

FORAGING ECOLOGY OF TWO PISCIVORES IN WOODY HABITAT AND EFFECTS OF
THEIR INTRODUCTION ON LAKE ECOSYSTEMS

BY

COREY S. DEBOOM

THESIS

Submitted in partial fulfillment of the requirements
for the degree of Master of Science in Natural Resources and Environmental Sciences
in the Graduate College of the
University of Illinois at Urbana-Champaign, 2012

Urbana, Illinois

Advisor:

David H. Wahl, PhD

ABSTRACT

Predation is a major ecological force affecting the abundance and species composition of natural communities. Predation from piscivorous fish is a strong driver of these patterns in freshwater aquatic communities. My research is directed at testing whether the introduction and augmentation of piscivore populations, as well as the alteration of littoral habitats, in Illinois lakes affects the consequences of predation for other ecologically and recreationally important species in these ecosystems. Some studies in lentic ecosystems have found large effects of introducing piscivores to systems that previously lacked them, as well as, to the artificial enhancement of piscivore populations. While the evidence for such “trophic cascades” is plentiful, a large body of subsequent research has suggested that certain properties of lakes found in lower latitude systems in the central and southern United States may buffer these systems from cascading effects of piscivore manipulations. Therefore, there is a need to test the generality of cascading trophic interactions in these lower latitude lentic ecosystems. Thus, in chapter 1 I tested for the effects of supplemental piscivore enhancements on the food webs of several Illinois lakes in a series of whole-lake experiments incorporating unmanipulated control systems. I found that piscivore enhancements in Illinois lakes did not cause the predicted pelagic food web changes predicted by the traditional trophic cascade theory; however, there was a significant effect upon littoral macroinvertebrates. This effect was driven by a reduction in the abundance of small bodied littoral fishes (primarily juvenile bluegills) after the initiation of supplemental largemouth bass stocking. My results highlight the importance of system-specific characteristics in determining the effects of piscivore enhancement measures. In addition to piscivore enhancement, there is a need to better understand the effects of introducing new piscivore species. Previous studies suggest that the introduction of new species can drive a nearly

limitless array of food web consequences, with the most common including direct and indirect interactions between top predators and changes in prey mortality rates. In a controlled experimental design, I tested for changes in population characteristics including size structure, condition, and relative abundance of several ecologically and recreational important resident fish species in response to muskellunge introduction across several Illinois lakes. I found that contrary to popular concerns, the dominant resident piscivore largemouth bass generally increased in relative abundance in response to muskellunge introduction. I also found few effects of introduced muskellunge on common prey species, with the exception of *Pomoxis* spp., which exhibited increases in size structure and/or decreases in relative abundance. My results indicate that the current trend of muskellunge introduction in lower Midwestern lakes does not appear to be significantly harming resident populations; however, much future work remains in this area. Physical habitat can be an important determinant of the strength of piscivory on freshwater fish populations. Thus, I conducted a manipulative laboratory experiment to test for the effects of coarse woody habitat complexity on the piscivore-prey interaction between four species with contrasting predatory and anti-predatory behavioral traits. I found that woody habitat in the form of deadfall conifer branches did not reduce total prey fish mortality rates inflicted by piscivores in experimental arenas. I did find an increase in mortality rate with increasing coarse woody habitat complexity for an obligate shoaling prey fish. Furthermore, there were significant effects of coarse woody habitat complexity on foraging efficiency of piscivores, which may influence metabolic costs and therefore piscivore energy balance (as net energy for reproduction and growth is equal to energy consumption minus losses due to excretion, egestion and metabolism). Collectively, my results suggest that coarse woody habitat may influence piscivore-prey

interactions principally through behavioral mechanisms and subsequent effects of behavior on piscivore energy balance as defined above.

ACKNOWLEDGEMENTS

Many people contributed to the completion of my thesis research. I am especially thankful to the staff of the Kaskaskia and Sam Parr Biological Stations for field and lab assistance, especially J. Wisher, D. Oele, K. Schnake, and J. Clark. I am also grateful for assistance I received from Illinois Department of Natural Resources (IDNR) staff especially the staffs of the Little Grassy and Jake Wolf Fish hatcheries for raising largemouth bass and muskellunge used in these projects. S. Pallo, J. Ferencak, M. Conlin, L. Dunham S. Krueger, T. Hayes, and A. Brandenburg were especially helpful in dealings with the IDNR. I am also grateful to a number of dedicated undergraduate students who worked tirelessly in the lab, especially Jeff Langefeld, Lou Depasqua, A.J. Repp, Hallie Kyreas, Mary Youpe, and Michelle Collins. J. Stein, R. Illyes and D. Phillipp aided with access and use of the Illinois FAS database. Most importantly I would like to thank my advisor David H. Wahl, for giving me the opportunity to pursue my academic goals. I would also like to thank Lisa Einfalt for her help in caring for fish in the laboratory. Funding for these projects was provided in part by Federal Aid in Sportfish Restoration Projects F-135-R and F-151-R administer by the Illinois Department of Natural Resources. The Illinois Natural History Survey and the Department of Natural Resources and Environmental Sciences, University of Illinois, also provided support.

TABLE OF CONTENTS

CHAPTER 1: INTRODUCTION	1
LITERATURE CITED	5
CHAPTER 2: EXPLORING RESPONSES OF EUTROPHIC LAKES TO SUPPLEMENTAL LARGEMOUTH BASS INTRODUCTIONS: A FIELD TEST OF TROPHIC CASCADE THEORY	10
ABSTRACT	10
INTRODUCTION	11
MATERIALS AND METHODS	15
RESULTS	21
DISCUSSION	25
LITERATURE CITED	32
CHAPTER 3: EFFECTS OF MUSKELLUNGE (ESOX MASQUINONGY) INTRODUCTION ON POPULATION CHARACTERISTICS OF RESIDENT FISH SPECIES IN ILLINOIS LAKES	52
ABSTRACT	52
INTRODUCTION	53
MATERIALS AND METHODS	56
RESULTS	61
DISCUSSION	63
LITERATURE CITED	69
CHAPTER 4: EFFECTS OF COARSE WOODY HABITAT COMPLEXITY AND SPECIES SPECIFIC BEHAVIORS ON PISCIVORE-PREY INTERACTIONS OF FOUR FRESHWATER FISH SPECIES	87
ABSTRACT	87
INTRODUCTION	88
MATERIALS AND METHODS	92
RESULTS	98
DISCUSSION	105
LITERATURE CITED	113
CHAPTER 5: CONCLUSION	127

CHAPTER 1: INTRODUCTION

Biologists have long been interested in the suite of morphological and behavioral adaptations that have arisen in the balance between predators and prey over evolutionary time. It has been recognized that these adaptations (eg. crypsis, mechanical defenses) provide indirect evidence for the importance of predation as a major ecological force structuring animal communities (Morin 1999). In addition to the indirect evidence, a large body of empirical research has shown strong effects of predation in a variety of ecosystems (reviewed by Sih et al. 1985). Predators influence prey communities principally by direct mortality of individuals, which can be a strong driver of prey population abundance and dynamics (see Brooks and Dodson 1965, Paine et al. 1974, Krebs et al. 1995, Gilg et al. 2006). In addition to direct mortality, predation can have strong indirect effects on communities through changes in prey behavior and trophic interactions (Carpenter and Kitchell 1985, Lima 1998). The effects of predation can have large consequences, such as determining community structure and influencing important ecosystem processes (Sih et al. 1985, Carpenter and Kitchell 1992).

Among the greatest effects of predation pressure on community structure are cascading trophic interactions or the “three trophic level effect” (Carpenter and Kitchell 1985, Hairston and Hairston 1993). In a trophic cascade, the abundance of a consumer species or multiple species has effects on the abundance or biomass of organisms across more than one trophic level (often due to predation) and can eventually influence primary production (Hodgson 2005). Examples of such cascading effects have been found in numerous ecosystems from freshwater lakes and streams to individual pitcher plants, the open ocean, and tropical forests (see Pace et al. 1999 and references therein). While the occurrences of such cascading effects of predation have been

shown over a broad range of ecosystems, it does not imply that such interactions are common within those ecosystems (Polis and Strong 1996, Persson 1999). Recent work on the prevalence of cascading interactions has shown that a number of food web and ecosystem properties can dampen the ability of predation pressure to cascade beyond the immediately impacted prey population (Polis et al. 2000).

