then mixed, filtered through 64 μm mesh, and fixed in Lugol's solution until zooplankton

could be identified and enumerated. Four random locations in each pond were sampled for benthic invertebrates with a 20 cm diameter stovepipe sampler (McPeck 1990). The samples were filtered through a 600 μm mesh, preserved in an ethanol/rose bengal solution, and afterwards the benthic invertebrates were identified and counted. A subset of invertebrates were digitized and measured so that total benthic invertebrate biomass estimates could be made for each pond using established length-weight regression equations for each order (Sample et al. 1993; Smock 1980). Separate integrated water samples were used to determine total phosphorus content and phytoplankton biomass from chlorophyll *a* concentration (Welshmeyer 1994). Water transparency was also determined weekly using Secchi disk depths and then averaged for each month. To reduce the number of possible covariates and account for correlations in variables among months, all habitat variables were averaged for the early summer (May-June) and late summer (July-August).

Data Analysis

Differences in total numbers, biomass, and mean size of juvenile bass found in the fall between control and treatment ponds were tested using a one-way ANOVA, blocked by year. For each of these analyses, I tested for the significance of each habitat variable as covariates. T-tests were used to determine if the treatment influenced average hatch dates and overall egg scores. To more closely examine the factors that may drive largemouth bass reproduction, growth, and survival in the ponds, I then used regression models to examine these variables independent of treatment type. Each predictor variable (summer chlorophyll *a* concentration, phosphorus concentration, secchi depth, zooplankton density, benthic invertebrate biomass, and vegetation density for both the early summer and late summer) was tested for its ability to account for

variation in juvenile largemouth bass numbers and biomass, midsummer average length, and fall average length. The tournament angling treatment was also included in these analyses. Because of small sample size, tested models only included one predictor variable. AIC scores were used to determine the best model(s), with models having scores within two units of the “best” model AIC score were considered parsimonious and of equal predictive power (Burnham and Anderson 2002). A separate analysis was also conducted to examine the relationship between number of fish caught per pond and variables associated with the juvenile bass population. These tests were carried out similarly to the other regression analyses, but only included treatment ponds.

RESULTS

In total, 210 adult bass were angled from treatment ponds over the course of the experiment (112 in 2010, 98 in 2011). The number angled from each pond was relatively consistent (range of 17-37), and the sex ratio of angled fish was approximately equal to the ratio initially stocked (112 females, 98 males). Fifteen fish (7%) perished due to either hooking mortality or mortality from livewell confinement.

The initial effect of the treatment was evident in a lower pond-wide egg score of all successful nests in the treatment ponds (6.3) as compared to the unfished controls (12.8, $P = 0.01$). There was no difference in the average hatch date of aged individuals between the treatment groups ($P = 0.31$, Figure 1.1). There was a pronounced difference in hatch dates between years, with fish from 2011 averaging a birth date about eight days later than the previous year ($P < 0.001$). Covariates were not significant for any parameters of the juvenile largemouth bass population except for the number of recruits, where early zooplankton density was a significant covariate. The mean number of recruits per pond did not differ between control

ponds ($4,237 \pm 1,205$) and their angled counterparts ($2,588 \pm 1,205$, $P = 0.35$). In contrast, juvenile bass biomass differed and was greater in control ($17,433\text{g} \pm 2,735$) than treatment ponds ($9,009\text{g} \pm 2,735$, $P = 0.048$, Figure 1.2). I did not see a significant relationship, however, between the number of fish caught per treatment pond and either juvenile bass numbers ($R^2 = 0.14$) or juvenile bass mass ($R^2 = 0.02$).

The difference between treatments in number of recruits and the biomass of those recruits was due to differing size distributions between treatments. No differences existed in average length of juveniles sampled in early July ($P = 0.99$) and at time of draining ($P = 0.77$) between treatments. No differences existed between numbers of fish in small size classes ($P = 0.43$, Figure 3), but there were significantly more fish present in the control ponds that were larger than 120 mm ($P = 0.04$, Figure 1.4). Although the numbers of these larger fish was low, their exponentially greater weight had an effect on pond-wide biomass estimates.

Regression analysis using AIC selection criteria indicated that environmental variables were generally more influential predictors of largemouth bass growth and recruitment than the treatment (Table 1.1). Early (May-June) macrozooplankton density was strongly correlated with juvenile largemouth bass numbers ($R^2 = 0.70$, Figure 1.2). The tournament treatment had the most influence on juvenile largemouth bass biomass among possible predictor variables, although this model had relatively low predictive power ($R^2 = 0.24$). Average length of individuals in early July was best predicted by early summer turbidity, whereas early phosphorus concentration was the best predictor variable for average lengths of individuals in the fall. The treatment had little effect on average juvenile length in summer and fall (Table 1.1). Raw data used for these analyses can be found in Table 2.

DISCUSSION

There was evidence that tournament-style angling affected some metrics of largemouth bass populations under my experimental conditions. Overall number of juvenile bass was not influenced by the treatment, but initial number of eggs and final biomass were lower in treatment ponds, and I observed a low level of hooking- and confinement-induced mortality in adults consistent with rates found in other studies (Driscoll et al. 2006; Wilde 1998). The overwhelming majority of recruits in largemouth bass are composed of the earliest successful broods from the largest males (Parkos et al. 2011), and many of these early broods could have been eliminated by the tournament treatment, as they have been shown to also be the most vulnerable to angling (Sutter et al. 2012). This could allow later spawned broods to flourish instead. Lack of success of some early broods could explain the lack of large individuals surviving to fall. Health and size of broodfish could have also been diminished by stress to the parental adult (Ostrand et al. 2004; Schreck et al. 2001). However, the lack of differences in hatch dates of juveniles between treatment and control ponds suggests that early broods were not lost differentially in the angled ponds. Also, there has been little documented correlation between hatch dates and end-of-year lengths in largemouth bass, with other factors such as timing of the switch to piscivory being more important in determining resulting lengths (Rogers and Allen 2009; Post 2003; Post et al. 1998).

Greater size and biomass in control ponds could also result from cannibalism among faster-growing cohorts of young-of-year largemouth bass in the summer and early fall. Cannibalism is common among many piscivorous fishes, and has been documented among black basses (Smith et al. 2009; Swenson 2002; Pine et al. 2000; Johnson and Post 1996). The large individuals present in controls may have been cannibals that affected end of summer juvenile

numbers and size distributions. When densities of conspecifics were high, lower growth should have resulted due to competition for finite resources (Slaughter et al. 2008), but my results do not support this hypothesis. In Eurasian perch (*Perca fluviatilis*), cannibalism among juvenile fish led to significantly lower survival at high juvenile densities (Kestemont et al. 2003). Periods of prey resource limitation contributed to promoting cannibalism by forcing some individuals to change food preference and limiting growth of others (Bystrom et al. 2012). Victim density must also be great to make cannibalism profitable (Huss et al. 2010). The relationship I observed between zooplanktonic prey resources and juvenile fish abundance suggests resource limitation, at least during the period when zooplanktons were the preferred prey resource. High nest success observed in control ponds compared to angled ponds also suggests that initial juvenile bass densities were high in controls. These two factors could combine to cause high cannibalism rates in control ponds, explaining greater juvenile biomass estimates and altered size distributions, but not greater overall numbers between treatments and controls.

Greater size prior to the first winter provides fish a significant advantage to survive over smaller counterparts for naturally reproduced (Shoup and Wahl 2011; Fullerton et al. 2000) and stocked fish (Diana and Wahl 2009). However, especially in the southern regions of the largemouth bass range, little size-selective mortality has been observed (Rogers and Allen 2009; Ostrand et al. 2005; Jackson and Noble 2000), and when it has, predation has been the most important size-selective force (Garvey et al. 2004; Garvey et al. 1998). Although winter severity also plays a role (Fullerton et al. 2000), prey assemblage is a major factor in the survival of juvenile fish regardless of size (Jacobs et al. 2012; Micucci et al. 2003). In some cases smaller fish with lower energy requirements may be favored (Garvey et al. 1998). As a result, size

differences of juveniles going into the winter months that I observed may not affect recruitment to age-1.

Even though I found that simulated tournaments affected some aspects of largemouth bass recruitment, other environmental factors were also important. Abundance of food items during larval and juvenile stages is a common driver of recruitment success and juvenile growth in many fish species (Kaemingk et al. 2012; Nunn et al. 2012; Redman et al. 2011; Graeb et al. 2004; Mayer and Wahl 1997), and zooplankton and prey fish abundance have been implicated as limiting young-of-year largemouth bass growth and survival in some systems (Parkos and Wahl 2002). Because of the multitude of factors that influence juvenile bass survival and growth, and the complex interactions of these factors, constructing definitive models predicting bass population growth and survival has been ultimately unsuccessful (Parkos and Wahl 2010; Shoup et al. 2007; Jackson and Noble 2000; Ludsin and DeVries 1997). I found that high early zooplankton densities positively influenced overall numbers of juvenile largemouth bass, although the mechanism remains unclear. Although zooplankton constitute the primary prey item of newly hatched individuals, they also provide food for other prey fish, which are then utilized by piscivorous fish such as largemouth bass as they switch to piscivory (Olson 1996; Olson et al. 1995). I had difficulty quantifying young-of-year bluegill abundances because many were too small to be captured at draining, and other gears attempted throughout the summer were ineffective with high vegetation abundance. The positive correlation that I found between clear water in spring/early summer with lengths of juvenile bass was expected, as foraging success of black bass decreases under increasingly turbid conditions (Carter et al. 2010; Sweka and Hartman 2003; Reid et al. 1999). Turbidity typically limits foraging of bluegills as well (Aday et al. 2003; Miner and Stein 1993), which usually leads to reduced growth among both species

(Wolfe et al. 2009). Turbidity had little effect on the size of juvenile fish in the early fall, with early phosphorus the most significant correlate to juvenile length at that time. Greater phosphorus concentrations presumably led to increased growth and production of prey for largemouth bass, including zooplankton, benthic invertebrates, and juvenile bluegill (Cole 1994). However, neither turbidity nor phosphorus was a definitive predictor of growth, and it is likely a suite of biotic and abiotic factors that influenced growth of juvenile fish (Parkos and Wahl 2010; Garvey et al. 2002). My results suggest that prey abundance and abiotic habitat factors are important for early life stages of largemouth bass.

It is clear that catch-and-release angling and tournament angling practices cause an overall reduction in individual nest-success of fish (Siepker et al. 2009; Hanson et al. 2008; Philipp et al. 1997). However, similar to my findings, several examples exist demonstrating a lack of a relationship between adult spawning stock and largemouth bass recruitment (Allen et al. 2011; Parkos and Wahl 2010; Jackson and Noble 2000), and large adult stocks do not necessarily lead to high recruitment (Post et al. 1998). However, tournament-related effects on size-structure of recruits to age-0 in the fall could still be important, especially in northern latitudes where juvenile size is more important to overwinter survival than in southern regions (Slaughter et al. 2008). My results suggest that catch-and-release and tournament angling can influence some aspects of recruitment, and the effects of tournament angling during the spawning season should be considered in lakes where largemouth bass recruitment is low. Systems that are already known to have attributes that limit recruitment (e.g. water level fluctuation, lack of prey resources) may be at further risk of recruitment problems from tournament angling. Indeed, there are systems with conditions where regulations would benefit largemouth bass fisheries (Gwinn and Allen 2010). In these situations, regulations limiting

tournament pressure during the spawn or the establishment of refugia so that some fish can reproduce undisturbed may be warranted.

My results are most applicable to small systems with simple community structure, and extrapolation of these results to larger lakes and reservoirs must be made with caution. The ponds were comprised entirely of littoral habitat ideal for bass spawning and use as nursery grounds for young fish, which differ considerably from large reservoirs with little shallow water, vegetation, and structure. Still, my conclusions are likely generally applicable and supported by previous studies; the number of nests is not directly correlated with some aspects of recruitment, environmental factors play a major role, and there are density-dependent interactions present in young-of-year largemouth bass. The mechanisms and specific factors driving these broad generalities at larger scales will need to be examined further. I was unable to accurately quantify juvenile bluegill production in my ponds, which may be a vital variable in determining juvenile bass production and growth. Although I have no reason to assume that bluegill production varied widely between ponds, aspects of the prey fish population should be closely monitored in subsequent studies to determine the relationship between largemouth bass juveniles and juvenile bluegill. I speculate that I may have observed cannibalism in some ponds, but additional work should be aimed at verifying this with stomach content analysis. If confirmed, research should focus on the prevalence of cannibalism in larger systems, and what factors promote cannibalism in largemouth bass. More definitive studies are needed to determine what factors influence growth and survival of young bass, including tournament angling at larger spatial scales. Also needed is the development of predictive models of the minimum spawning stock or number of nests needed to sustain a given level of recruitment with variable abiotic and biotic factors such as lake size, littoral area, and productivity. Long-term tournament pressure data on a number of

lakes with annual estimates of largemouth bass recruitment, sub-adult and adult size structure, and adult fish densities would be valuable in quantifying the effects of tournament-style angling.

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TABLES

Table 1.1. Sets of best models for response variables as determined by DeltaAIC model selection. Variables available for inclusion were early and late summer chlorophyll *a* concentrations, phosphorus concentrations, secchi depths, zooplankton densities, benthic invertebrate biomass, and vegetation density. Parsimonious models within two DeltaAIC units of the best model are shown for each response variable. Models containing the tournament treatment are also shown for each variable for comparison.

Parameter	Model R ²	Δ AIC
Juvenile Bass Number		
Early zooplankton density	0.70	-
Tournament treatment	0.05	+ 10.2
Juvenile Bass Mass		
Tournament treatment	0.24	-
Early chlorophyll <i>a</i>	0.20	+ 0.8
Late vegetation	0.18	+ 1.3
Summer Juvenile Length		
Early secchi depth	0.32	-
Tournament treatment	<0.001	+ 6.3
Fall Juvenile Length		
Early phosphorus	0.54	-
Tournament treatment	0.01	+ 11.3

Table 1.2. Raw values for environmental and response variables for all experimental ponds in 2010 and 2011. The environmental variables were evaluated for their use as possible covariates and their effects on the measured response variables. Zooplankton densities (#/L), phytoplankton abundance (measured as chlorophyll *a* concentration, $\mu\text{g/L}$), total phosphorus concentration ($\mu\text{g/L}$), vegetation density (g/m^2), secchi depth (m), and benthic invertebrate biomass (mg/m^2) were measured each month and averaged for the early (May-June) and late (July-August) season. Number of recruits, recruit biomass (g), average length of juveniles in the midsummer (mm), average lengths of recruits in the fall (mm), and cumulative egg score were examined for their relationship with the environmental factors. The relationship between response variables and the number of fish angled in each treatment pond was also evaluated.

Table 1.2.

Year	Type	Pond ID	Early Zoop	Late Zoop	Early chl a	Late chl a	Early P	Environmental Variables						Angled fish	
								Late P	Early Veg	Late Veg	Early Secc	Late Secc	Early benth.		Late benth.
2010	Control	3A	6	24	15	23	367	144	1030	1267	1.1	1.3	696	463	0
		4A	8	101	18	19	104	143	674	1183	1.3	1.0	452	1301	0
		5A	3	10	4	6	140	120	349	1638	1.1	1.0	298	337	0
		8A	11	74	23	11	168	152	491	226	1.0	1.0	523	559	0
	Treatment	1A	2	29	4	43	172	270	1244	371	1.5	0.7	457	1097	37
		2A	8	97	6	52	114	155	651	1474	1.4	1.2	508	921	27
		6A	10	126	16	14	237	90	535	1597	1.3	0.9	362	549	26
		7A	4	99	4	37	136	86	476	1293	1.2	1.0	390	582	23
2011	Control	1B	6	28	7	47	154	263	1836	334	1.4	0.7	640	1175	0
		2B	42	78	5	42	46	113	425	0	1.4	0.9	437	556	0
		6B	8	112	8	38	64	63	436	4536	1.4	1.7	717	676	0
		7B	30	73	4	37	76	176	2076	2007	1.7	0.8	390	1081	0
	Treatment	3B	24	44	3	26	52	143	4138	3042	2.0	1.3	274	1128	35
		4B	18	82	5	13	104	82	813	4119	1.4	1.4	518	890	23
		5B	65	380	7	30	87	28	4124	1791	1.8	0.8	371	506	23
		8B	7	154	9	24	79	117	3556	451	1.5	1.1	857	763	17

Table 1.2 (cont.)

Year	Type	Pond ID	Bass #	Response Variables			Egg score
				Bass mass	Summer length	Fall length	
2010	Control	3A	1559	27399	36.1	71.7	7.5
		4A	3071	32870	37.8	58.4	17.5
		5A	1325	14412	31.0	53.8	19.5
		8A	1352	12697	31.3	54.0	5
	Treatment	1A	698	8762	37.4	65.0	10
		2A	2531	14570	36.6	60.7	2
		6A	2397	11833	34.7	61.0	10
2011	Control	7A	692	3730	31.2	59.6	10.5
		1B	1233	8574	35.7	59.1	15.5
		2B	16089	28950	42.0	57.2	10
		6B	3788	5036	30.7	47.9	17
	Treatment	7B	5479	9527	40.5	52.6	10
		3B	2386	6307	39.6	52.8	2
		4B	3037	6895	34.9	55.7	3.5
		5B	6311	8271	34.9	47.0	6
		8B	2654	11705	35.6	60.3	6.5

FIGURES

Figure 1.1. Hatch dates of aged largemouth bass (*Micropterus salmoides*) from control (dark bars) and treatment ponds (open bars) from two years, A) 2010 and B) 2011. Error bars represent the complete range of hatch dates for fish in each pond. There were no differences in hatch dates between treatment and control ponds ($P = 0.31$), but a difference was present between years ($P = 0.001$).

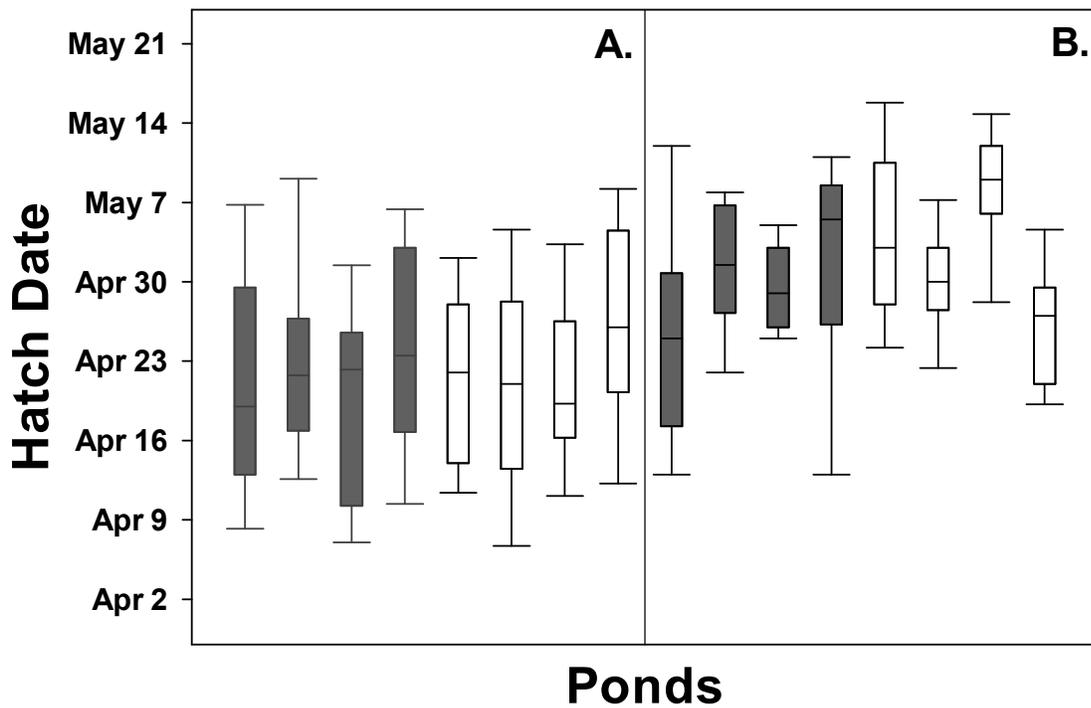


Figure 1.2. The relationship between May-June macrozooplankton density and the number of largemouth bass (*Micropterus salmoides*) recruits surviving to the fall in each pond. Control ponds are represented by open circles and treatment ponds are represented as darkened circles. Early macrozooplankton abundance was used as a covariate for the test of treatment effect on recruitment.

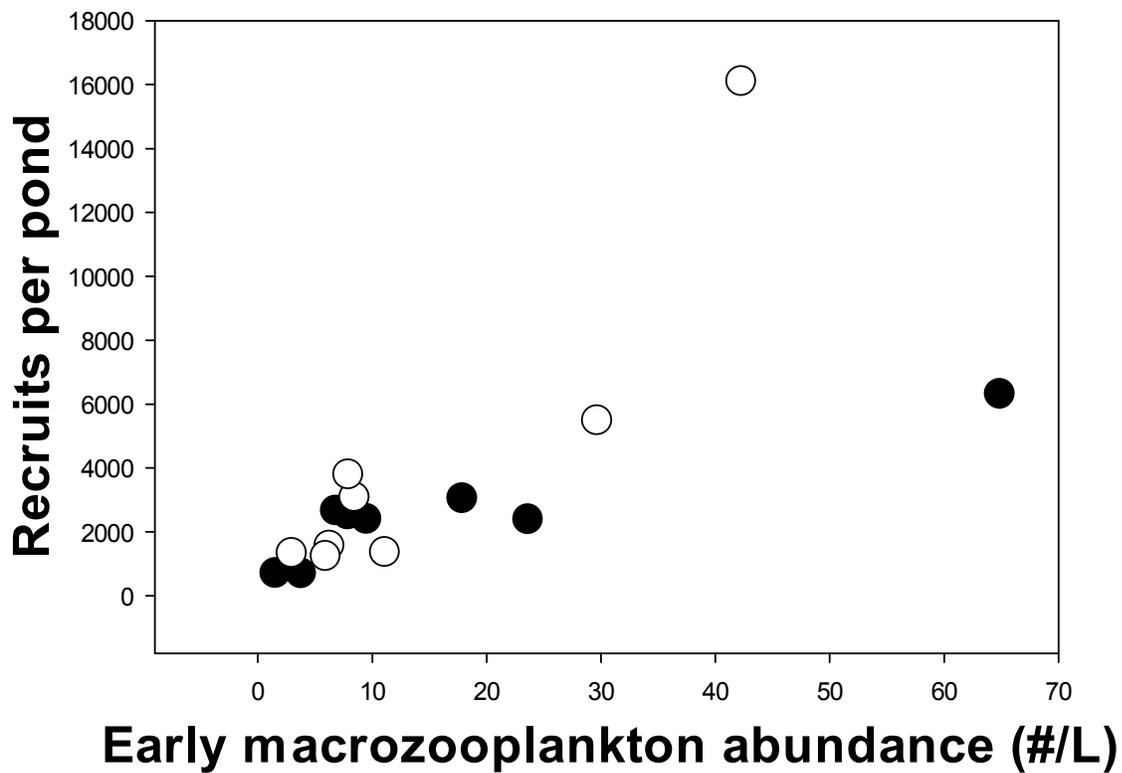


Figure 1.3. Number and biomass of largemouth bass (*Micropterus salmoides*) recruits between treatment and control ponds. The adjusted means for the number of recruits were produced from a model incorporating yearly effects and early zooplankton abundance. The means for biomass were adjusted for year only. No significant difference was observed for number of recruits ($P = 0.17$), but a difference was detected between treatments for recruit biomass ($P = 0.05$).

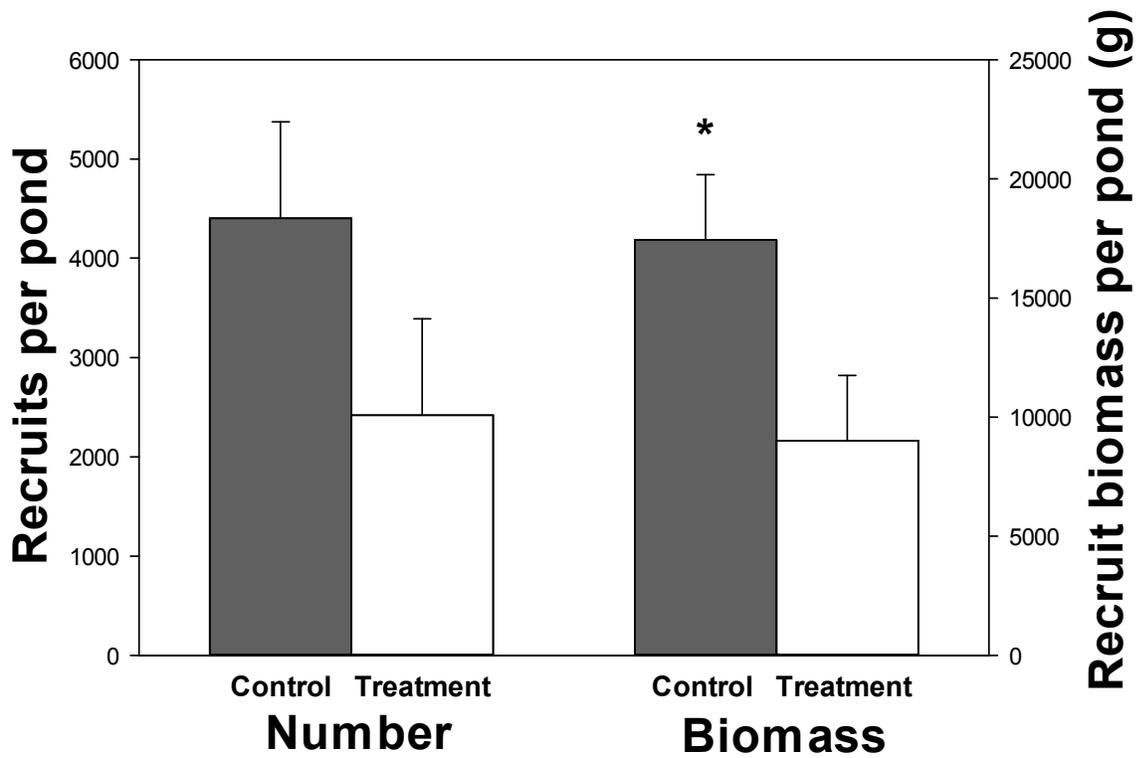


Figure 1.4. Average number of largemouth bass (*Micropterus salmoides*) recruits per size class in control (dark bars) and treatment (open bars) ponds for individuals less than 120mm. Error bars represent 95% confidence limits. No difference was present between treatments for these smaller individuals ($P = 0.43$).

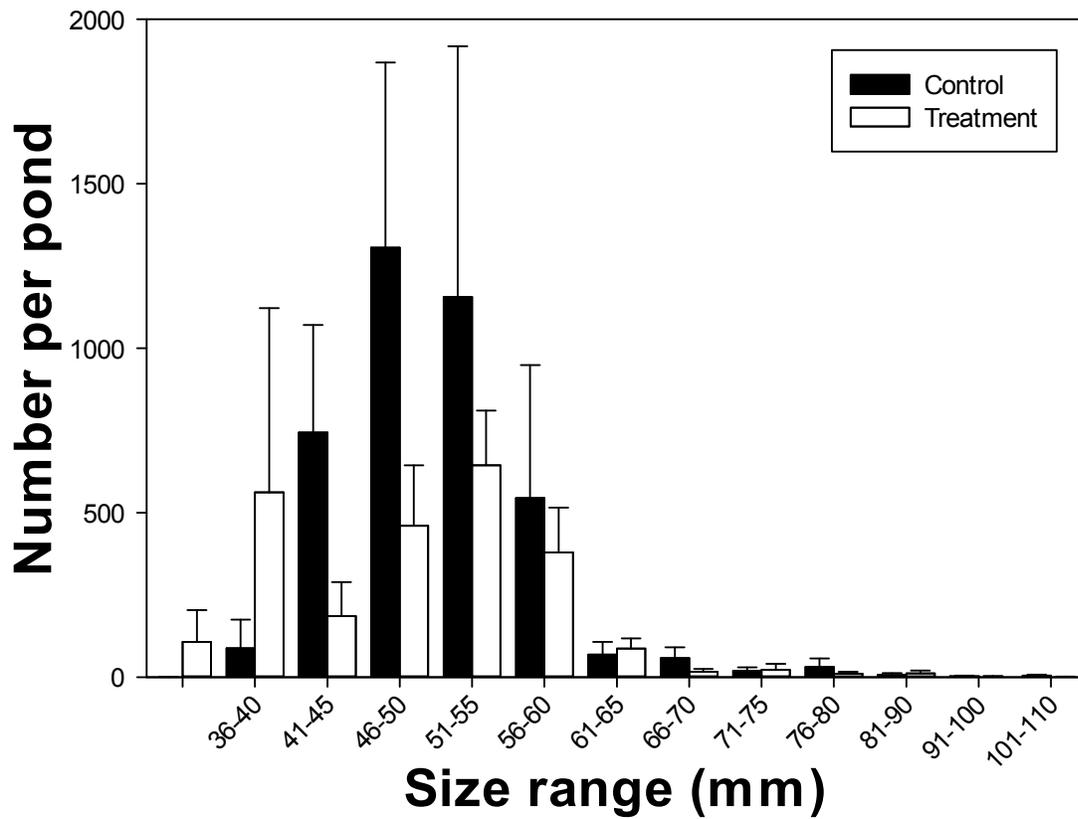
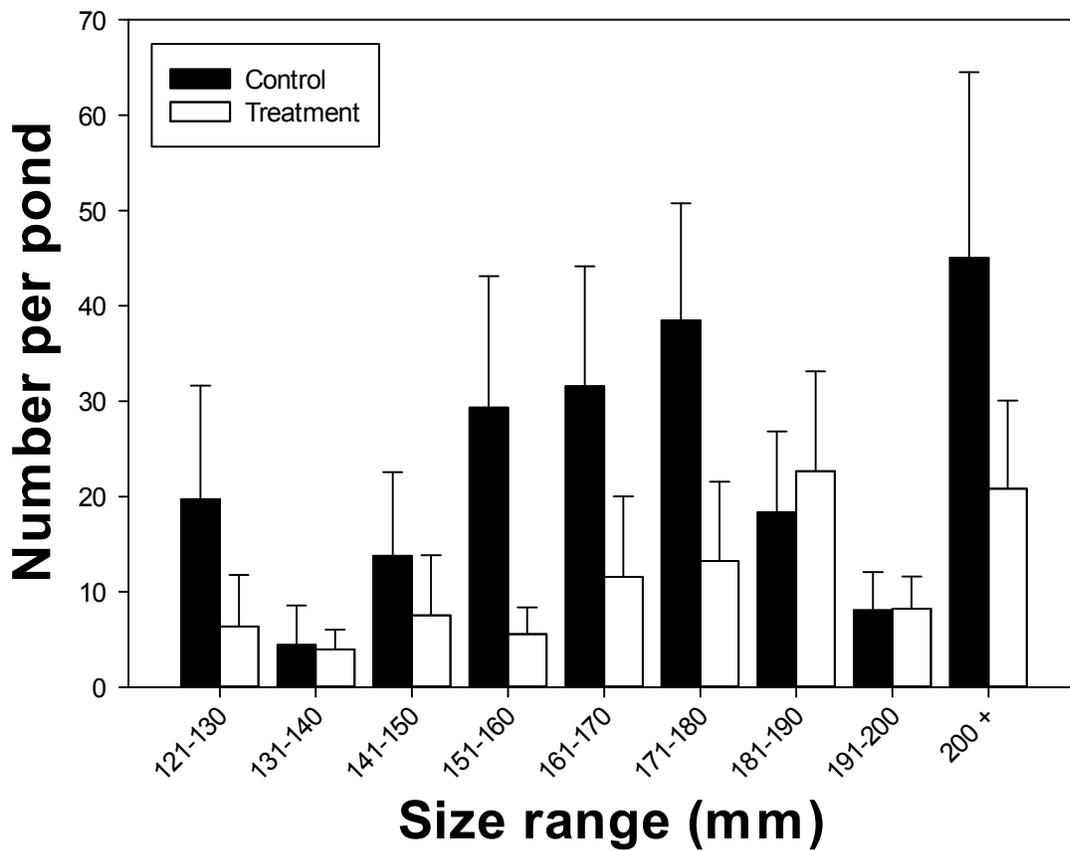


Figure 1.5. Average number of largemouth bass (*Micropterus salmoides*) recruits per size class in control (dark bars) and treatment (open bars) ponds for individuals larger than 120mm. Error bars represent 95% confidence limits. Unfished control ponds had more large individuals than the angled treatment ponds ($P = 0.04$).