Properties of food webs thought to dampen cascading interactions include food web complexity, the development of predator resistant prey populations and predation refuges (Polis and Strong 1996, Pace et al. 1999). The ability of predation to cause cascading changes in the biomass of lower trophic levels depends on the degree to which food webs are trophically stratified and the relative strength of these interactions (Paine 1980, Polis and Strong 1996, Polis et al. 2000). As prey species diversity within a trophic level increases, the effects of predators produce more diffuse (and therefore weaker) effects on population abundances (Duffy et al. 2007). In addition, more diverse prey assemblages increase the probability that a less vulnerable prey species will become dominant and fill the void left by the more vulnerable prey (Elser et al. 1991, Persson 1999). These compensatory responses can occur when species possess chemical and physical defenses (toxins, large body sizes, spines) or flexible antipredatory behaviors such as use of structural refuges (Sih 1987).

Structural refuges can have strong effects on predator prey dynamics and are generally considered a stabilizing force moderating the ability of predators to control prey populations (Krivan 1998, Arthur et al. 2005). While a considerable body of empirical research on predator-prey interactions has supported this generalization (see Savino and Stein 1982, Sanders et al. 2008, Grabowski et al. 2008), there are several recent exceptions (Andruskiw et al. 2008, Mattila et al. 2008, Horinouchi et al. 2009, Kon et al. 2009). Habitat structure typically affects predator

prey relationships by decreasing foraging efficiency of predators or altering prey distribution (Crowder and Cooper 1982, MacRae and Jackson 2001, Sass 2006b). The ability of habitat structure to function as a predation refuge is however dependent on the behavioral flexibility of the species in question, which can be limited by phylogenetic and physiological constraints (Sih et al. 1987, Sih 1992). Such behavioral constraints can cause differential responses to the presence of structural refuges and predation risk between species (see Ryer et al. 2004, Scharf et al. 2006, and Michel and Adams 2009) and may ultimately determine the strength of predation pressure on that species.

In this thesis, I present three experiments investigating the ecology of piscivore-prey interactions in Illinois lake ecosystems. Predation has particularly strong effects in aquatic communities (Tonn and Magnuson 1982, Hairston and Hairston 1993, Macrae and Jackson 2001) and is thought to be one of the primary factors shaping the structure of freshwater fish assemblages (Jackson et al. 2001, He and Kitchell 1990). The traits that make predation a strong characteristic of aquatic communities also contributes to the strong trophic cascades found in some lake ecosystems (Carpenter et al. 1985, Polis and Strong 1996). Illinois lakes however are significantly more trophically complex and nutrient rich than the northern lakes where strong trophic cascades have been documented. In addition, these lakes contain fish species with strong antipredatory behavior and the ability to escape piscivory through use of structural refuges or attainment of large body sizes (Hambright 1994, Stein et al. 1995). In chapters one and two, I test for community and fishery effects of stocking two popular piscivorous sportfish into various Illinois lakes. These experiments represent an opportunity to test the prevalence of piscivory related effects (including cascading effects) in lower latitude, eutrophic waters using replicated whole-lake manipulations. Full-scale assessments of the influence of piscivores on communities

are relatively scarce in these types of systems (McQueen 1989). Combined with laboratory investigations of piscivore and prey behavior (chapter three), these experiments will add to my understanding of the strength and effects of piscivory in Illinois lakes.

In chapter three, I present a laboratory experiment testing for species-specific behavioral responses of piscivores and prey to habitat complexity. In lake ecosystems, complex littoral habitats in the form of aquatic macrophytes and coarse woody debris serve as important predation refuges for small bodied freshwater fish (Savino and Stein 1982, Werner and Hall 1988, Hosn and Downing 1994). Recent research has found that lake shoreline development results in loss of this habitat (Christensen et al. 1996, Scheuerell and Schindler 2004) and changes in lake littoral habitat complexity have been shown to have important consequences for piscivore-prey interactions in several studies (Schindler et al. 2000, Sass et al. 2006a, Ahrenstorff et al. 2009). While the existing studies have largely corroborated the theoretical predictions of refuges' influence on piscivore-prey dynamics, the survivorship of individual prey species in response to habitat change can vary due to the differing tactics used by piscivore species (Eklov and Diehl 1994) or the specific anti-predator behaviors of prey (Christensen and Persson 1993, Flynn and Ritz 1999, Ryer et al. 2004, Scharf et al. 2006). In this study, I incorporate species with contrasting predatory tactics and antipredatory behaviors common to Illinois lakes, thus adding to my understanding of the influence of species-specific behavior in determining responses of piscivore-prey dynamics to habitat change. Results of such laboratory experiments can provide hypotheses for larger field studies and/or provide potential mechanistic explanations for field patterns (Huston 1999).

LITERATURE CITED

- Ahrenstorf, T.D., G. G. Sass, and M. R. Helmus. 2009. The influence of littoral zone coarse woody habitat on home range size, spatial distribution, and feeding ecology of largemouth bass (*Micropterus salmoides*). *Hydrobiologia* 623:223-233.
- Andruskiw, M., J. M. Fryxell, I. D. Thompson, and J. A. Baker. 2008. Habitat-mediated variation in predation risk by the American marten. *Ecology* 89(8):2273-2280.
- Arthur, A. D., R. P. Pech, and C. R. Dickman. 2005. Effects of predation and habitat structure on the population dynamics of house mice in large outdoor enclosures. *Oikos* 108(3):562-572.
- Brooks, J. L., and S. I. Dodson. 1965. Predation, body size, and composition of plankton. *Science* 150(3692):28-35.
- Carpenter, S. R., J. F. Kitchell, and J. R. Hodgson. 1985. Cascading trophic interactions and lake productivity. *BioScience* 35(10):634-639.
- Carpenter, S. R., and J. F. Kitchell. 1992. Trophic cascade and biomanipulation – interface of research and management - reply. *Limnology and Oceanography* 37(1):208-213.
- Crowder L.B., W.E. Cooper. 1982. Habitat structural complexity and the interaction between bluegills and their prey. *Ecology* 63:1802–1813.
- Christensen, B. and L. Persson. 1993. Species-specific antipredatory behaviors: effects on prey choice in different habitats. *Behavioral Ecology and Sociobiology* 32: 1-9.
- Christensen, D. L., Herwig, B. R., Schindler, D. E., Carpenter, S. R. 1996. Impacts of lakeshore residential development on coarse woody debris in north temperate lakes. *Ecological Applications* 6: 1143-1149.
- Duffy J. E., B.J. Carinale, K.E. France, P.B. McIntyre, E. Thebault, and M. Loreau 2007. The functional role of biodiversity in ecosystems: incorporating trophic complexity. *Ecology Letters* 10:522–538
- Eklöv, P. and S. Diehl. 1994. Piscivore efficiency and refuging prey: the importance of predator search mode. *Oecologia* 98: 3440-353.
- Elser, J. J., and C. R. Goldman. 1991. Zooplankton effects on phytoplankton in lakes of contrasting trophic status. *Limnology and Oceanography* 36(1):64-90.
- Flynn, A. J. and D. A. Ritz. 1999. Effect of habitat complexity and predatory style on the capture success of fish feeding on aggregated prey. *Journal of the Marine Biological Association of the United Kingdom*. 79: 487-494.