CHAPTER 2. EFFECTS OF HEATED EFFLUENT ON MIDWESTERN U.S. LAKES: IMPLICATIONS FOR FUTURE CLIMATE CHANGE

ABSTRACT

Numerous simulation studies have considered the effects of impending climate change on lakes. Predictive models exist for the responses of a multitude of variables to a warmer climate, and potential effects on food webs and ecosystem functions. Although these predictions are numerous, there is a need for manipulative experiments testing for the effects of warming on actual lake systems. I used power plant lakes across the central Midwestern U.S. as a substitute for lake systems that may result from climate change. These treatment lakes receive heated effluent and are typically 2-6° C warmer than other regional lakes. I collected data from 1997-2010 on a number of abiotic and biotic variables from three of these treatment lakes and six control lakes that were of similar size and location but did not have an artificial thermal regime. Phosphorus and phytoplankton concentrations were similar between treatment groups, although treatment lakes had greater phosphorus and less phytoplankton in September. No differences existed in turbidity (measured as Secchi depth transparency). Zooplankton were less abundant in treatment lakes than in control lakes throughout my sampling period (May – October), with differences in cladocerans driving this disparity. There was evidence of earlier spawning of gizzard shad (*Dorosoma cepedianum*) due to the warmer temperature regime, but not for bluegill (*Lepomis macrochirus*). Average sizes of juvenile bluegill were larger in warmed systems in July and August. Juvenile largemouth bass (*Micropterus salmoides*) were larger in heated systems in June, but no differences existed in July or August. Growth of adult largemouth bass was greater in systems with a warmer thermal regime. My results provide insights into patterns that can be expected in the future, and may be used to further understand the wide-reaching implications of climate change.

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INTRODUCTION

The effect of climate change on the natural world is a great uncertainty, as shifts in weather patterns may have pronounced effects on global ecosystems. A multitude of models have been developed to predict global changes in temperature; there is general agreement that mean global air temperatures will rise by 0.5-6° C in the next century (IPCC 2007; Cox et al. 2000), that are often mirrored in water temperatures. Although research has predicted (and observed, in some cases) the result of elevated water temperatures, most studies ignore the multitude of effects that may occur with rising temperatures (Harrington et al. 1999). Species ranges may shift poleward as preferred temperature regimes diverge from the equator (Britton et al. 2010; Daufresne et al. 2003; Meyer et al. 1999) and species occupying relatively rare, delicate habitats could be at risk of regional extirpation and possible extinction (Matthew and Zimmerman 1990). Other results of warming may be the exacerbation of existing forms of thermal pollution (McKee et al. 2003; Schindler 2001; Hauer et al. 1997), elevated levels of

biomagnification of anthropogenic toxicants (Moore et al. 1997), and increased invasion of exotic species (Dulvy et al. 2008; Scavia et al. 2002; Ricciardi and MacIsaac 2000).

Climate change could affect trophic levels of aquatic systems in a variety of complex ways. Accelerated denitrification due to higher temperatures may lead to a higher prevalence of blue-green algae blooms that already plague some systems (Markensten et al. 2010; Pascual et al. 2008; Beisner et al. 2003). The positive effect of increasing temperature on photosynthetic capacity of such algae would only compound this problem (Robarts and Zohary 1987). More phosphorus could also be released if lethally high summer temperatures kill aquatic organisms (Correll 1998). Warmer temperatures may also cause an earlier onset and prolonged stability of lake stratification (Hondzo and Stefan 1993), leading to increased disassociation of phosphorus bound in sediments because of higher occurrences of anoxic conditions (Amirbahman et al. 2003; Jensen et al. 1992), accelerating internal phosphorus loading (Sondergaard et al. 2003; Stauffer 1985). Markedly greater phosphorus concentrations in lakes may then occur (Feuchtmayr et al. 2009).

Shifts in the chemical balance of aquatic systems may have their most profound effect at the bottom of lake food webs (Yvon-Durocher et al. 2011; Hader et al. 1995). Although the effects of climate change will undoubtedly vary among regions, most research predicts that a warming trend will favor phytoplankton- or cyanobacteria-dominated systems (Feuchtmayr et al. 2009; Johnk et al. 2008; Mooij et al. 2005; McKee et al. 2003). Growth and survival of young-of-year planktivorous fish would generally increase with greater temperatures (Jeppesen et al. 2003), potentially putting more predation pressure on large zooplankton that may limit phytoplankton density. These factors, coupled with exacerbated cultural eutrophication from runoff expected from increased precipitation (Schindler 2001), may cause lakes to transition to a

turbid state (Mooij et al. 2005; Jeppesen et al. 2003). However, alternative hypotheses suggest that warmer mean temperatures could promote prolonged clear-water seasons and less overall turbidity, caused mainly by increased performance of macrophytes with higher temperatures (Rooney and Kalff 2000). Also, increased algal production could be negated by higher performance of herbivorous zooplankton, leading to no discernible change in turbidity (Straile 2002). If increased temperatures further upset the current equilibrium of stable states in many lake systems (Scheffer and Carpenter 2003), predicting the consequences becomes progressively more difficult.

Temperature increase from climate change may have a range of effects moving up trophic levels, but due to the complexity of interactions and the wide range of ecosystem variables, these effects are difficult to speculate on and nearly impossible to predict (DeStasio et al. 1996). Warmer temperatures, specifically in spring, may cause zooplankton populations to peak earlier in the year, possibly suppressing spring phytoplankton blooms through grazing pressure. Less phytoplankton would be available to benthic invertebrates, triggering noticeable effects in higher trophic levels (Smith et al. 2010). However, it is also possible that greater temperatures could also cause phytoplankton peaks to occur outside the critical reproduction periods for zooplankton, thus suppressing zooplankton populations through lack of food (George and Harris 1985). If water temperatures influence temporal aspects of the life histories of plankton, small fish, and large fish differently, mismatches between reproductive periods and prey availabilities could occur throughout the food web (Genner et al. 2009). Depending on how potential changes in temperature and lake stratification effect vertical migration of zooplankton and habitat use of young fish, there may be changes in habitat overlap shared by larval fish and their prey (Mehner 2000; DeStasio et al. 1996).

Due to these uncertainties, the influence of climate change on sportfish populations is a topic of great interest, as the effects of such change on the carrying capacity of all trophic levels is unknown (Mooij et al. 2005). For some fishes at the northern extent of their range, warming may increase year-class strength and population abundance (Casselman et al. 2002; Shuter et al. 1985). Growth of a common sportfish, largemouth bass (*Micropterus salmoides*), is positively correlated with temperature (Rypel 2009), as is the case for almost all fish within their thermal optima. Warmer temperatures generally advance spawning dates in centrarchids, as well as reduce overwinter mortality (Rogers and Allen 2009; Mooij et al. 2008). However, thermal refugia may become limited for some cold water species (Williams et al. 2009; Jacobson et al. 2008). Because of inherent difficulty in modeling these influences on fish life histories, making definitive predictions on the outcome of an altered temperature regime is quite difficult (Meyer et al. 1999).

Uncertainty concerning the effect of climate change on aquatic ecosystems argues for further research (Ficke et al. 2007; Roessig et al. 2004). To test for the outcome of warmer temperatures on lakes of the Midwestern U.S., I developed a unique study design using artificially warmed systems common in the region. Treatment lakes were ones with power plants that draw in water from their respective lake, use it to cool generators, and discharge the heated effluent back into the lake. As a result, average temperatures in these lakes are 1-4° C warmer than nearby systems of similar size and morphometry. Because these elevated temperatures are consistent with models predicting temperature shifts in the next century (IPCC 2007), I used these power plant lakes as examples of systems that could result from climate warming. I compared artificially warmed lakes against ‘natural’ lakes in the region for a host of abiotic and biotic variables to provide insight into how a warmer environment may affect lakes. Historical

data from treatment and control lakes allowed me to test whether warmer temperatures influenced selected variables, and how warmer systems and their resident populations may adapt to prolonged temperature changes.

METHODS

Three power plant cooling lakes in central Illinois were used in the study: Clinton Lake (DeWitt Co.), Newton Lake (Jasper Co.), and Coffeen Lake (Montgomery Co., Figure 2.1). The nuclear plant at Clinton has been in operation since 1987 and the coal plants at Newton since 1977, and at Coffeen since 1965. These three lakes were compared with six control lakes of similar biotic community and location: Forbes Lake (Marion Co.), Lake Shelbyville (Shelby Co.), Lake Paradise (Coles Co.), Pierce Lake (Winnebago Co.), Lake Mingo (Vermilion Co.), and Lake Charleston (Coles Co., Figure 1). I included a wide range of lake sizes in the study to maximize my inference space (Table 1).

Quantification of the temperature regime of each system was accomplished using temperature loggers stationed centrally in each lake at a depth of 1 meter. Loggers were active on Clinton Lake from 2009-2012, Coffeen Lake from 2003-2006, Newton Lake from 2003-2006, Forbes Lake from 2006-2010, Lake Mingo from 2003-2007, and Pierce Lake from 2002-2007. Loggers were not installed on the remaining lakes, but temperatures at 1 m were taken biweekly from 2002-2011. Average temperatures for each Julian day were then calculated for each lake for standardization across years. Treatment lakes were about 5° C warmer than controls during the summer and fall, and much greater (>7°) during the winter and spring (Figure 2.2).

Lakes were sampled for several abiotic and biotic variables from 1997 to 2010. From late spring to early fall, biweekly sampling was conducted to assess phosphorus and chlorophyll

concentrations, zooplankton and larval fish densities, and juvenile fish size structure. Samples for water chemistry analysis were collected using an integrated water sampler at the deepest part of each lake and returned for laboratory analysis to determine total phosphorus and chlorophyll *a* concentrations (Welschmeyer 1994). Secchi depths were also taken at this location. Zooplankton communities were assessed using a Wisconsin zooplankton net (50 cm diameter, 64 μm mesh) pulled vertically through the water column at eight sites randomly distributed throughout each lake (Murphy and Willis 1996). Samples were preserved in Lugol's solution until they could be analyzed in the laboratory, where individual zooplankton were identified to family and enumerated to provide density and relative abundance estimates. Larval fish densities were assessed with a 0.5 m diameter bow-mounted push-net with 500 μm mesh, which was pushed for 2.5 min inshore and 2.5 min offshore at six fixed transects on each lake (Claramunt et al. 2005). Collected fish were then stored in ethanol until identification to genus in the laboratory. Densities were determined using distance values from flowmeters fixed to each net. Juvenile fish were collected using a 10 m bag seine with 3 mm mesh pulled for 10 m at four fixed sites that represented a range of habitats on each lake. Captured fish were counted and up to 50 of each species were measured to estimate size structure. Study lakes were also sampled using standard electrofishing procedures to collect adult largemouth bass (*Micropterus salmoides*) for age assessment. After weighing and measuring, scales were taken from each fish before release. Ages from scales were then determined by two independent readers, and only scales with agreed upon ages were used in subsequent analyses.

Because of the use of historical data that was collected for a diverse number of other studies, sampling did not occur on all lakes for all examined variables for the duration of the study period. However, the data sets were extensive and each power plant lake was

comprehensively sampled during a subset of years from the complete sampling period (1998-2010), whereas the majority of control lakes were sampled for all variables continuously. Water chemistry variables, zooplankton, larval fish densities, and juvenile size structure was measured on the control lakes of Forbes, Shelbyville, Pierce, and Charleston from 1998 to 2010. These data were gathered at Lake Paradise from 1999 to 2010 and at Lake Mingo from 1999 to 2004 and 2007. Clinton Lake was sampled for these data from 1999 to 2007. Zooplankton was sampled in Newton Lake in 1998 and Lake Coffeen in 2010, and juvenile fish size was measured from both lakes from 1997 to 2001 and in 2004. No water chemistry or larval fish data was available for either Coffeen or Newton Lake. Largemouth bass caught via electrofishing and aged were available from the control lakes of Pierce, Paradise, Shelbyville, and Charleston and at Clinton Lake from 2005 to 2010. These data were available from Coffeen and Newton from 1997 to 2000, as well as 2004.

Data Analysis

I tested for differences in phosphorus and chlorophyll concentrations, Secchi depths, zooplankton and larval fish densities, and sizes of juvenile largemouth bass and bluegill (*Lepomis macrochirus*) between heated and control lakes using linear contrasts in a mixed model framework. Each analyzed variable was modeled as a function of its associated treatment, lake nested within treatment, month of sampling, the interaction between treatment and month, and blocked by year. I then tested for the overall mean difference between treatment lakes and controls, as well as differences between lake groups within individual months using linear contrasts for each month. Because monthly contrasts may not be sensitive enough to examine differences in spawning times from larval fish densities, months were split into early and late

periods for analysis of that variable. Known-age largemouth bass from scales were used to create a von Bertalanffy growth curve for each lake. Treatment and control lakes were then compared using the parameter ω , a measurement of early growth, which has been suggested for use in statistical comparisons of von Bertalanffy growth curves from different populations (Gallucci and Quinn 1979).

RESULTS

Several abiotic and biotic differences were observed between the control lakes and the thermally influenced power plant lakes. Analysis of water nutrients showed few differences between Clinton lake and controls in annual average phosphorus concentrations ($P = 0.28$), but concentrations in Clinton lake were greater than controls in September ($F = 21.74$, $P < 0.0001$, Figure 2.3). Control lakes had greater chlorophyll *a* concentrations in September ($F = 3.55$, $P = 0.05$, Figure 2.3), but not in other months. No differences existed between lake types in either monthly or annual means for Secchi depth (all $P > 0.05$, Figure 2.4).

Zooplankton communities exhibited relatively large differences between lake types. Overall mean densities of macrozooplankton were greater in control lakes (61 individuals / L) than treatments (17 individuals / L, t-test $F = 8.57$, $P = 0.004$, Figure 2.5). The power plant lakes also lacked the spring/early summer peaks present in the controls, as mean values in May and June were significantly lower than controls (May $F = 6.04$, $P = 0.01$; June $F = 11.91$, $P < 0.001$), and not significantly different in other months.

Differences in zooplankton densities were due to lower concentrations of the most prevalent zooplankton groups, including cladocerans and copepods (Figure 2.6). Cladocerans were abundant in control lakes in the early summer, whereas they were much lower in power

plant lakes in May ($F = 5.88$, $P = 0.02$) and June ($F=8.02$, $P = 0.005$). Copepod populations stayed relatively stable in control lakes throughout the sampling period, but copepod populations in the power plant lakes were much lower than control lakes during the midsummer (June $F=5.48$, $P = 0.02$; July $F=3.64$, $P = 0.06$; August $F=2.97$, $P = 0.08$; September $F=3.79$, $P = 0.05$). Similar patterns existed in rotifer densities as well, where overall densities were lower in treatment lakes than controls ($F=10.49$, $P = 0.001$, Figure 2.5), and treatment lakes had lower densities during the summer months (June $F=5.60$, $P = 0.02$; July $F=9.81$, $P = 0.002$; August $F=6.19$, $P = 0.01$).

Juvenile and adult fish abundance and size differed between lake groups, whereas larval fish responses varied by species. Larval densities of *Lepomis* species were not different in annual or monthly means ($F=2.59$, $P = 0.11$, Figure 2.7). Larval gizzard shad (*Dorosoma cepedianum*) densities were also not different in overall annual means ($F=0.67$, $P = 0.41$), but densities were greater in control lakes than heated systems in early June ($F=4.41$, $P = 0.04$). Gizzard shad appeared to spawn earlier in the power plant lakes than in control lakes (Figure 2.7). Although larval largemouth bass were not collected with my gears, there was evidence of earlier spawning in this species based on sizes in the early summer. Juvenile bass were longer in treatment lakes in June ($F=5.36$, $P = 0.02$), but those differences disappeared by the late summer (Figure 2.8). There were also differences in the sizes of juvenile *Lepomis*, with larger fish present in treatment lakes in July ($F=7.12$, $P = 0.01$) and August ($F = 6.77$, $P = 0.01$, Figure 2.8). Von Bertalanffy growth curves showed that growth for largemouth bass was more rapid in the thermally influenced power plant lakes ($P = 0.03$, Figure 2.9). Coffeen and Newton lakes, the warmest systems used in the study, had significantly higher mean length at age for largemouth bass in all

age classes, whereas growth was consistently lower and relatively similar in all control lakes and Clinton Lake.

DISCUSSION

I observed several differences and many similarities between control lakes and thermally warmed lakes. Water chemistry variables examined were similar between lake types for most of the year, which disagrees with previous suggestions of negative effects of warming on water quality variables (Feuchtmayr et al. 2009; Magnuson et al. 1997; Hondzo and Stefan 1993). Although greater temperatures should lead to increased internal loading of phosphorus, I found few differences in phosphorus concentrations for most of the year. My study lakes lacked increasingly prevalent anoxic conditions associated with most predictions for phosphorus (Mooij et al. 2005; Sondergaard et al. 2003; Stauffer 1985). Predictions are that total phosphorus levels in most water bodies will increase as a result of climate change, but these are partly based on expectations that increases in precipitation will facilitate higher levels of external loading from runoff (Mooij et al. 2005). I found greater phosphorus concentrations in thermally influenced lakes in September only, and the variation associated with this monthly estimate was relatively high. September usually marks the last full month of summer stratification in regional lakes, and is often accompanied with the highest levels of anoxic conditions. Warmer water, coupled with warmer air temperatures at that time of year may have resulted in greater concentrations as phosphorus dissociated from substrates in warm, anoxic conditions (Amirbahman et al. 2003; Jensen et al. 1992).

Despite expectations that warmer temperatures will lead to an increase in total phytoplankton abundance (Feuchtmayr et al. 2009; Mooij et al. 2005; McKee et al. 2003), my

results mirror those of others that contradict that prediction (Straile 2002; Weyhenmeyer 2001). Warmer waters did not have greater phytoplankton concentrations for most of the year, although similar to phosphorus concentrations, chlorophyll *a* was different between lake types in September. In contrast to predictions, there was less chlorophyll in the warmer systems during this month, again suggesting that phytoplankton populations were not affected by increased temperatures. Although this is contrary to the typical correlation between chlorophyll and phosphorus, it provides additional evidence that phytoplankton populations were not affected by thermal effluent. Greater spring temperatures may initiate earlier algal production, but increases in herbivore performance may negate algal production and lead to increased herbivore growth (Straile 2002). Although mean abundance of phytoplankton may not change, there would presumably be changes in community composition, although this is not universally supported (see Wilde 1997). I did not specifically examine taxa-specific differences in my study, but heat-tolerant species may dominate in the warmed systems (Scheffer and van Nes 2007).

Due to relatively similar concentrations of phytoplankton between lakes, differences in zooplankton densities were surprising. Although extremely high temperatures can have a negative influence on zooplankton communities, moderate temperatures have been shown to have little effect (Taylor et al. 1993). Still, high mortality has been observed in some species with temperatures in excess of 30 ° C (Carlson 1973). Greater spring temperatures could cause a mismatch between photoperiod cues and ideal temperatures for some life stages. Zooplankton densities may be limited in heated lakes, as hatchling abundance of some cladocerans has been shown to be negatively affected by early onset of high spring temperatures (Dupuis and Hann 2009). Reproductive success may also be limited because energy is converted into egg production and not larvae (Threlkeld 1979). Other research has suggested that elevated

temperatures may limit the availability of thermal refugia for temperature-sensitive zooplankton (Moore et al. 1996). Zooplankton limitation could also be explained by increased grazing pressure on zooplankton from planktivores, because warmer temperature should enhance planktivorous fish growth as well (Jeppesen et al. 2003; Moore et al. 1997). A warmer thermal regime should accelerate the onset of peaks for phytoplankton and zooplankton. Expected peaks may have occurred earlier in the year (Metzke and Pederson 2012; Nicolle et al. 2012) and my sampling may have missed these peaks. Because greater temperatures and earlier onset of spring can be beneficial to zooplankton populations in some cases (Schindler et al. 2005), the effects of temperature on zooplankton densities appear to be region-specific. I found that cladocerans were very low in the treatment lakes, which is contradictory to work suggesting that warmer temperatures will favor cladocerans over other zooplankton types (Ekvall and Hansson 2012). Microzooplankton did not follow predictions, as rotifers, being more tolerant to heat, did not thrive in warmed systems as expected (Leeper and Taylor 1995). However, if the treatment also had an effect on rotifer size, my results could be unreliable, as my methods may have underestimated numbers of smaller individuals (Chick et al. 2010).

Timing of spawning of fishes and switches in ontogeny of juvenile fish are universally expected to be influenced by a changing climate (Rogers and Allen 2009; Bradshaw and Holzapfel 2008; Mooij et al. 2008; Shuter et al. 1985). I have evidence of earlier spawning among fish in heated systems. In gizzard shad, there was an apparent shift in the peak spawning period to May in treatment lakes, with larval shad being almost completely absent in samples later in the year. In control lakes, larval shad appeared in moderate numbers throughout June and even into July. Interestingly, I did not find evidence of shifted spawning time in bluegill, which may have been due to high variation within months between years. There was a general pattern

of lower densities of larval bluegill in thermally influenced lakes throughout the sampling period, which has been shown previously in comparisons of lakes from southern and northern latitudes (Jolley et al. 2009).

Although I did not find differences in spawning times of bluegill as measured by larval fish densities, I observed larger age-0 fish in thermally influenced lakes. These size differences are probably due in part to earlier spawning, but faster growth among resident fish has been noted in systems receiving power plant effluent (Galloway and Kilambi 1988). Since I observed marginally lower densities of juvenile bluegill in treatment lakes, differences in growth rate could have been influenced by density dependent factors as well. Increases in grazing pressure of juvenile fish on zooplankton, which would have led to faster growth, could be the mechanism behind low densities of large zooplankton in treatment lakes (Carpenter et al. 1985). Food limitation during the late summer, coupled with high temperatures, explain why differences in sizes of juvenile largemouth bass present in June disappeared by July and August. However, Von Bertalanffy growth curves of largemouth bass showed differences existed for adult fish as well. Temperate species such as black basses have shown elevated growth during warmer years as compared to colder ones (King et al. 2012; Morrongiello et al. 2011; Rypel 2009). Relaxation of cold winter temperatures and an extended growing season are likely the cause of enhanced somatic growth (Stefan et al. 2011; Bradshaw and Holzapfel 2008). However, any differences in adult largemouth bass density or density of forage fish, factors that were not included in this study, could have influenced growth.

There were several differences between power plant lakes and natural systems. I conclude that dynamics of zooplankton populations may be altered as a result of climate change, although if these changes will be shifts in density, timing of peaks and reproduction, or a

combination of both factors, is unclear. Spawning of some fish is also likely to begin earlier in the year, but may vary on a species or familial basis. Because most temperate species exist in more southern, warmer regions, I expect increases in growth of most species at northern latitudes in response to global climate changes. However, shifts in lower trophic levels will undoubtedly affect the growth of predatory fish, and extremely warm summer temperatures could also be detrimental. Negative effects of extreme summer temperatures may be negated by the extended growing season allowed by a warmer winter. These patterns cannot be universally applied to all systems, as regional variability in resident biota make each fish community susceptibility to climate change different.

My experimental approach provides unique insights into the possible effects of a warmer climate that does not require estimating model parameters of previous approaches and expands the limited inference space of small, manipulative experiments. However, aspects of climate change other than temperature, such as precipitation and increased incidence of strong storms, were not assessed in my study. Also, the thermal influence of power plants is strongest in the winter, when the difference between effluent and air temperature is the greatest. Though cold overwinter temperatures will be relaxed, global climate change will likely be more proportionate seasonally. Because of logistical limitations, my sampling was restricted to other seasons and future work should include the winter period. Warming has been shown to move up the onset of spring phytoplankton peaks (Winder and Schindler 2004), which may have occurred outside of my sampling regime. Phytoplankton communities may also shift to more heat-tolerant species. Another focus of future study should be how systems adapt over time. My study used a simple approach of examining lakes that have been constantly exposed to an artificial thermal regime for many years. In reality, climate is expected to slowly change over the course of the next

hundred years and beyond (IPCC 2007). How biota adapts to a changing climate over a long time period, and how these adaptations change or stabilize food web processes, must be addressed. It is possible that, although many individual factors may change, the overall result may be little or no effect on ecosystem function. Lastly, global models, supported with data from experiments like ours, are needed to test how lake processes may change as a result of a myriad of changes in individual variables. I believe my results provide valuable insight into the potential effects of climate change in the Midwestern U.S. and can be used to further prepare for potential changes in ecosystem functions associated with a warmer temperature regime.

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TABLES

Table 2.1. Physical characteristics of lakes used in this study, including treatment lakes that were thermally influenced and lakes that were not thermally affected that were used as controls.

Lake	Surface area (ha)	Mean depth (m)	Max depth (m)	Shore length (km)
<i>Control Lakes</i>				
Charleston	132	2.4	4.9	6
Forbes	226	4.6	9.5	36
Mingo	72	3.7	10.1	15
Paradise	58	2.6	4.9	6
Pierce	61	3.4	10.1	7
Shelbyville	4492	4.9	20.4	277
<i>Treatment Lakes</i>				
Clinton	1983	5.9	14.6	219
Coffeen	120	5.8	17.9	77
Newton	688	6	15.5	96

FIGURES

Figure 2.1. Map of Illinois showing the distribution of lakes used in this study. Control lakes are indicated with circles, and power plant lakes are shown with squares.

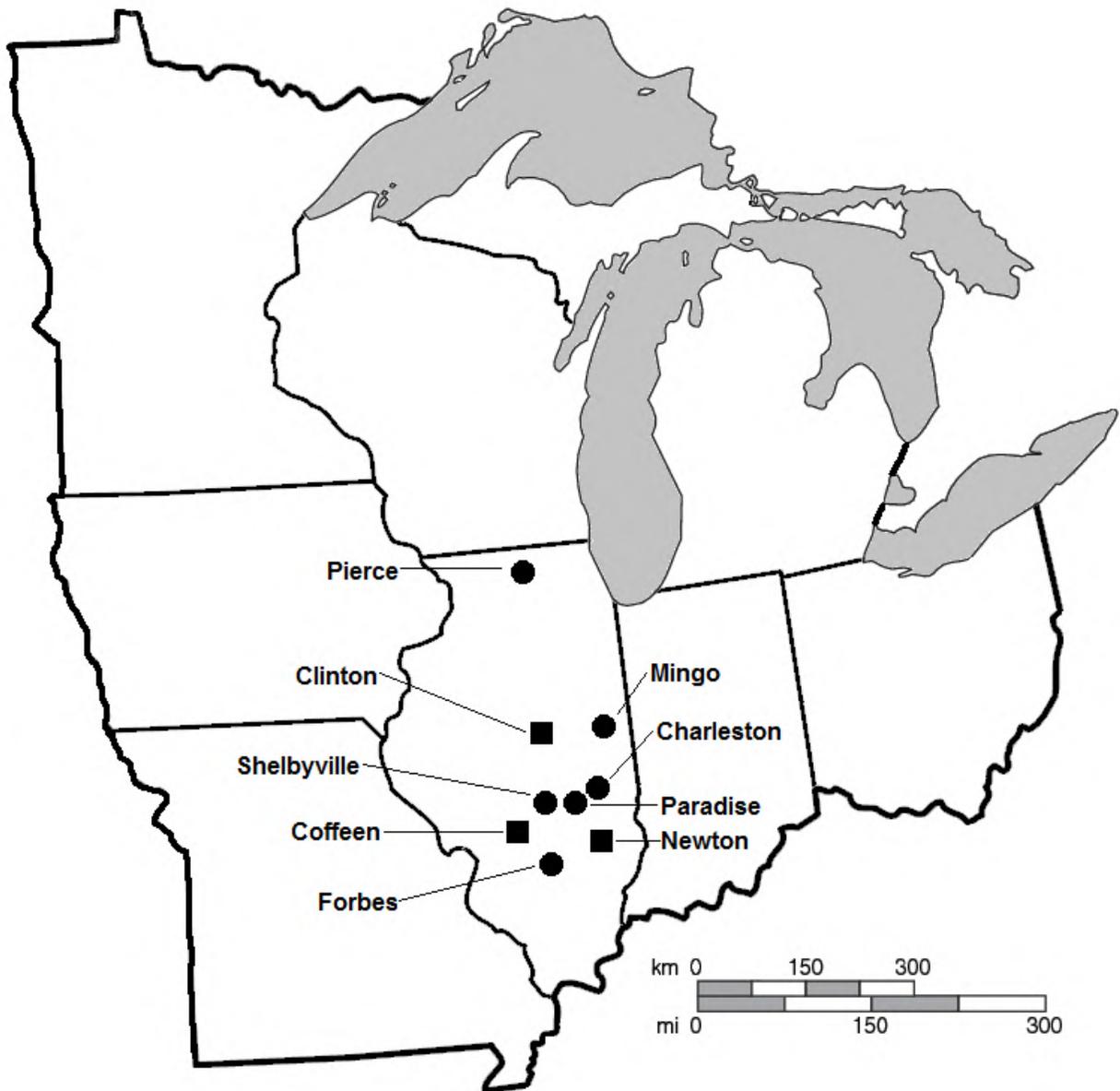


Figure 2.2. Average annual temperature (C°) regime for each power plant (gray lines) and control lakes (black lines) as determined from temperature loggers and temperature probes located at 1 m of depth.