- Gilg O., B. Sittler, B. Sabard, A. Hurstel, R. Sane, P. Delattre, I. Hanski. 2006. Functional and numerical responses of four lemming predators in high arctic Greenland. *Oikos* 113:193–216
- Grabowski, J. H., A. R. Hughes, and D. L. Kimbro. 2008. Habitat complexity influences cascading effects of multiple predators. *Ecology* 89(12):3413-3422.
- Hairston Jr., N. G. and N.G. Hairston Sr. 1993. Cause effect relationships in energy flow, trophic structure, and interspecific interactions. *American Naturalist* 142: 379-411.
- Hambright, K. D. 1994. Morphological constraints in the piscivore-planktivore interaction implications for the trophic cascade hypothesis. *Limnology and Oceanography* 39(4):897-912.
- Hodgson, J. Y. 2005. A trophic cascade synthesis: review of top-down mechanisms regulating lake ecosystems. *Bios* 76:137-144.
- Horinouchi, M., N. Mizuno, Y. Jo, M. Fujita, M. Sano, and Y. Suzuki. 2009. Seagrass habitat complexity does not always decrease foraging efficiencies of piscivorous fishes. *Marine Ecology-Progress Series* 377:43-49.
- Hosn, W.A. and J. A. Downing. 1994. Influence of cover on the spatial-distribution of littoral fishes. *Canadian Journal of Fisheries and Aquatic Sciences* 51:1832-1838.
- Huston, M. A. 1999. Microcosm experiments have limited relevance for community and ecosystem ecology: Synthesis of comments. *Ecology* 80(3):1088-1089.
- Jackson, D.A., P. R. Perez-Neto, and J. D. Olden. 2001. What controls who is where in freshwater fish communities - the roles of biotic, abiotic, and spatial factors. *Canadian Journal of Fisheries and Aquatic Sciences* 58: 157-170.
- Kasprzak, P., R. C. Lathrop, and S. R. Carpenter. 1999. Influence of different sized *Daphnia* species on chlorophyll concentration and summer phytoplankton community structure in eutrophic Wisconsin lakes. *Journal of Plankton Research* 21(11):2161-2174.
- Klopfer, P. H. 1973. Natural regulation of animal populations - McLaren, Ia. *Social Biology* 20(1):121-122.
- Kon, K., H. Kurokura, and P. Tongnunui. 2009. Do mangrove root structures function to shelter benthic macrofauna from predators? *Journal of Experimental Marine Biology and Ecology* 370(1-2):1-8.
- Krebs, C. J., S. Boutin, R. Boonstra, A. R. E. Sinclair, J. N. M. Smith, M. R. T. Dale, K. Martin, and R. Turkington. 1995. Impact of food and predation on the snowshoe hare cycle. *Science* 269(5227):1112-1115.

- Křivan, V. 1998. Effects of optimal antipredator behavior of prey on predator-prey dynamics: the role of refuges. *Theoretical Population Biology* 53: 131-142.
- Leibold, M. A. 1989. Resource edibility and the effects of predators and productivity on the outcome of trophic interactions. *American Naturalist* 134(6):922-949.
- Lima, S. L. 1998. Nonlethal effects in the ecology of predator-prey interactions. *Bioscience* 48(1):25-34.
- MacRae P.D., and D.A. Jackson. 2001. The influence of smallmouth bass (*Micropterus dolomieu*) predation and habitat complexity on the structure of littoral zone fish assemblages. *Canadian Journal of Fisheries and Aquatic Sciences* 58: 342–351.
- Mattila, J., K. L. Heck Jr., E. Millstein, E. Miller, C. Gustafsson, S. Williams, and D. Byron. 2008. Increased habitat structure does not always provide increased refuge from predation. *Marine Ecology-Progress Series* 361:15-20.
- McQueen, D. J., M. R. S. Johannes, J. R. Post, T. J. Stewart, and D. R. S. Lean. 1989. Bottom-up and top-down impacts on fresh-water pelagic community structure. *Ecological Monographs* 59(3):289-309.
- Michel, M.J., and M.M. Adams. 2009. Differential effects of structural complexity on predator foraging behavior. *Behavioral Ecology* 20:313-317.
- Morin, P. 1999. Predation and communities: empirical patterns. Pages 105-135 *In* *Community Ecology*. Blackwell Publishing. Malden, MA.
- Pace, M. L., J. J. Cole, S. R. Carpenter, and J. F. Kitchell. 1999. Trophic cascades revealed in diverse ecosystems. *Trends in Ecology & Evolution* 14(12):483-488.
- Paine, R. T. 1980. Food webs: linkage, interaction strength and community infrastructure. *Journal of Animal Ecology* 49:667–685.
- Paine, R. T. 1974. Intertidal community structure - experimental studies on the relationship between a dominant competitor and its principal predator. *Oecologia* 15(2):93-120.
- Persson, L. 1999. Trophic cascades: abiding heterogeneity and the trophic level concept at the end of the road. *Oikos* 85(3):385-397.
- Polis, G. A., A. L. W. Sears, G. R. Huxel, D. R. Strong, and J. Maron. 2000. When is a trophic cascade a trophic cascade? *Trends in Ecology & Evolution* 15(11):473-475.
- Polis, G. A., and D. R. Strong. 1996. Food web complexity and community dynamics. *American Naturalist* 147(5):813.

- Ryer, C. H., A. W. Stoner, and R. H. Titgen. 2004. Behavioral mechanisms underlying the refuge value of benthic habitat structure for two flatfishes with differing anti-predator strategies. *Marine Ecology-Progress Series* 268:231-243.
- Sanders, D., H. Nickel, T. Grutzner, and C. Platner. 2008. Habitat structure mediates top down effects of spiders and ants on herbivores. *Basic and Applied Ecology* 9(2):152-160.
- Sass, G.G., J.F. Kitchell, S.R. Carpenter, T.R. Hrabik, A.E. Marburg, and M.G. Turner. 2006a. Fish community and food web responses to a whole-lake removal of coarse woody habitat. *Fisheries* 31(7):321-330.
- Sass, G.G., C. M. Gillie, J. T. Hinke, and J. F. Kitchell. 2006b. Whole lake influences of littoral structural complexity and prey body morphology on fish predator-prey interactions. *Ecology of Freshwater Fish* 15(3):301-308.
- Savino, J. F., and R. A. Stein. 1982. Predator-prey interaction between largemouth bass and bluegills as influenced by simulated, submersed vegetation. *Transactions of the American Fisheries Society*. 111:255-266.
- Scharf, F. S., J. A. Buckel, P. A. McGinn, F. Juanes. 2003. Vulnerability of marine forage fishes to piscivory: effects of prey behavior on susceptibility to attack and capture.
- Scheuerell, M. D. and D. E. Schindler. 2004. Changes in the spatial distribution of fishes in lakes along a residential development gradient. *Ecosystems* 7:98–106.
- Schindler, D. E., Geib, S. I., and M. R. Williams. 2000. Patterns of fish growth along a residential development gradient in north temperate lakes. *Ecosystems* 3: 229-237.
- Sih, A. 1992. Integrative approaches to the study of predation – general thoughts and a case-study on sunfish and salamander larvae. *Annales Zoologici Fennici* 29:183-198.
- Sih, A. 1987. Prey refuges and predator-prey stability. *Theoretical Population Biology* 31:1–12
- Sih, A., P. Crowley, M. McPeck, J. Petranka and K. Strohmeier. 1985. Predation competition and prey communities: A review of field experiments. *Annual Review of Ecology and Systematics* 16:269-311.
- Stein, R. A., D. R. DeVries, and J. M. Dettmers. 1995. Food-web regulation by a planktivore: Exploring the generality of the trophic cascade hypothesis. *Canadian Journal of Fisheries and Aquatic Sciences* 52(11):2518-2526.
- Strong, D. R. 1992. Are trophic cascades all wet? Differentiation and donor-control in speciose ecosystems. *Ecology* 73(3):747-754.
- Tonn W.M., and J.J. Magnuson 1982. Patterns in the species composition and richness of fish assemblages in northern Wisconsin lakes. *Ecology* 63:1149–1166

- Tonn, W. M., C. A. Paszkowski, and I. J. Holopainen. 1992. Piscivory and recruitment: mechanisms structuring prey populations in small lakes. *Ecology* 73(3):951-958.
- Vadas, R. L. 1990. The importance of omnivory and predator regulation of prey in freshwater fish assemblages of North America. *Environmental Biology of Fishes* 27(4):285-302.
- Vanni, M. J., and D. L. Findlay. 1990. Trophic cascades and phytoplankton community structure. *Ecology* 71(3):921-937.
- Werner, E. E., and D. J. Hall. 1988. Ontogenetic habitat shifts in bluegill - the foraging rate predation risk trade-off. *Ecology* 69(5):1352-1366.

CHAPTER 2: EXPLORING RESPONSES OF EUTROPHIC LAKES TO SUPPLEMENTAL LARGEMOUTH BASS INTRODUCTIONS: A FIELD TEST OF TROPHIC CASCADE THEORY

ABSTRACT

I conducted a replicated whole lake experiment designed to test for the effects of supplemental piscivore introduction on the food webs of lakes dominated by one of two common, deep-bodied, planktivore species, either bluegill *Lepomis macrochirus* or gizzard shad *Dorosoma cepedianum*. Thirteen Illinois lakes were monitored for a number of food web parameters for two years before (1998-1999) and 6 years after (2000-2005) initiation of annual largemouth bass introductions using a multiple before-after control-impact (MBACI) design. Lakes were classified into those with and without gizzard shad. A significant decrease in the relative abundance of juvenile planktivorous fish and an increase in total benthic macroinvertebrate density were observed in lakes without gizzard shad. However, no changes in adult planktivore populations, planktonic invertebrates, or water quality were detected in these same lakes. In contrast, lakes with gizzard shad exhibited no significant responses to piscivore manipulations. My results are consistent with the findings of previous experiments conducted over shorter time periods and smaller spatial scales, and suggest that food webs in lakes dominated by deep-bodied prey species respond weakly to piscivore enhancement measures. In addition, my findings support the hypothesis that gizzard shad may weaken cascading food web responses in lake ecosystems.

INTRODUCTION

Empirical research in freshwater environments has demonstrated that consumer control of resources is a common phenomenon in a number of habitats and over several major trophic linkages (Brooks and Dodson 1965; Benndorf et al. 1984; Hrbáček et al. 1986; Power 1990). Strong consumer control has the potential to alter the biomass of trophic levels across more than one link in a food chain (Hairston et al. 1960; Hrbáček et al. 1961). In some cases, this phenomenon (known as a trophic cascade; Carpenter et al. 1985) can reach from apex predators down to primary producers and ultimately affect system-wide primary productivity (Carpenter et al. 1985; Power 1990). Although the existence of community wide trophic cascades in some lakes is not disputed (Pace et al. 1999), trophic cascade models have been criticized by a number of researchers as an oversimplification of complex lake food web dynamics (Polis and Strong 1996, Persson 1999, Wetzel 2001). Trophic cascade and lake food web research has suggested that the effects of apex predators may weaken across trophic levels in some systems with consumer control being stronger at the top of the food web (McQueen et al. 1986; Leibold et al. 1989; De Melo et al. 1992; Elser and Goldman 1991; Hambright 1994; Shurin et al. 2002). Owing to the conflicting outcomes of many published studies, identification of the specific lake ecosystems where trophic cascades are found has been identified as an important ecological question (Polis and Strong 1996). Adding to the interest in trophic cascades has been the idea of using these processes as a tool in water quality management (reviewed by Reynolds 1994, Hanson et al. 1998; Drenner and Hambright 2002, and Sierp et al. 2009).

Manipulation of fish communities as a tool in water quality management (called biomanipulation; Shapiro et al. 1975) is based on the theory that decreasing the abundance of planktivorous fish in lake ecosystems will lead to increases in the size and abundance of

herbivorous zooplankton (because fish are size selective predators on the zooplankton; Brooks and Dodson 1965), and cause decreases in algal biomass (because larger zooplankton are more efficient grazers) through a trophic cascade (Shapiro et al. 1975, Carpenter and Kitchell 1988, Carpenter et al. 1995). Several authors have suggested using piscivorous fish introductions as a tool to decrease planktivore abundance (Shapiro et al. 1975; Carpenter et al. 1995) and the approach is often implicit in discussions of biomanipulation as a restoration technique (Drenner and Hambright 2002). Biomanipulation theory has converged with basic trophic cascade ideas and lead to debate concerning the structure and dynamics of aquatic food webs (De Melo et al. 1992 vs. Carpenter et al. 1992; Mazumder 1994; Polis et al. 2000; Jeppesen et al. 2003). The merging of these two parallel lines of inquiry has resulted in a large body of research focused on the specific conditions that may limit the strength of consumer control and cascading interactions in lakes (Benndorf et al. 2002; Jeppesen et al. 2003).

Productivity and planktivore assemblages have been found to affect the strength of consumer control and trophic cascades in lake ecosystems. For example, comparative studies in systems of differing nutrient status have found that more productive systems display a weakening of consumer control at the zooplankton-phytoplankton linkage due to the development of grazing resistant blue-green algae (Elser and Goldman 1991; Kazprzak et al. 1999 *but see* Carpenter et al. 1995) or eutrophication induced changes in the zooplankton community structure (Haberman et al. 2007). In addition to the effects of productivity, a number of studies have found that cascading effects are reduced when systems contain planktivorous fish species able to outgrow piscivore gape sizes (Hambright et al. 1991; Hambright 1994; Nowlin et al. 2006). A recent meta-analysis of piscivore manipulation studies indicated that top-down control of phytoplankton appeared to be related to body sizes of planktivores (Drenner and

Hambright 2002). A comparative study across 66 eutrophic European lakes containing piscivores and deep-bodied prey species found no evidence for consumer control of prey fish density by piscivores (Mehner 2010). Collectively, these studies suggest that lakes with increased nutrient loads and dominance of deep-bodied prey species should show weaker cascading interactions and therefore may be less responsive to biomanipulation measures.

The presence of species able to regulate community structure through unique adaptations is another potential mechanism affecting the strength of consumer control and cascading interactions in lakes because such species can drive community wide patterns regardless of their position in the food web (Pimm 1988; Hunter and Price 1992). In lower latitude lentic systems of North America, the gizzard shad (*Dorosoma cepedianum*) has been identified as such a “community regulator” (Stein et al. 1995). Several aspects of gizzard shad biology allow them to dominate the food webs of eutrophic lakes and reservoirs. For example, while gizzard shad have been shown to feed on and reduce zooplankton abundance when available (Dettmers and Stein 1996; Drenner et al. 1996; Schaus et al. 2002), their ability to meet their caloric needs by consuming detritus buffers them from the effects of low zooplankton abundance and allows them to maintain a high biomass in situations where other planktivore populations would become resource limited (Schaus et al. 2002; Vanni et al. 2005; Smoot and Findlay 2010). This reliance on detrital carbon may also decouple gizzard shad populations from zooplankton as it has been shown that populations of gizzard shad in some impoundments derive over 80% of their carbon from detrital sources (Higgins et al. 2006). Furthermore gizzard shad presence reduces piscivore abundance through several mechanisms. Gizzard shad can reduce piscivore abundance through increased competition for zooplankton during early life stages (Garvey and Stein 1998) and because detrital feeding transports nutrients to the water column increasing algal turbidity and

reducing piscivore foraging ability (Vanni et al. 2005). Gizzard shad also indirectly reduce piscivore recruitment by reducing young of year abundance of other planktivores through competition and simultaneously quickly outgrowing piscivore gape limitation (Garvey and Stein 1998). In this way gizzard shad reduce the availability of critical fish prey which reduces piscivore recruitment and combined with their own rapid growth and fecundity allows their populations to escape consumer control by piscivores (Stein 1995; Garvey and Stein 1998b). Collectively these aspects of gizzard shad biology may limit the strength of trophic cascades in systems where gizzard shad are present and limit the utility of biomanipulation measures in these systems (Stein 1995; Dettmers and Stein 1996).

In North America, a latitudinal gradient in productivity of lentic systems exists with relatively nutrient poor natural lakes in the north and nutrient rich impoundments in the south (Thornton 1990). Lower latitude lakes often contain fewer small-bodied planktivore species than northern lakes, as well as, increased abundance of less vulnerable, large bodied prey species capable of outgrowing the gape limitation of piscivores (O'Brien 1990). In addition, gizzard shad often dominate fish assemblages in lakes in the midwestern and southeastern United States (Johnson et al. 1988). Therefore, lower latitude lentic systems in North America contain at least two of the major ecosystem properties thought to limit cascading trophic interactions and biomanipulation effectiveness. These systems are also prime candidates for restoration due to issues with eutrophication brought on by agricultural land use and relatively large watershed – lake area ratios (Thornton 1990). Therefore, there exists a need for experiments to test for the relative sensitivity of lower latitude lentic ecosystems dominated by deep-bodied planktivorous fishes to piscivore manipulations.