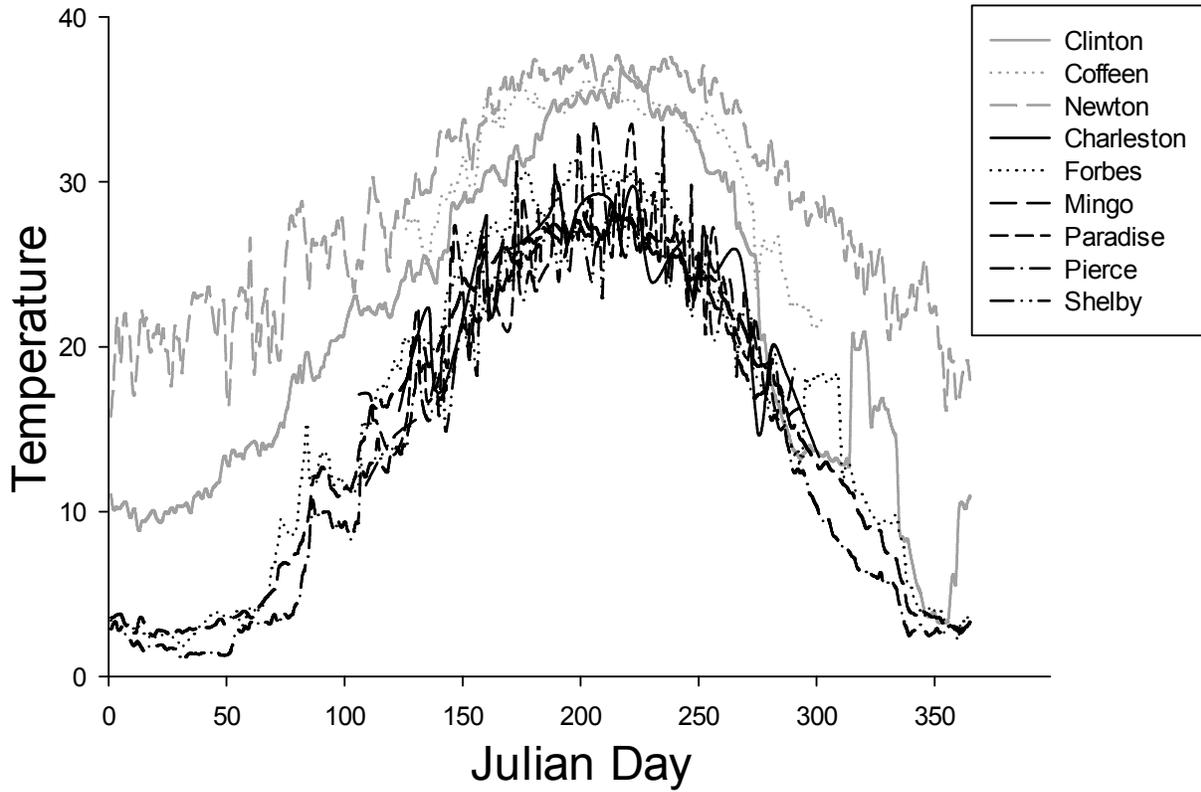


Figure 2.3. Average phosphorus and chlorophyll concentrations among control lakes (dark circles) and Clinton Lake (open circles) between 1999 and 2007. Error bars represent 95% confidence limits. Monthly differences across years are indicated with asterisks.

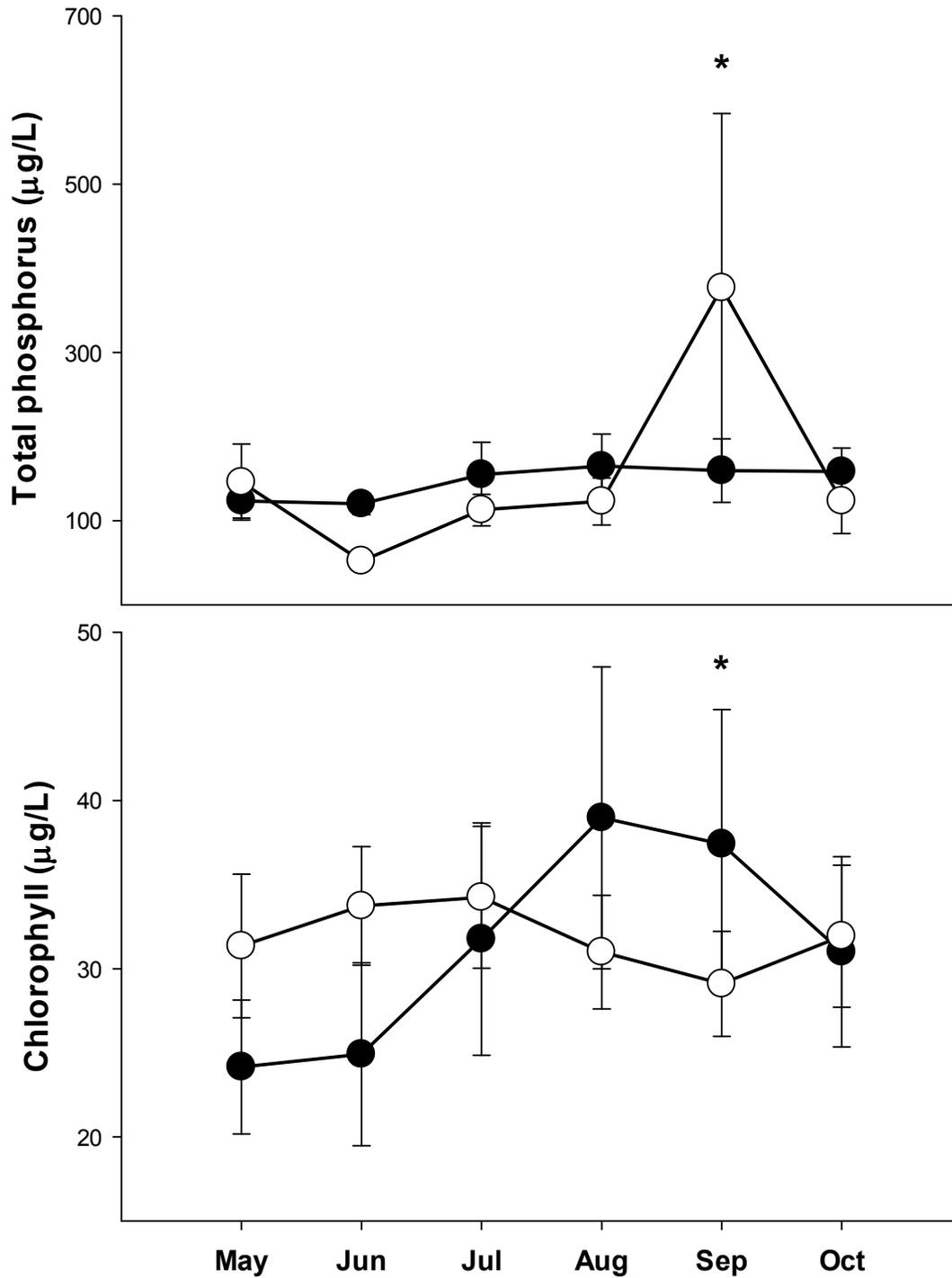


Figure 2.4. Average Secchi depths among control lakes (dark circles) and thermally influenced Clinton Lake (open circles) between 1999 and 2007. Error bars represent 95% confidence limits.

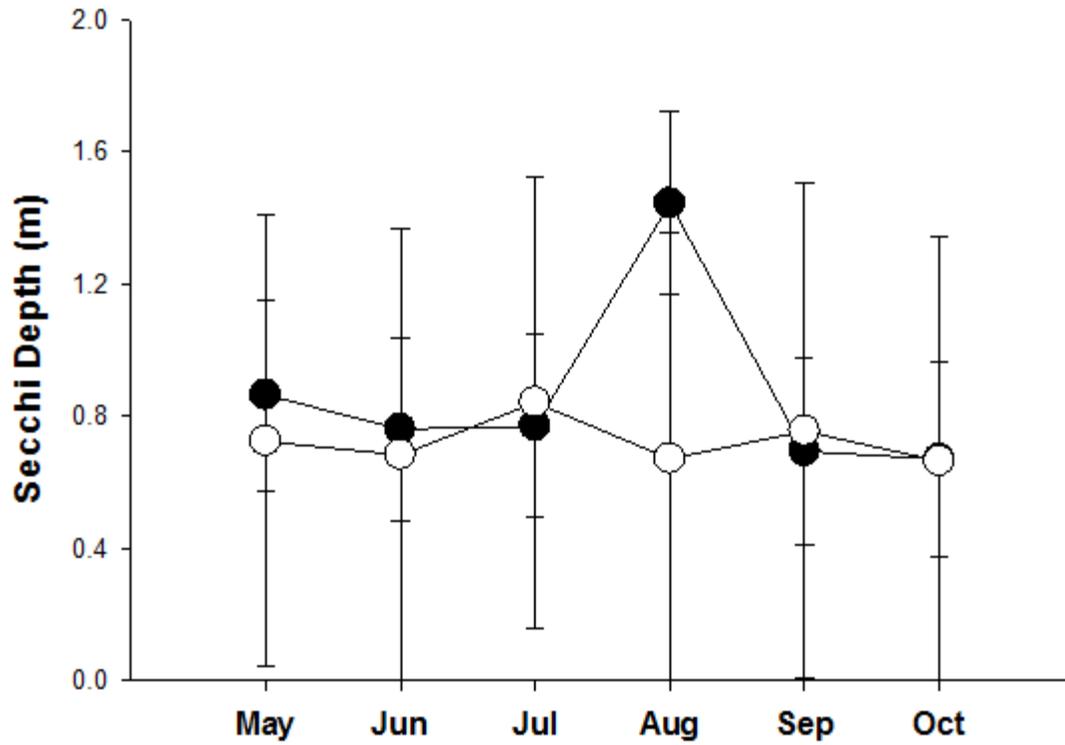


Figure 2.5. Macrozooplankton (left panels) and rotifer (right panels) density per month between control lakes (dark circles) and power plant lakes (open circles). Error bars represent 95% confidence limits. Monthly mean densities are shown for Clinton Lake versus controls for 1997-2007 (A and D), Newton Lake versus controls in 1999 (B and E), and Coffeen Lake versus controls in 2010 (C and F).

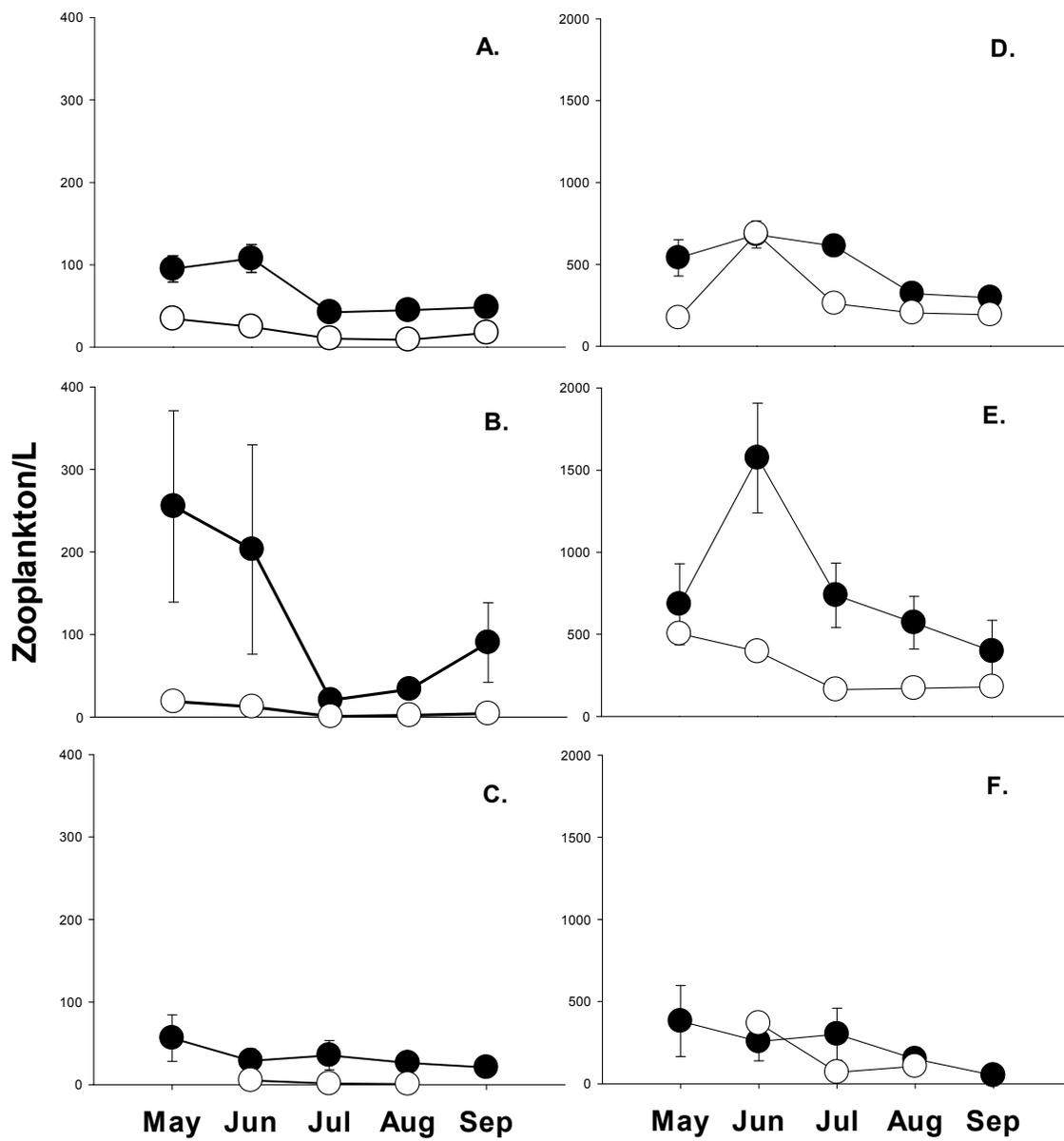


Figure 2.6. Summer macrozooplankton communities of the most abundant groups in control (C; no thermal influence) and treatment (T; thermally influenced) lakes.