Although some studies have attempted to investigate the cascading effects of piscivores in lower latitude systems, these studies have been based on correlational evidence, conducted at small spatial scales (ponds, mesocosms), over short time periods (< 2 years), or in unreplicated studies of single lakes (e.g. Drenner et al. 2002). These issues of scale and duration are problematic and several researchers have argued that true tests of food web theory can only be accomplished via whole-lake manipulations covering significant time periods (Carpenter et al. 1995, Ramcharan et al. 1995; Schindler et al. 1998). In this study, I present such an experiment carried out through the use of long-term (6 year) introductions of largemouth bass *Micropterus salmoides*. My objectives were to test for the potential of piscivore manipulations to affect the food webs of eutrophic lakes common in the lower Midwestern United States and to compare the responses of lakes dominated by two common, deep-bodied, prey species, bluegill *Lepomis machrochirus* and gizzard shad *Dorosoma cepedianum*. I hypothesized that due to the differences in food web characteristics of Illinois lakes relative to systems where strong trophic cascades have been found, piscivore enhancements in Illinois lakes would not induce a classic trophic cascade from piscivores to phytoplankton as predicted by the trophic cascade hypothesis. Furthermore, I hypothesized that if any changes in food web characteristics were found due to piscivore enhancement, these effects would be strongest in systems lacking gizzard shad due to the unique effects of this species on food web dynamics.

MATERIALS AND METHODS

Study Sites and experimental design

To test for the effects of supplemental largemouth bass introductions, I sampled 13 Illinois lakes over an 8-year period from 1998 – 2005 (Figure 1.1). Lakes were grouped into

those with ($n = 7$) and without ($n = 6$) gizzard shad and a subset of these were then selected to serve as reference systems (Table 1.1). Lakes were monitored for a number of parameters including relative abundance (number collected per hour of electrofishing) of piscivore and prey fish, zooplankton and invertebrate predator concentrations, benthic macroinvertebrate densities, total phosphorous concentration, secchi disk depth and water column chlorophyll a concentrations for two years before (1998-1999) and 6 years after (2000-2005) initiation of annual largemouth bass introductions. Data were collected to test a number of *a priori* predictions of trophic cascade and biomanipulation theory and included all major trophic levels. With the exception of gizzard shad and smallmouth bass (Table 1.2), the fish communities of these impoundments were similar with largemouth bass and bluegill being the most abundant species. Other potential piscivorous, zooplanktivorous, or benthivorous fishes were present at low densities (less than 6% of total electrofishing catch; Table 1.2). Lakes were less than 12 m deep and ranged in surface area from 16-218 ha. All study lakes were eutrophic to hypereutrophic, with average summer total phosphorous concentrations ranging from 45-463 ug/L (Table 1.1).

Largemouth bass introductions and evaluation

Beginning in the late summer (August) of 1999 and each year thereafter, treatment lakes received introductions of juvenile largemouth bass at a target size of 100 mm (mean \pm SE = 102 ± 1 mm TL) and target density of 60 fish per hectare (59 ± 2 fish/ha). Fish were given pelvic fin clips (left pelvic, right pelvic, or both pelvic fins, alternating by year) to allow for future identification and to assist in aging. Each spring (April-May) following stocking (2000-2005), the relative contribution of stocked fish to each year class (age-1 and age-2 spring) was

determined in each lake via three-phase AC boat mounted electrofishing conducted on 2-3 dates per lake. Three fixed one-half hour transects were sampled in each lake on each date. All largemouth bass were netted and measured for total length. Scales were collected from all fin clipped individuals to assist in assigning age classes to stocked fish. To assign ages to wild fish, largemouth bass length frequencies were analyzed using RMIX an “R”-based version of the “MIX” software (MacDonald and Pitcher 1979; MacDonald and Green 1988). Data from each spring sample were analyzed separately with initial inputs of cohort mean lengths estimated from length frequency plots. Distributions were fit by allowing the standard deviation of the oldest cohort to vary to accommodate the larger variation in this group (Du 2002). This method of length frequency analysis has been found to effectively assign ages to early largemouth bass cohorts (ages 0-2) in Illinois lakes relative to ages based on scale samples (Riedel and Bailey 1999). From this data, I calculated the proportional contribution of stocked fish to each age-1 and age-2 cohort for each lake and year (2000-2005). I chose age-1 and age-2 spring proportions as my measure of stocked fish contribution as previous studies have found that largemouth bass year class strength is established by this point (Kramer and Smith 1962; Parkos and Wahl 2011) and to avoid issues with fin regeneration in older fish which would make estimates unreliable.

Data collection

I monitored fish community responses through standardized sampling in all study lakes each fall (September – October) from 1998-2005. Adult fish populations were assessed using three-phase AC boat mounted electrofishing, whereas juvenile fish were sampled using a 9.2 m bag seine pulled along the shoreline at six fixed transects. Electrofishing samples consisted of sampling three one-half hour fixed shoreline transects in each lake on each of 2-3 dates to ensure

standardized sampling effort among lakes and within lakes over time. All fish collected were identified to species, counted, and a subsample of each species (up to 50 individuals) was measured for total length. I then calculated electrofishing catch per unit effort (CPUE; number per hour) of adult and density (number per square meter in seine samples) of juvenile planktivorous and benthivorous fishes for each lake and year.

Zooplankton and water quality samples were collected once per month from June-August of each year. Zooplankton was sampled at four fixed offshore and four fixed inshore sites while water quality variables including secchi disk depth, chlorophyll *a*, and total phosphorous were measured from a single fixed site at the deepest point in each lake. This zooplankton and water quality sampling regime was similar in both spatial coverage and sampling frequency to many previous studies examining the effects of fish manipulations on zooplankton populations in lakes (Shapiro and Wright 1984; Mittelbach et al. 1995; Drenner et al. 2000; Lathrop et al. 2002; Findlay et al. 2005; Potthoff et al. 2008). Zooplankton samples were collected using vertical tows of a 0.5-m-diameter, 64- μ m-mesh zooplankton net taken from the thermocline (or lake bottom if not stratified) to the surface, preserved in a 4% Lugol's solution and taken back to the laboratory for processing. Samples were processed by adjusting to a constant volume (100 ml) and subsampled by 1 ml (0.01) aliquot. Whole subsamples were counted until reaching 200 animals from the major taxonomic groups or until 10% of the total sample was counted (Welker et al. 1994). A subset of each zooplankton taxa ($n = 30$) was measured for total length (not including spines or appendages) with the aid of a digitizing pad. Water samples for chlorophyll-*a* and total phosphorous analysis were collected using an integrated water sampler lowered to twice the Secchi depth (to sample the entire photic zone). Chlorophyll-*a* was measured in a flourometer with an acetone extraction technique (Welshmeyer 1994). Total phosphorous was

analyzed according to Wetzel and Likens (1991) and was quantified using a spectrophotometer. Each water quality parameter was summarized for analysis by calculating a mean value for each lake and year for the summer period (June-August). I summarized zooplankton data by pooling samples from all sites within each lake to calculate lake-wide average concentrations of invertebrate predators (Chaoboridae), as well as, *Daphnia* species and average cladoceran length over the summer period (June-August) each year. This approach of summarizing data as monthly values for each lake and comparing seasonal averages is consistent with several previous biomanipulation studies (Drenner et al. 2002; Findlay et a. 2005; Potthoff et al. 2008).

Benthic invertebrates were sampled in June and August in each lake and year at six fixed littoral sites with a modified stovepipe sampler (Merritt and Cummins 1996; 20 cm diameter). Samples were passed through a 250- μm -sieve bucket and preserved in a 70% ethanol and rose bengal solution. Samples were returned to the laboratory where all organisms were identified to family and enumerated. I calculated average total macroinvertebrate density, as well as, the density of the two most common invertebrate families (Chironomidae and Ceratopogonidae) for each lake and year.