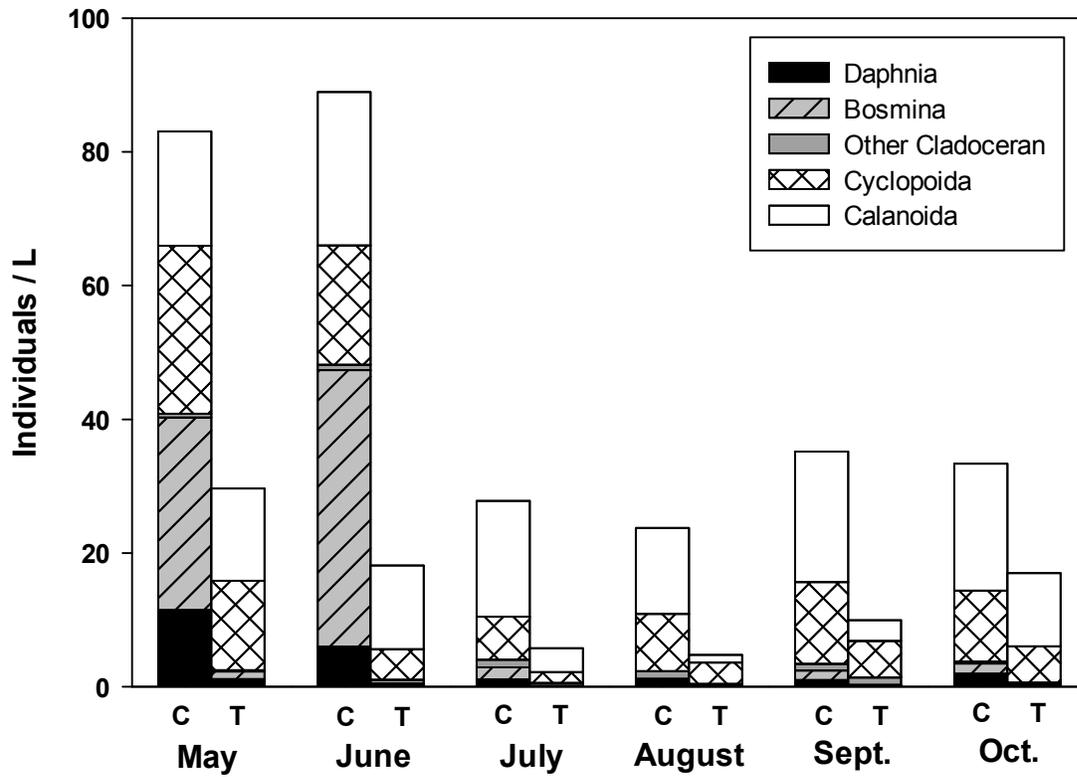


Figure 2.7. Average larval *Lepomis* and gizzard shad (*Dorosoma cepedianum*) densities in control lakes (dark circles) and Clinton Lake (open circles) between 1999 and 2007. Error bars represent 95% confidence limits. Monthly differences are indicated with asterisks.

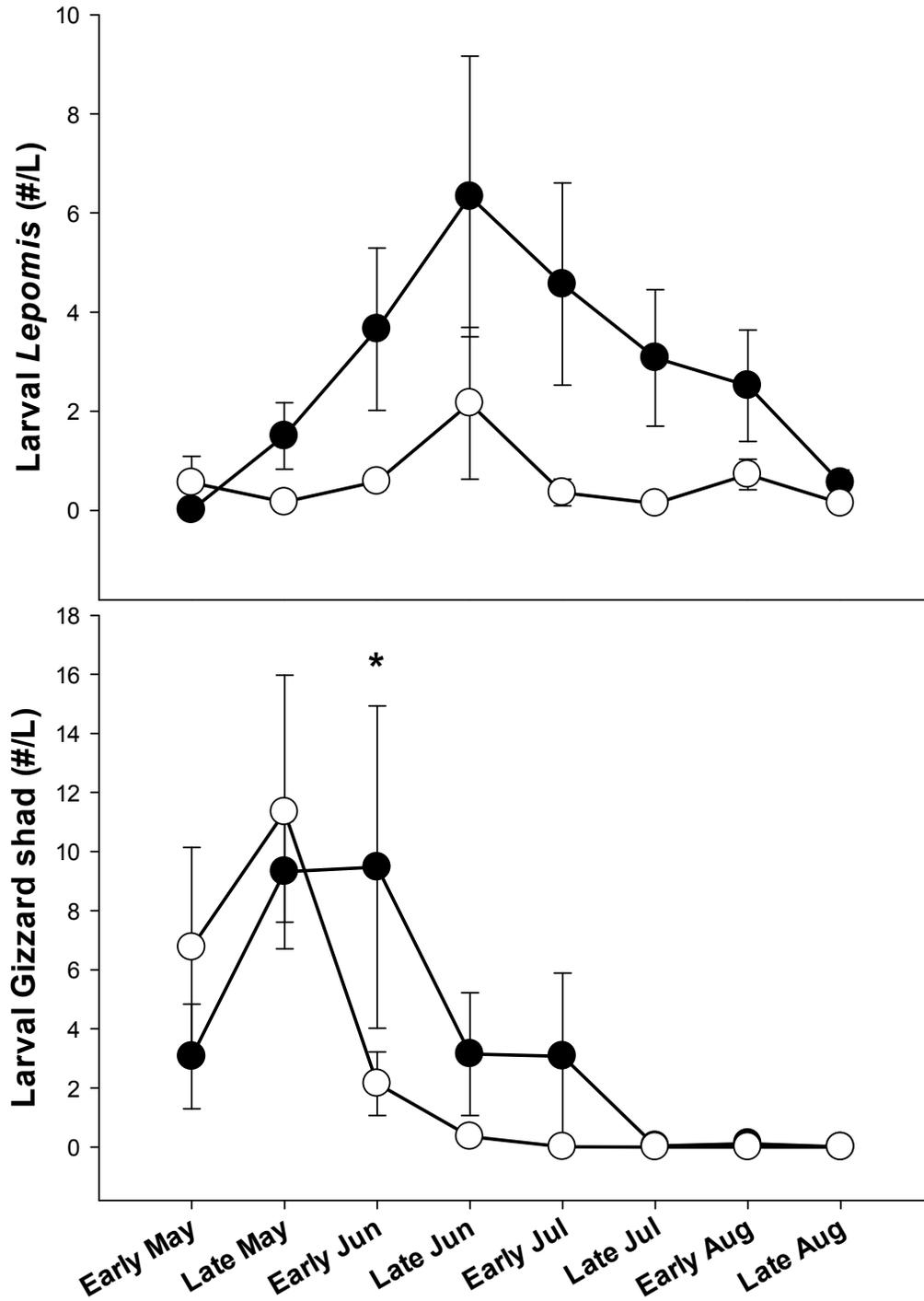


Figure 2.8. Average size of young-of-year bluegill (*Lepomis macrochirus*) (A) and largemouth bass (*Micropterus salmoides*) (B) in power plant (open circles) and control (dark circles) lakes between 1998 and 2007. Error bars represent 95% confidence limits. Monthly differences are indicated with asterisks.

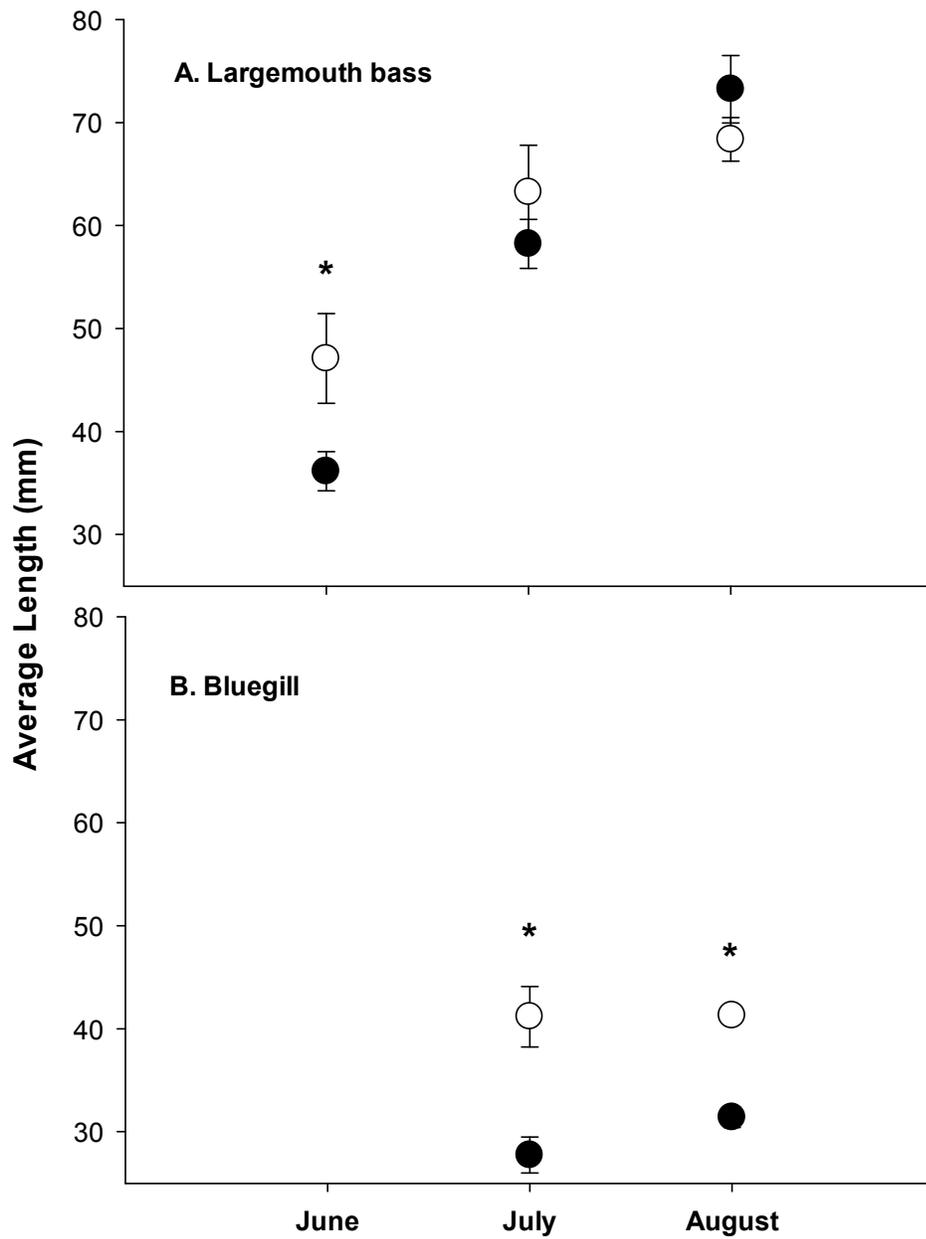
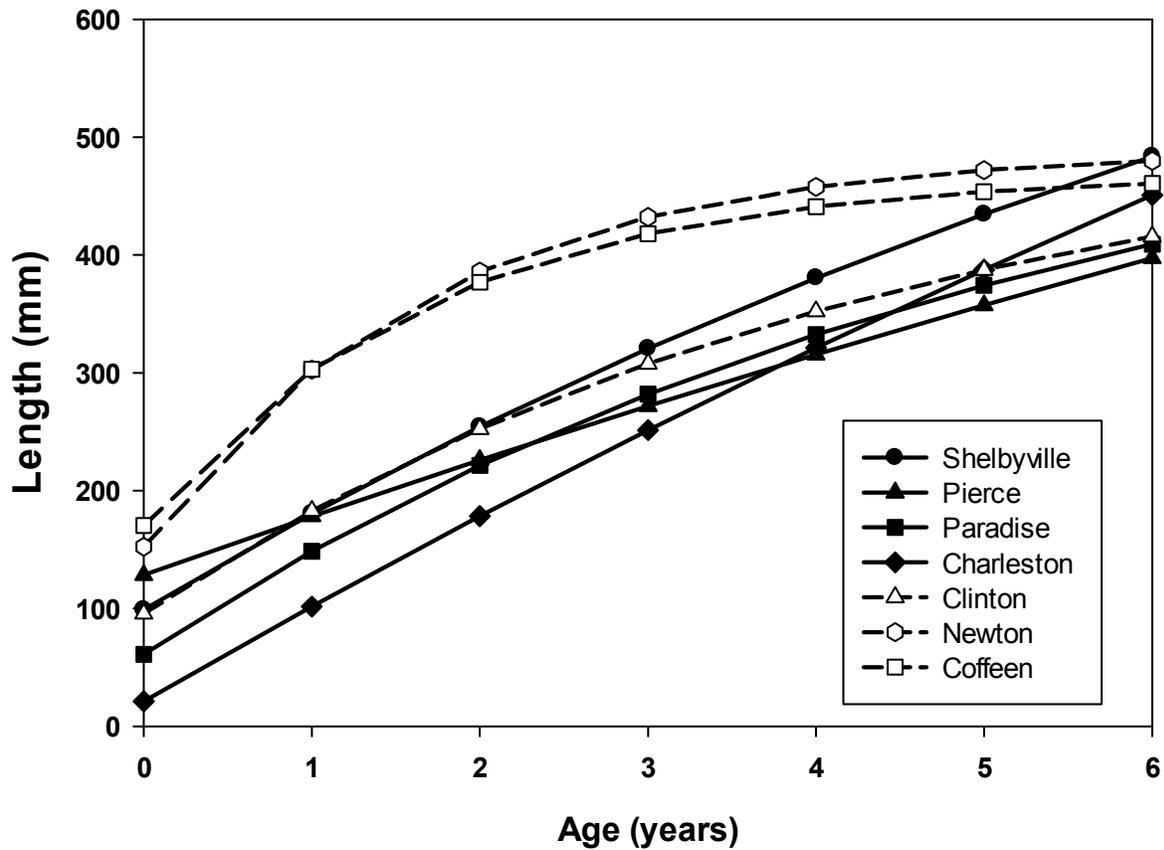


Figure 2.9. Von Bertalanffy growth curves for largemouth bass (*Micropterus salmoides*) from control (solid lines) and power plant (dotted lines). A t test of the ω parameters showed that growth was significantly greater for largemouth bass in the heated lakes ($P = 0.03$).



CHAPTER 3. RESPONSE OF FISH FROM DIFFERENT THERMAL ENVIRONMENTS TO INCREASED WATER TEMPERATURE

ABSTRACT

Due to concerns of global climate change, additional research is needed to quantify the thermal tolerance of species, and how organisms are able to adapt to changes in thermal regime. I quantified the thermal tolerance and thermal stress response of a temperate sportfish from two different thermal environments. One group of largemouth bass (*Micropterus salmoides*) inhabited thermally enhanced reservoirs (used for power plant cooling), with water temperatures typically 2-5° C warmer than nearby reservoirs that are not. I tested both groups of fish for chronic thermal maxima and reaction to a heat shock (8° C) using three common physiological indices of stress. I observed no evidence of differences between groups in thermal maxima. I also found no difference in baseline or response to heat shock in levels of plasma cortisol, plasma glucose, or packed cell volume of whole blood. My results disagree with research suggesting differences due to adaptation to different thermal environments. I speculate that behavioral modifications, lack of adequate time for genetic divergence, or the robust genetic plasticity of largemouth bass explains the lack of difference between treatment groups.

INTRODUCTION

Thermal tolerance assessments on individual fish and fish populations have been used to address a range of questions, including home range expansion and contraction, as well as suitability of new habitats to colonization (Kimball et al. 2004; Dunham et al. 2003; Hostetler 1991). Knowledge of preferred temperature is also important to the development of bioenergetics models (Chipps and Wahl 2008; Hansen et al. 1993). Intraspecific differences have also been used to answer questions concerning the effects of stressors (Morgan et al. 2001), latitudinal variation (Eliason et al. 2011; Fangue et al. 2006), and effects of fish size (Rodnick et al. 2004). With the growing concern of impending climate change, temperature tolerances of many cold and cool water species have also been used to predict effects on fish communities (Britton et al. 2010; Somero 2010; Mohseni et al. 2003; Eaton and Scheller 1996).