Statistical analyses

Comparisons before and after largemouth bass introductions were made between treatment and reference lakes using a replicated before-after control-impact (MBACI) design suited to a repeated measures analysis of variance (Underwood 1994, Kough and Mapstone 1995). The MBACI design was chosen because it is among the most scientifically defensible for detecting disturbances in natural systems (Downes et al. 2002). Separate analyses were performed for lakes that contained gizzard shad and those that did not. These analyses were

conducted by fitting a linear mixed model with main factors of treatment (Trt; with introductions or without), and before-after (Period), with lakes (L) nested in Trt and years (Y) nested in Period. The full ANOVA model contained the terms Trt, Period, Trt x Period, L(Trt), L(Trt) x Period, Y(Period), Y(Period) x Trt, and L(Trt) x Y(Period). The three terms containing lake (L) were considered random (because lakes were a random effect in the model) and the remaining terms were considered fixed. The Y(BA) term was considered the repeated factor and L(Trt) was the subject. The Trt*Period interaction measures any change associated with the onset of the largemouth bass introductions (Kough and Mapstone 1995). All errors were tested for normality (Shapiro-Wilk test) and were natural log transformed where necessary to meet the assumptions of ANOVA. Serial correlation among years (nonzero covariance) due to repeated measurements was accounted for by fitting various covariance structures to the data (SAS[®]; PROC MIXED) and choosing the structure that generated the best model based on the corrected Akaike's information criterion (AICC; Littell et al. 2000). All analyses were conducted using the SAS[®] system (Statistical Analysis System Version 9.0; SAS Institute, Cary, North Carolina). The MBACI model tests two null hypotheses specific to either changes in mean values or changes in temporal trends coincident with piscivore introductions (Kough and Mapstone 1995). The first null hypothesis was that there was no change in the average value of the parameter of interest in lakes receiving piscivore introductions that was not also present in control systems given the background patterns of variation among the systems. This hypothesis was tested with the Trt*Period interaction from the statistical model and indicates a longer term or cumulative effect of piscivore introduction. The second null hypothesis was that there were no changes in the temporal trends in the parameter of interest between lakes receiving piscivore introductions and control systems relative to the background patterns of variation among the systems. This

hypothesis was tested with the Y(Period) x Trt term from the statistical model and is sensitive to more immediate changes in the time profiles (Kough and Mapstone 1995). In cases of significant Y(Period) x Trt interactions we used linear contrasts between control and treatment systems to aid in interpreting the temporal differences between groups of lakes. Significance was declared at an alpha equal to or less than 0.05.

RESULTS

Largemouth bass introductions

In lakes with and without gizzard shad, largemouth bass stocking did not greatly contribute to the age 1 and 2 year classes. In lakes that did not contain gizzard shad, the average annual proportional contribution of introduced largemouth bass ranged from 7-34% of age-1 fish and 4-17% of age-2 fish (Figure 2.2A). Across years, stocked fish made up an average of 19(\pm 5)% of age-1, and 10(\pm 4)% of age-2 largemouth bass collected in spring surveys from these lakes.

In lakes containing gizzard shad, the average annual proportional contribution of introduced largemouth bass ranged from 13-40% of age-1 fish and 8-33% of age-2 fish (Figure 2.2B). Across years, stocked fish comprised an average of 31(\pm 5)% of age-1 and 23(\pm 5)% of age-2 largemouth bass collected in spring surveys from these lakes.

Fish populations

There was a significant decrease in the average fall density of juvenile littoral prey fish in lakes receiving piscivore introductions for lakes that did not contain gizzard shad (R-ANOVA, Trt x Period; $F_{1,4} = 8.5$; $P = 0.04$; Figure 2.3A). Examination of the time series (Figure 2.3B)

revealed that the decline in littoral fish density in fall seine samples was not due to any abrupt change in temporal patterns (Y(Period) x Trt; $F_{6,24} = 1.20$; $P = 0.35$). In contrast to juvenile prey, there was no significant change in the relative abundance of adult prey fish collected via fall electrofishing in response to largemouth bass introductions (Trt x Period; $F_{1,4} = 0.01$; $P = 0.93$; Figure 2.3C). This lack of change was also evident in the time series (Y(Period) x Trt; $F_{6,24} = 0.56$; $P = 0.53$; Figure 2.3D).

There was no significant change in average juvenile littoral prey fish density in lakes containing gizzard shad (Trt x Period; $F_{1,5} = 0.11$; $P = 0.75$; Figure 2.4A). The lack of change in lakes containing shad was also evident in the time series (Y(Period) x Trt; $F_{6,30} = 1.17$; $P = 0.35$). Figure 2.4B). Similarly, there was no effect of largemouth bass introduction on the average relative abundance of adult prey fish collected via fall electrofishing in lakes containing gizzard shad ($F_{1,4} = 1.07$; $P = 0.36$; Figure 2.4C) and the lack of a change was also apparent in the time series (Y(Period) x Trt; $F_{6,30} = 0.72$; $P = 0.64$; Figure 2.4D).

Zooplankton

In lakes where gizzard shad were absent, there was no significant change in the average concentration of *Daphnia* over the summer period in response to largemouth bass introduction (Trt x Period; $F_{1,4} = 2.12$; $P = 0.22$; Figure 2.5A). Examination of the time series indicated an abrupt increase in *Daphnia* concentration following initial introduction that was not present in the control lakes (Y(Period) x Trt; $F_{6,24} = 2.53$ $P = 0.05$). *Daphnia* concentration in treatment systems increased in the second year (2001) after initiation of largemouth bass introductions relative to controls (linear contrast; $F_{1,24} = 7.8$; $P = 0.01$); however, densities returned to their previous levels in the later years of the study (linear contrasts for all other years before and after

introduction; $P > 0.05$; Figure 2.5B). Similarly, there was no significant change in the average size of cladoceran zooplankton in response to largemouth bass introduction in lakes which did not contain gizzard shad (Trt x Period; $F_{1,4} = 3.95$; $P = 0.12$; Figure 2.5C). The time series indicated no change in this metric in treatment lakes over the duration of the study in these gizzard shad free lakes (Y(Period) x Trt; $F_{6,24} = 0.52$; 0.78 ; Figure 2.5D). There was also no significant change in the average (Trt x Period; $F_{1,4} = 0.64$; $P = 0.47$;) or temporal trend (Y(Period) x Trt; $F_{6,24} = 1.67$; $P = 0.17$) in the concentration of invertebrate predators of the family Chaoboridae after initiation of largemouth bass introductions (Figure 2.5E-F).

In gizzard shad lakes, I found no significant change in average *Daphnia* concentration after initiation of largemouth bass introduction (Trt x Period; $F_{1,5} = 0.16$; $P = 0.71$; Figure 2.6A). There was a significant change in the temporal trends in *Daphnia* concentration after initiation of piscivore introduction (Y(Period) x Trt, $F_{6,30} = 2.94$; $P = 0.02$), however this change was unlikely to be a result of piscivore introduction as it was due to changes in both control and treatment lakes (Figure 2.6B). *Daphnia* concentration was greater in treatment lakes in 2001 (linear contrast; $F_{6,30} = 7.29$; $P = 0.02$) and was greater in control lakes in 2005 (linear contrast; $F_{6,30} = 4.19$; $P = 0.05$). There was no significant change in average cladoceran length in response to piscivore introduction (Trt x Period; $F_{1,5} = 0.75$; $P = 0.43$; Figure 2.6C). Similarly, there were no significant changes in temporal patterns in cladoceran length (Y(Period) x Trt; $F_{6,30} = 0.73$; $P = 0.63$; Figure 2.6D). Both the average (Trt x Period; $F_{1,5} = 0.61$; $P = 0.47$) and temporal trends (Y(Period) x Trt; $F_{6,30} = 1.28$; $P = 0.30$) in concentration of invertebrate predators of the family Chaoboridae also were unchanged after the initiation of largemouth bass introductions (Figure 2.6E-F).