Due to uncertainties concerning the effects of a changing climate on fish populations, evaluation of the stress response of organisms to environmental variables subject to shift in the near future is necessary. Predicting how organisms may respond to a warmer environment is also needed, and examining differences in populations from variable thermal regimes can inform these predictions. Beneficial acclimation theory suggests that fish from warmer systems will be best adapted to those systems (LeRoi et al. 1994) and therefore should demonstrate higher temperature tolerance and potentially a different physiological response to thermal stress than fish from cooler water bodies. However, there are questions concerning the generality of this theory (Huey et al. 1999). Chronic exposure to poor environments, potentially those with disruptively high temperatures, may cause a steady decrease in organismal condition (Woods and Harrison 2002), and hide any beneficial acclimation to the environment.

Predicting the effects of climate change, and how organisms may adapt, is also problematic because of difficulties recreating climate change scenarios to test hypotheses (Meyer et al. 1999). Most predictive studies are based on lab experiments and models, as forecasting changes to long-term temperature shifts is logistically difficult. For this study, I have proposed new study systems to be used as surrogates for aquatic environments affected by climate change. For decades, large reservoirs have been used to cool electric generators of power plants, causing water temperatures to be warmer than ambient. Research has demonstrated that power plant effluent can have effects on fish distribution and behavior (Cooke et al. 2004), reproductive abilities (Luksiene et al. 2000), and thermal tolerance (Meffe et al. 1995). However, using these warmed systems as a proxy for lakes of the future is a somewhat novel approach. Many power plants on these lakes have been in use for half of a century, so resident biota have been chronically exposed to a warmer, artificial temperature regime for decades. This makes these systems ideal for examining how organisms may be affected by a different temperature regime, since nearby lakes have fish communities with a similar genetic composition, but have had a different thermal experience for generations. I used these power plant lakes to gain insights into changes in thermal tolerance, but their value for all applications concerning climate change should not be overlooked.

Many questions concerning the impacts of climate change on organisms are highly dependent on characteristics of the organism in question. As climate regimes shift, organisms that are the most able to rapidly adapt physiologically (Hoffman and Sgro 2011; Somero 2010), or migrate to remain in optimal climates (La Sorte and Jetz 2012; Angert et al. 2011), will be the most successful in a quickly changing world. Species currently inhabiting a wide range of habitats and temperature regimes are the most likely to exhibit these traits, and are therefore

excellent organisms to study for physiological adjustments and tolerance to habitat variables. Largemouth bass, *Micropterus salmoides* (Lacepede 1802), are a prominent sportfish throughout North America and have been introduced worldwide. Although a temperate species, they have been shown to thrive in a variety of environments, from Canadian Shield lakes to Mediterranean wetlands (Page and Burr 2011; Scalici et al. 2009). Previous research has established largemouth bass demonstrate plasticity sufficient to adjust its metabolic rate / temperature dynamics to maximize growth and survival in markedly different climates (Gaulke et al. In Press; Venables et al. 1977). Largemouth bass are likely to be better adjusted to deal with a changing climate than many other fishes, as their range and apparent plasticity are traits needed to adapt to rapid change (Somero 2010). Like other widespread eurythermal species, largemouth bass also demonstrate significant phenotypic plasticity, as life history variation can be a consequence of different developmental environments (Meffe 1992). Because of the ability of this eurythermal fish to flourish in variable environments, it is an ideal candidate for a study into the adaptive ability of a fish to a changing climate.

There have been a variety of methods used to characterize temperature tolerance and temperature-induced stress. Whole-body responses to temperature treatments have used thermal maxima treatments (first described by Cowles and Bogert (1944)) to ascertain tolerance. Typically, these types of experiments subject individuals to progressively greater temperatures until a response (loss of equilibrium or death) is induced. Because starting temperatures and rate of heating can be variable, the chronic thermal maxima of fish are relative values and artifacts of a given experimental design. However, it is an effective method for characterizing the temperature tolerance of fish (Becker and Genoway 1979) and commonly used to test for

differences among fish species and populations (Galbreath et al. 2004; Currie et al. 1988; Fields et al. 1987).

Another common practice to assess stress caused by disturbances such as elevated temperatures is to measure physiological parameters (Diaz et al. 2007; Suski et al. 2006; Vanlandeghem et al. 2010). For example, the steroid hormone cortisol, which promotes energy metabolism and is a widely used indicator of stress in fish (Wendelaar Bonga 1997), increases in fish exposed to a stressor, including hypoxia and undesirable temperatures (Vanlandeghem et al. 2010; Tanck et al. 2000; Cataldi et al. 1998), as well as angling, handling, and confinement (Rapp et al. 2012; Suski et al. 2003; Carmichael et al. 1984). Plasma hemoglobin and packed cell volume can also be informative for characterizing secondary responses to sub-lethal stressors (Furimsky et al. 2003), and blood glucose levels have also been shown to rise in response to acute temperature stress (Mesa et al. 2002).

My goal was to evaluate the response of a temperate teleost fish to multiple temperature stressors from systems that differ significantly in their respective thermal regime. I used largemouth bass as my study organism, and compared fish from artificially warmed systems to others from systems of similar size and location, but without the artificial thermal regime. I assessed fish for thermal maxima and three common physiological parameters associated with response to stressful conditions.

METHODS

Study systems

To quantify differences in thermal tolerance between fish from different thermal regimes but similar latitudes, I used two artificially heated reservoirs. Clinton Lake (1,983 ha., DeWitt

Co., IL) and Newton Lake (688 ha., Jasper Co., IL) function as power plant cooling lakes, and typically have water temperatures 2-8° C greater than nearby water bodies (Figure 3.1). The nuclear power plant at Clinton Lake has been in use since 1987, and the coal plant at Newton Lake has been operational since 1977. Each power plant lake was then paired with a control lake of similar size and location not receiving thermal effluent. Lake Shelbyville (4,492 ha., Shelby Co., IL) was paired with Clinton Lake, and Forbes Lake (226 ha., Marion Co., IL) was paired with Newton Lake. With the two by two paired experimental design, I was able to isolate the effects that the thermal regimes have on resident populations without the influence of regional differences.

Quantification of the temperature regime of each system was accomplished using temperature loggers stationed centrally in each lake at a depth of 1 meter. Loggers were active on Clinton Lake from 2009-2012, Newton Lake from 2003-2006, and Forbes Lake from 2006-2010, and were programmed to record temperature measurements every hour. Loggers were not installed on Lake Shelbyville, but temperatures at 1 m were taken biweekly from 1999-2012. Average temperatures for each Julian day were then calculated for each lake for standardization across years. Treatment lakes were about 5° C warmer than controls during the summer and fall, and much greater (>7°) during the winter and spring (Figure 3.1).

I chose largemouth bass (*Micropterus salmoides*) as my study organism due to their widespread range, prevalence in nearly all regional water bodies, and value as a sportfish (Schramm et al. 1991; Siepker et al. 2007). All bass used in experiments were collected using standard electrofishing procedures from 2009 to 2011, brought to the Kaskaskia Biological Station (Moultrie Co., IL) and acclimated for one to three weeks at 25° C. To minimize differences associated with fish size, all fish were between 250-370 mm. Fish were fed to

satiation with fathead minnows (*Pimephales promelas*) three times per week, and starved for 48 hours prior to experimental use.

Thermal maxima

Thermal maxima experiments were conducted in an environmental chamber with temperature and light control. The chamber contained 16 (75 L) aerated aquaria wrapped in black plastic to eliminate visual disturbance. I chose to use a slow heating rate of 2° C per day to determine chronic thermal maxima (Beitinger et al. 2000; Galbreath et al. 2006). More gradual heating rates are more sensitive for detecting differences among populations, specifically with fish of the same species (Galbreath et al. 2004).

Each trial included eight fish from one of the power plant lakes and eight fish from its associated control lake. Four trials were conducted so that each lake pair was completed twice. Because of inherent seasonal changes in physiology that influence thermal tolerance (Chipps et al. 2000), data analysis included each trial as a block. Because larger fish have been shown to sometimes have lower thermal tolerances (Currie et al. 1998; Rodnick et al. 2004), fish length was also recorded for use as covariate. No differences in fish length were observed between Clinton Lake and Lake Shelbyville ($P = 0.98$), or between Forbes Lake and Newton Lake ($P = 0.35$). One trial was also conducted without the thermal treatment to test whether stress associated with confinement in experimental aquaria caused mortality independent of temperature.

Experimental fish for each trial were randomly distributed among the environmental chamber aquaria, and allowed to acclimate an additional 24 hours at 25° C. The treatment was then administered, and fish were checked every four hours for loss of equilibrium, when time

and temperature were recorded. Dissolved oxygen concentrations in the aquaria were also monitored, with lower oxygen concentrations observed at higher temperatures, mirroring natural processes (Cross and Rawding 2009). Throughout the trial period, 25% of the water in each aquaria was replaced each day with fresh water of equal temperature. Each trial persisted until all fish had lost equilibrium.

Physiological comparison

Physiological parameters were measured in response to an acute 8° C heat shock (25° C to 33° C) sustained for six hours. The magnitude of the heat shock was chosen to be large enough to illicit a stress response, but based on preliminary trials not too severe to lead to mortality in largemouth bass. Although it is unlikely that fish would encounter a rapid temperature increase of this magnitude in the wild, differences in physiological reaction may provide valuable insights on how these fish populations may respond to climatic changes (Somero 2011). The heat shock was administered by a closed-circuit system designed so that water temperatures in eight, 18 L plastic aquaria could be closely regulated, similar to the methods used by Suski et al (2007). Each aquaria was aerated, covered, and isolated from one another with plastic dividers so that treatment fish were not visually disturbed. Water from one of two large, central basins was pumped into all aquaria and allowed to overflow into fiberglass raceways holding these containers. The raceways then returned water to the central basin, thus closing the system. One basin contained water kept at 25° C, and the other held heated water maintained at 33° C. A valve in the flow-through system allowed for changing of the active basin.

Eight fish from each lake were randomly designated to receive the heat shock treatment, and eight others were used as controls. Each trial could accommodate eight fish, so four fish from each lake of the two lake pairs were included in each experimental run that was either a control or heat shock treatment. Experimental fish were placed into one of the eight aquaria and allowed to acclimate to the new environment, during which water was constantly flowing from the 25° basin. After 24 hours of acclimation in heat shock treatment runs, temperatures were quickly raised by 8° and held constant at 33° for six hours. In control runs, temperatures were held constant at 25° for the complete 30 hour period. After the allotted time, flow to individual containers ceased and each fish was euthanized with a lethal dose (250 mg/L) of 3-aminobenzoic acid ethyl ester methanesulfonate (MS-222) buffered with 500 mg/L of sodium bicarbonate (Summerfelt and Smith 1990). Following cessation of opercular movement, a 20-gauge hypodermic needle rinsed with lithium heparin (Houston 1990) was used to draw blood from the gill arch of each fish. To assess packed cell volume (PCV%), a portion of the blood was put into microcapillary tubes in duplicate and centrifuged at 15,800 rpm for three minutes using a hematocrit microcentrifuge, and the PCV% was ascertained using a hematocrit reader (CritSpin Models CS22 and CSD2, Iris International Inc., Chatsworth, CA). The remaining blood was centrifuged at 2,000 x gravity for two minutes to separate plasma from red blood cells. Plasma was pipetted out and put into two 1.5 mL microcentrifuge tubes, and then immediately stored in -80° C liquid nitrogen until lab processing (Iwama et al. 1998). Plasma cortisol concentration was determined using a commercially available kit (Kit # 900-071; Assay Designs, Ann Arbor, MI, USA) previously validated for use on largemouth bass (Sink et al. 2008), and plasma glucose was determined enzymatically following the methods of Lowry and Passonneau (1972) using a

spectrophotometer (Spectra Max Plus 384, Model # 05362; Molecular Devices, Union City, CA, USA).

Statistical Analysis

For chronic thermal maxima analyses, time from beginning of a given trial to cessation of opercular movement was used as the response variable. Use of time instead of temperature eliminates error associated with minor deviations from the linear heating rate of 2° C/day as suggested by Galbreath et al (2004). Because chronic thermal maxima trials were conducted at different times during the year, and because of seasonal variation expected in fish physiology and metabolism regardless of acclimation temperatures (Chipps et al. 2000), each trial was treated as a block. Because each trial only contained fish from one of the two possible lake pairs, a separate ANOVA was conducted for each lake pair, blocked by trial, with fish length as a covariate, since fish size has been shown to influence thermal tolerance in some cases (Cook et al. 2006; Galbreath et al. 2006; Becker and Genoway 1979).

Because of the relative temporal proximity of trials assessing physiological response to heat shock, blocking by trial was ineffective and therefore not used in subsequent analyses. For each physiological variable measured, an ANOVA was conducted that included thermal environment and treatment type (heat shock vs. control) as binary class variables, the interaction between the two, and lakes nested within environments. In this way, I could test for differences in physiological parameters between thermal environments for baseline levels and the relative change in these levels between control and treatment trials. Fish length was also tested as a covariate, and was not different between thermal environments ($P = 0.98$).

RESULTS

No significant differences were observed between fish from the different thermal environments in chronic thermal maxima. Individual variation in largemouth bass was much greater than any differences between populations. Chronic thermal maxima experiments showed no significant differences between either lake pair. The average time until cessation of opercular movement was slightly greater for the warmed Newton Lake (156.2 hours) than for the control lake of Forbes (144.8 hours), but this difference was not statistically significant ($P = 0.16$, Figure 3.2). The average times for thermally enriched Clinton Lake (137.6 hours) and control lake Shelbyville (139.3 hours) were also not statistically different ($P = 0.75$, Figure 3.2). For both comparisons, the blocking factors were highly significant. Control trials lasted 168 and resulted in no fish mortality.

Physiological variables also showed no differences between heated and control lakes. PCV values were not different between environments for baseline values ($P = 0.12$) or response to treatment ($P = 0.53$). Cortisol levels were similar between environments for baselines ($P = 0.20$) and reactions to heat shock ($P = 0.45$). Likewise, the heat shock did not induce different blood glucose responses ($P = 0.81$) or were the initial baseline levels different ($P = 0.39$, Figure 3.3). Among all fish, the heat shock caused a significant increase in blood glucose levels ($P = 0.04$), but there was no change in PCV ($P = 0.89$) or plasma cortisol ($P = 0.87$) as a result of the treatment.

DISCUSSION

Contrary to my expectations, I saw little evidence of differences in thermal tolerance between fish from lakes with different thermal regimes. From the measured metrics, I conclude

that the populations assessed are not different in their response to rapid heat shock or to gradually rising temperatures. Other studies have suggested that animals raised at different temperatures should demonstrate different tolerance at some level (Ayrinhac et al. 2004; Sokolova and Portner 2003; Tomanek and Somero 1999). My results also disagree with other studies examining response to thermal challenges for different fish populations of the same species, including research conducted with sockeye salmon (*Oncorhynchus nerka*) (Eliason et al. 2011) and tropical fishes (Newton et al. 2010).

Several plausible explanations exist for why largemouth bass populations from different thermal environments demonstrated similar thermal tolerance. Beneficial acclimation theory, suggesting that fish from the warmer systems should perform better in tolerance tests due to their acclimation in higher temperatures, has been scrutinized and failed to have been supported in many cases (Woods and Harrison 2002; Huey et al. 1999). The ability to flourish in a variety of thermal environments has been linked to ideal temperatures during early life stages (Cohet and David 1978). The ‘optimal developmental temperature hypothesis’ could explain my results, if the temperature regime in power plant reservoirs is suboptimal (i.e. too warm) during the early development of largemouth bass. Differences between populations may also not be present due to behavioral modifications of fish in the warmed environments, referred to as the Bogert Effect (Huey et al. 2003). In the power plant lakes, resident fish may be actively avoiding uncomfortably warm water (Zimmerman et al. 1989; Block et al. 1984), and spawning earlier so that young past the critical development stage by the warmest summer temperatures. This seems likely because cooling reservoirs, including those in this study, are characterized as having a temperature gradient across the lake, in which the warmest temperatures are found at the effluent outflow, and gradually drop with distance from the outflow. Previous research has demonstrated

that fish captured close to power plant effluent have lower body condition than fish captured farther away (Gibbons et al. 1978). Also, I have observed that juvenile bass are larger in the early summer in power plant lakes when compared to their cooler counterparts, possibly indicating that spawning occurs earlier in the power plant reservoirs (Mulhollem et al. unpublished). I also may not have observed differences in the populations due the relatively short evolutionary time scale (25-35 yrs.) in which the power plants on the study lakes have been operational. Even if the unnatural temperature regime is causing changes in fish populations, it is possible that more time is needed before these changes become perceptible.