Benthic invertebrates

A significant increase in average total macroinvertebrate density was observed in response to largemouth bass introduction in lakes without gizzard shad (Trt x Period; $F_{1,4} = 11.47$; $P = 0.03$; Figure 2.7A). The time series indicated an increase in total macroinvertebrate density in treatment lakes in two of the five years after beginning piscivore introductions (Y(Period) x Trt; $F_{6,24} = 2.68$; $P = 0.03$). Total macroinvertebrate density was significantly greater in lakes receiving largemouth bass introductions than control lakes in 2000 (linear contrast; $F_{1,24} = 4.26$; $P = 0.05$) and 2005 (linear contrast; $F_{1,24} = 5.18$; $P = 0.03$). Similar to the results for *Daphnia* concentration, total macroinvertebrate densities appeared to return to pre-manipulation levels in the later years of the study (linear contrasts all other years before and after piscivore introduction; all $P > 0.05$; Figure 2.7B). Individual macroinvertebrate groups were variable and there were no significant changes for average densities (Trt x Period; $F_{1,4} = 5.35$; $P = 0.08$) or temporal trends (Y(Period) x Trt; $F_{6,24} = 0.81$; $P = 0.57$) for choronomidae (Figure 2.7C-D) or ceratopogonidae (Trt x Period; $F_{1,4} = 2.89$; $P = 0.16$; Y(Period) x Trt; $F_{6,24} = 1.54$; $P = 0.21$; Figure 2.7E-F).

Lakes containing gizzard shad exhibited no change in average total benthic invertebrate density after initiation of supplemental largemouth bass introduction (Trt x Period; $F_{1,5} = 3.33$; $P = 0.13$; Figure 2.8A) and this lack of response was reflected in the time series (Y(Period) x Trt; $F_{6,30} = 1.83$; $P = 0.13$; Figure 2.8B). Individual groups showed a significant effect on average density (Trt x Period; $F_{1,5} = 8.08$; $P = 0.04$) and temporal patterns (Y(Period) x Trt; $F_{6,30} = 2.81$; $P = 0.03$) in Chironomidae (Figure 2.8C-D); however, these effects were due to an increase in the control lakes that did not occur in the treatment lakes (Figure 2.8D). Chironomid density was significantly greater in treatment lakes (linear contrast; $F_{1,30} = 11.13$, $P < 0.01$) one year (1999)

prior to initiation of largemouth bass introductions whereas chironomid density increased in the following year (2000) in control systems being significantly higher than in treatment lakes (linear contrast; $F_{1,30} = 9.04$; $P = <0.01$). Chironomid densities were not significantly different between treatment and control lakes in any other year of the study (linear contrasts; all $P > 0.05$). As with total invertebrate density, there was no significant change in the average density (Trt x Period; $F = 0.36$; $P = 0.56$) or temporal trends (Y(Period) x Trt; $F_{6,30} = 1.10$; $P = 0.39$) of Ceratopogonidae in response to largemouth bass introduction in lakes containing gizzard shad (Figures 2.8E-F).

Nutrients and water quality

In lakes without gizzard shad there were no changes in summer means (Table 2.3) or annual trends for chlorophyll-a (Y(Period) x Trt; $F_{6,24} = 1.04$; $P = 0.42$), Secchi disk transparency (Y(Period) x Trt; $F_{6,24} = 0.22$; $P = 0.97$), or total phosphorous concentration (Y(Period) x Trt; $F_{6,24} = 1.36$; $P = 0.28$) in response to largemouth bass introduction. No change was mirrored in lakes containing gizzard shad where there was also no significant difference in summer means (Table 2.3) or annual trends for chlorophyll-a (Y(Period) x Trt; $F_{6,30} = 0.98$; $P = 0.46$), Secchi disk transparency (Y(Period) x Trt; $F_{6,30} = 1.79$; $P = 0.14$), and total phosphorous concentration (Y(Period) x Trt; $F_{6,30} = 0.77$; $P = 0.60$), in response to largemouth bass introduction.

DISCUSSION

Biomanipulation studies focused on lower latitude lakes in the Midwestern and Southern United States have been relatively few and my study represents a rare example of incorporating lake-scale replication. In addition, my study represents a unique account of a piscivore

enhancement experiment as the majority of previous biomanipulation studies involving piscivore enhancements have been confounded by concurrent planktivorous fish removal efforts or other simultaneous management actions (29 of 33 published studies; reviewed by Drenner and Hambright 2002). Although these features of my study create a novel approach, they likewise create difficulties in relating my results to other studies. A specific problem is placing my rate of piscivore introduction and consequent level of piscivore enhancement in the context of previous efforts as few studies have examined the community wide effects of piscivore enhancements in unconfounded studies (see Drenner and Hambright 2002, Lathrop et al. 2002). In addition, there is no current consensus on the level of piscivore enhancement required to trigger cascading trophic effects outside of a general statement that efforts should be “strong” (McQueen et al. 1990; Carpenter and Kitchell 1992; Seda 2000) and previous efforts toward determining empirical relationships have been unsuccessful (De Melo et al. 1992). In one of the only North American piscivore enhancement studies conducted to date (and one of the few non-confounded biomanipulation by piscivore enhancement studies), 270,000 walleye (~50 mm) and 170,000 northern pike fingerlings (~250 mm) were introduced into Lake Mendota, Wisconsin (3985 ha) over a period of 12 years at densities ranging from 120-162 fish/ha during the first 3 years and at much lower densities thereafter. Although the stocking rate was greater than in my study during the initial years, the average annual density of fish introduced over the duration of the study was very similar to my study averaging roughly 65 fish/ha (Lathrop et al. 2002). Published largemouth bass population density estimates in central Illinois impoundments average around 100 fish per hectare (Diana and Wahl 2009) and therefore my stocking density represents a number approximating 60% of the density of the standing population of a typical lake in this region. Despite this rate of stocking my estimates of contributions of introduced largemouth bass

to year class strength were not extremely large which could have influenced the degree to which the food webs of recipient lakes were affected. I believe my study is an appropriate first step in evaluating whole-system responses of lower latitude lakes to piscivore enhancements, but acknowledge that higher stocking rates or increased survival of introduced piscivores may show stronger effects and encourage consideration of such effects when making future decisions for research and management. It should be noted however that my rate of piscivore introduction was on par with one of the most intensive North American efforts to date and that densities in excess of these likely may be beyond the capacities of most lake managers. Furthermore, I assumed in my evaluation of piscivore enhancement that the proportional contribution of stocked fish was additive. While this assumption appears to be consistent with numerous previous studies of piscivore introductions (Brabrand and Faafeng 1993; Benndorf 1995; Berg et al. 1997; Lathrop et al. 2002) it should be noted that any compensatory increases in mortality rates of native fish would weaken the effects of such introductions and future studies should account for such possibilities.

In lakes without gizzard shad, I found that increased piscivory significantly reduced small bodied and juvenile fish density, but had little effect on adult populations of prey fish that were comprised mostly of bluegill. In experimental ponds, the presence of largemouth bass increased the size distribution of bluegill but caused only a slight (15%) decrease in bluegill biomass compared to piscivore free ponds (Hambright et al. 1986). Response of bluegill to largemouth bass predation is consistent with other studies focused on the effects of gape-limited piscivores foraging on deep-bodied prey species (Tonn et al. 1992; Hambright et al. 1994; Findlay et al. 2000). Combined, these results suggest that adult bluegill populations are resistant to consumer control by largemouth bass. Bluegills are known to outgrow the gape limitation of

largemouth bass (Lawrence 1957; Werner et al. 1988) and are commonly abundant in systems containing largemouth bass throughout the midwestern and southern United States. Due to their ability to outgrow the gape limitation of piscivores and associated behavioral and physical antipredator adaptations (Howick and O'Brien 1983), bluegills may limit the effectiveness of biomanipulation via piscivore enhancement. I cannot however rule out the possibility that higher densities or increased survival of introduced piscivores may have greater effects on bluegill populations.