The possibility exists that the populations differ in response to thermal stressors, but these differences were not measureable by my methods. Both of my techniques for determining temperature tolerance used a rapid change in temperature that is not necessarily indicative of the environmental conditions experienced by fish in cooling reservoirs. Largemouth bass are quite resilient in response to a moderate heat shock, and evidence suggests that short-term changes in physiological parameters may have returned to baseline levels during the six hour exposure to the stressor (Vanlandeghem et al. 2010). However, I induced a response in glucose that should have allowed me to detect differences if they existed. More lake pairs may be useful in eliminating random variation among populations, regardless of local thermal regime. Other physiological parameters may also identify differences that were undetected in my study. Heat shock proteins, for example, initiate cellular responses as a result of a stressor, and are not completely dependent on hormones released in the primary stress response (i.e., cortisol) (Iwama et al. 1998). Heat shock protein differences may exist between populations that may have masked differences in the variables I measured. Still, I would expect any physiological variation

between the populations to be manifested in the whole-body temperature tolerance experiment, in which I detected no differences.

My research demonstrated the plasticity in largemouth bass that may signify the ability of the species to thrive despite a changing climate (Somero 2011). Fish taken from two distinctly different environments demonstrated little difference in their response to a thermal stressor and overall temperature tolerance. I speculate that similar studies with eurythermal species would generate similar results, potentially indicating the hardiness of the species to adapt to varying environmental conditions. Results contrary to ours, in which organisms of the same species but inhabiting different environments reacted differently to a stressor, may indicate that one (or both) populations are occupying a sub-optimal environment. This may suggest that a population is at or near a threshold for some environmental variable, and that even minor changes in that variable could have significant effects on the population. Or, it may simply mean that the two populations are genetically distinct stocks that have evolved to different environmental conditions.

The assessment of thermal tolerance among all organisms has resurfaced as an important research area due to growing concerns about global climate change. Fish species are potentially at the greatest risk, due to constraints on mobility in aquatic environments. It has been predicted that fishes most adaptive to changing temperature will be the most likely to flourish despite climatic changes (Matthews and Zimmerman 1990). Future research should focus on the fitness of fish species in response to shifts in thermal regimes, and how changing temperatures may affect populations in variables other than the ones I measured. Determining thermal thresholds, those at which significant impairment occurs, for different fish species is also needed so that populations at risk can be identified and protected if local temperatures rise.

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FIGURES

Figure 3.1. Average annual temperature (C°) regime for each power plant (gray lines) and control lakes (black lines) as determined from temperature loggers and temperature probes used at 1 m of depth. For my analyses, largemouth bass (*Micropterus salmoides*) from lakes Shelbyville and Clinton (solid lines) were compared with each other, as were fish from lakes Forbes and Newton (dotted lines).

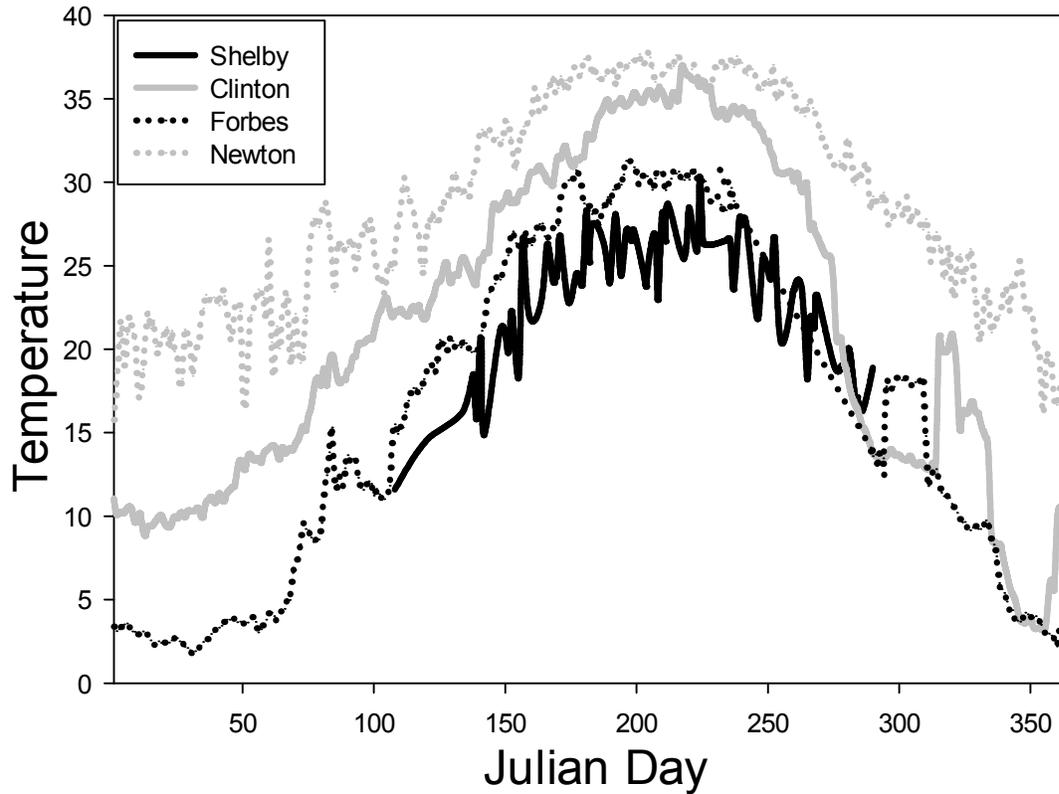


Figure 3.2. Elapsed time from the onset of chronic thermal maxima experiments until cessation of opercular movement for largemouth bass (*Micropterus salmoides*) from natural (gray bars) and heated (open bars) lakes. Error bars indicate 95% confidence limits. Neither lake pairing resulted in a significant difference between bass from the two environments. The number of bass used to calculate means are included for each bar.

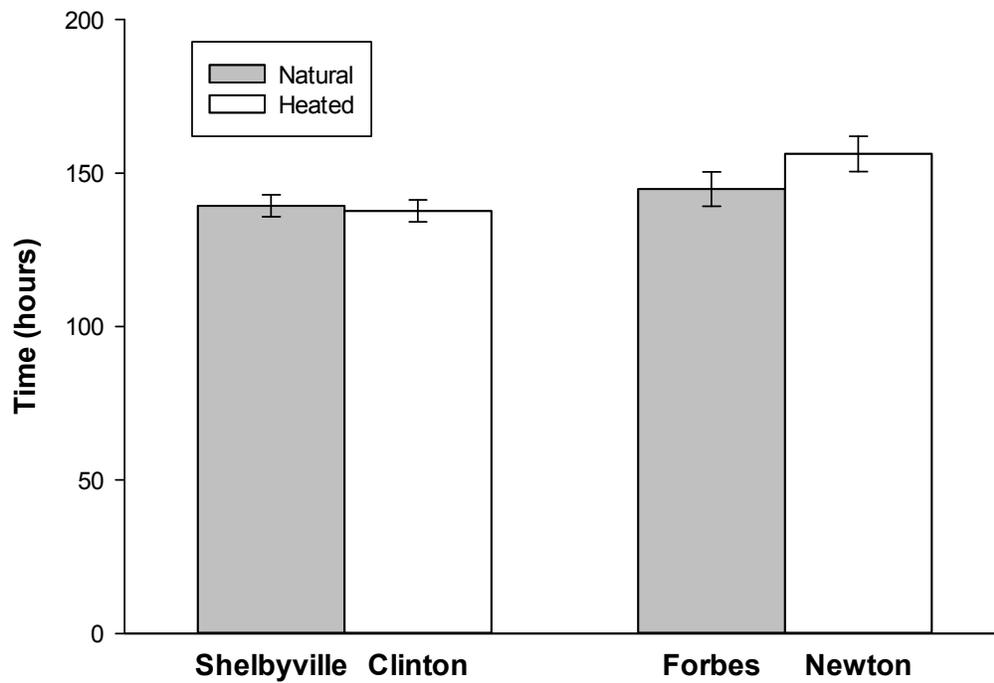
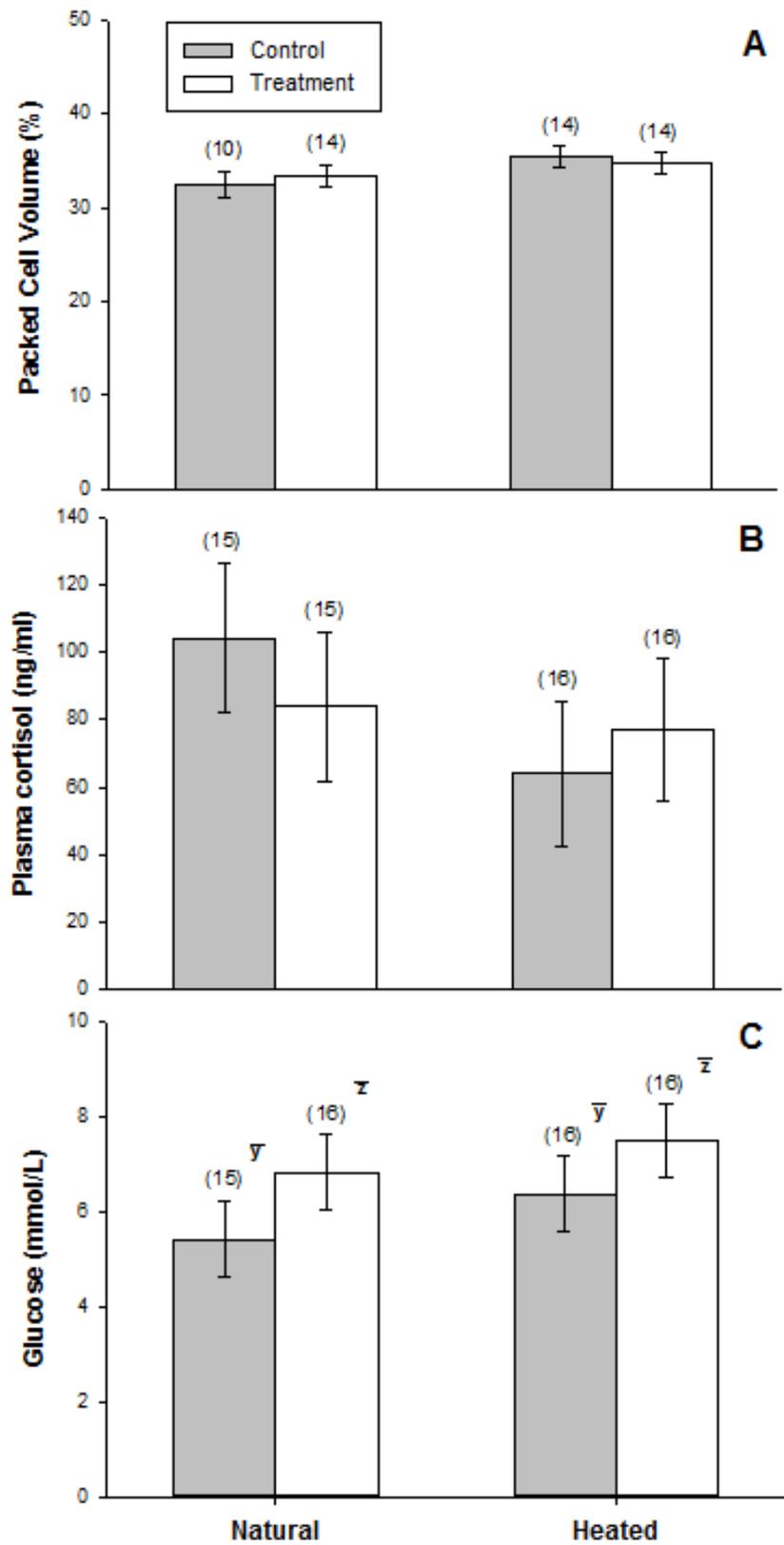


Figure 3.3. Packed cell volume (A), and plasma cortisol (B) and glucose (C) concentrations of largemouth bass (*Micropterus salmoides*) held at a control temperature of 25° C (gray bars) and heat shocked for six hours at 33° C (open bars). Fish are from control environments (natural), and from thermally enriched environments (heated). No significant differences existed between environments for either baseline values (control), or relative reaction to heat shock (treatment*environment) in any of the measured variables. A significant positive effect of treatment on glucose concentration is indicated with different letters. The number of fish used to calculate means are included above each bar.

Figure 3.3.



SUMMARY

My results and conclusions indicate that some stressors experienced in aquatic ecosystems and by resident biota could potentially cause negative effects. Still, ecosystems and fish populations are resilient and often able to mitigate negative effects brought on by changing abiotic variables (i.e. temperature regime) or anthropogenic influences (i.e. tournament angling of nesting adults). I found evidence of both scenarios.

Although it was clear that simulated tournament angling practices caused a reduction in individual nesting success of angled largemouth bass similar to many previous studies, there was no difference in gross recruitment to the fall between angled and control ponds, which is a much less established finding. I did, however, find that there were differences in the size structure of juvenile bass that could be attributed to the angling treatment. Recruitment and other variables associated with reproduction were correlated with habitat variables. This finding highlighted the importance of habitat and prey availability to successful largemouth bass populations. My final conclusion is that the effects of excessive tournament angling pressure would be variable and unique to each system. While systems with favorable habitat conditions for largemouth bass recruitment may be rather unaffected by the loss of some percentage of nests, the possibility exists that altered size structure of juvenile fish could have consequences on long term survivability.

The effects of warmer temperatures on lake ecosystems may be pronounced in some cases, but that will not necessarily mean that changes will be positive or negative. As has been suggested in previous studies, changes in the climate regime may shift many variables temporally, such as timing of zooplankton peaks and timing of spawning of fish. There may also be water clarity shifts and changes in nutrient concentrations and stoichiometry ratios, although

my results did not support these kinds of changes. I did observe changes in growth of some fish species, which would be expected of most warm water species in a temperate climate up to some thermal threshold.

Shifts at lower trophic levels and elevated summer temperatures did not appear to negatively affect growth top predator fish, as the extended growing season afforded by warmer winter temperatures may have contributed to increased fish growth. I ultimately conclude that systems in the Midwest may be resilient to the effects of a climate regime shift, but many variables are subject to change.

Examination of the temperature tolerance of largemouth bass from different thermal regimes demonstrated little difference between populations from the different environments. Largemouth bass from warmer systems were not different in thermal tolerance to bass from cooler systems when assessed with any of the temperature tolerance tests used in my study. Because largemouth bass are found worldwide in a variety of climates, they have proved to be superior at adapting to a range of temperatures. My results indicate that genetic plasticity present in eurythermal species such as largemouth bass may result in little genetic and phenotypic change between populations in different climates. Results may indicate that species with similar traits may be best suited to adapt and thrive to future climate scenarios.