The lack of fish community responses to piscivore enhancement in lakes dominated by gizzard shad is not surprising given the known effects of this species on reservoir food webs. Stein et al. (1995) argued that gizzard shad populations are not subject to consumer control by piscivores due to their high fecundity (Parrish and Vondracek 1989) and their ability to quickly outgrow the gape of piscivores (Hambright et al. 1991). These hypotheses have been supported by several studies using bioenergetics-based assessments of gizzard shad consumption by resident and introduced piscivore populations (Carline et al. 1984; Johnson et al. 1988; Dettmers et al. 1998). Additionally, a lack of cascading effects in gizzard shad dominated systems may be due to a lack of planktivory by juvenile and adult gizzard shad. While larval gizzard shad are obligate planktivores, juveniles and adults feed on zooplankton, detritus and phytoplankton and may facultatively switch between these resources depending on their relative abundance and nutritional value (Vanni and Headworth 2004; Higgins et al. 2006). Therefore one may not expect zooplankton to respond to changes in gizzard shad density if the bulk of the juvenile and adult populations are not feeding on zooplankton as has been found in some systems (Higgins et al. 2006). Future studies examining effects of piscivore enhancements on gizzard shad

dominated systems should include a detailed analysis of gizzard shad diets which may aid in determining mechanism for the presence or absence of effects on the pelagic food web.

Increases in littoral benthic invertebrate density and a lack of change in zooplankton communities are consistent with previous studies on foraging behavior of bluegill (the dominant planktivore/benthivore) in lower latitude lentic ecosystems. In contrast to northern natural lakes where adult bluegill inhabit pelagic areas and forage extensively on zooplankton (Werner et al. 1983; Werner and Hall 1988), several studies of bluegill diet and feeding behavior in reservoirs and natural lakes in the lower Midwest and southeastern United States have found that bluegills rely primarily on littoral macroinvertebrates independent of size or population density (Schramm and Jirka 1989; Dewey et al. 1997; Olson et al. 2003). These patterns in bluegill foraging may explain my observed effects on littoral benthic invertebrates and lack of effects on zooplankton. While our study cannot directly address why changes in bluegill density more strongly affected macroinvertebrates as compared to zooplankton, bluegills are known to facultatively shift their foraging from zooplankton to macroinvertebrates contingent upon spatial variation in predation risk as well as the relative profitability of prey items (Werner et al. 1981). Differences between lower latitude waterbodies and northern lakes such as changes in water clarity, littoral habitat and/or the relative profitability of zooplankton vs macroinvertebrates with increasing nutrient levels may alter these key determinants of foraging decisions and should be investigated further. Bluegill are known to structure invertebrate communities through predation (Hambricht et al. 1986) and several previous studies from North America and Europe have documented taxonomic increases in benthic invertebrate communities following reductions in the density of bluegill (Pierce and Hinrichs 1997) and other benthivorous fish (Svensson et al. 1999; Leppa et al 2003; Potthoff et al. 2008). My results suggest that littoral benthic invertebrate populations in several

Illinois lakes are subject to control by mid-level fish consumers and the strength of these effects may be influenced by piscivore abundance.

As recently demonstrated by Vadeboncoeur and Vander Zanden (2002) the focus of lake food web research (including the trophic cascade hypothesis) has been largely skewed toward a focus on pelagic processes which may limit the understanding of effects of ecosystem scale perturbations such as enhanced piscivory. While top down effects of fish on macroinvertebrates and responses in benthic algal biomass in streams has received some attention (Steinman 1996; Herbst et al. 2009) the links between these organisms in lakes is not well studied (Lowe 1996). Links between littoral benthic invertebrate populations, secondary fish consumers and piscivores may have important implications for understanding food web dynamics in Illinois impoundments. For example, my results which suggest that zoobenthos are under consumer control by secondary fish consumers in these lakes combined with the knowledge that these invertebrates can exhibit consumer control of benthic algae (Steinman 1996) suggests that changes in piscivore abundance in these systems may have the potential to influence benthic primary productivity. It is however unclear to what degree altered benthic algal biomass and production may influence lake-scale properties such as total primary production. For example, both theory and empirical evidence suggests that the relative contribution of benthic primary production to total primary production is reduced in more eutrophic lakes such as those found in Illinois (Vadeboncoeur et al. 2001; Wetzel 2001). In contrast, the contribution of benthic primary production is greater in smaller and shallower lake ecosystems (Lodge et al. 1998) and given that the majority of lakes (including those in the lower latitudes of North America) are relatively small and shallow (Wetzel 2001) we might predict a relatively important role of benthic primary producers in these systems. My results reinforce that the current lack of

understanding of links between piscivores, fish prey, benthic invertebrates and benthic primary production combined with the growing evidence of the importance of benthic energy pathways in lake food webs suggests these areas as an important topic of future study and should be considered in future studies of lake food web dynamics.

In lakes without gizzard shad, I found abrupt increases in benthic macroinvertebrates and *Daphnia* concentrations during early years after piscivore manipulation with densities returning to pre-manipulation levels in later years. Such initial responses have been attributed to compensatory mechanisms and have led others to argue for longer periods of observation such as ours in attempts to elucidate the role of piscivores in determining aquatic food web structure (Benndorf 1990; De Melo 1992; Ramcharan et al. 1995). Numerous studies have supported the role of compensatory mechanisms and time scales in determining outcomes of biomanipulation experiments (Benndorf et al. 1988; Drenner et al. 2002). For example, in one of the classic large-scale biomanipulation experiments conducted in North America, a large decline in planktivorous fish (cisco; *Coregonus artedii*) led to short-term increases in large daphnids and declines in algal biomass (Vanni et al. 1990). These effects on algae dissipated over subsequent years due to compensatory changes in phytoplankton community structure and later recruitment of planktivores (yellow perch; *Perca flavescens*) despite the development of large piscivore populations (Rudstam et al. 1993; Lathrop et al. 2002). Similar compensatory effects were found during a long-term biomanipulation experiment in the Bautzen Reservoir, Germany (Benndorf et al. 1988), as well as, in comparative studies in systems with and without piscivores (Power 1990; Ramcharan et al. 1995). Compensatory mechanisms may be an important factor determining the long-term success of biomanipulation measures and the influence of piscivores in structuring aquatic food webs.

While the lack of response of Illinois lakes to piscivore enhancement is not surprising based on many previous studies, it is now clear that longer term studies at greater spatial scales revealed no major differences from previous studies. Additionally, my results reinforce recent work that has demonstrated the importance of benthic and littoral energy pathways in lake food webs (Vander Zanden and Vadeboncoeur 2002; Vadeboncoeur et al. 2002). Limitations of my study design should be considered in the interpretations of my findings, as ecosystem-scale experiments often suffer from a combination of high between system and inter-annual variability in dependent variables (Carpenter 1989). These realities may have hampered my ability to detect changes in some key parameters. For example, several of my water quality variables (chlorophyll a, total phosphorous concentration) were highly variable between lakes resulting in large standard errors which approximated the magnitudes of mean values. My findings suggest that future such experiments will require larger numbers of replicates and/or more rigorous spatial and temporal sampling regimes to increase the power to detect changes in water quality parameters. Future studies should focus on identifying the importance of alternative mechanisms which may prevent piscivore effects from cascading down to the phytoplankton such as eutrophication- induced changes in phytoplankton or zooplankton community structure, compensatory responses such as increases in invertebrate predation or low survival of introduced predators.

LITERATURE CITED

Baca, R. M. and R. Drenner. 1995. Do the effects of piscivorous largemouth bass cascade to the plankton? *Hydrobiologia* 316:131-151.

- Benndorf, J., H. Schultz, A. Benndorf, R. Unger, E. Penz, H. Kneschke, K. Kossatz, R. Dumke, U. Hornig, R. Kruspe and S. Reichel. 1988. Food web manipulation by enhancement of piscivorous fish stocks: long-term effects in the hypertrophic Bautzen Reservoir. *Limnologica* (Berlin) 19:97–110.
- Benndorf, J., W. Böing, J. Koop, and I. Neubauer. 2002. Top-down control of phytoplankton: the role of time scale, lake depth and trophic state. *Freshwater Biology* 47(12):2282-2295.
- Benndorf, J., H. Schultz, A. Benndorf, R. Unger, E. Penz, H. Kneschke, K. Kossatz, R. Dumke, and U. Hornig. 1988. Food-web manipulation by enhancement of piscivorous fish stocks: long-term effects in the hypertrophic Bautzen Reservoir. *Limnologica* 19:97-110.
- Benndorf, J., H. Kneschke, K. Kossatz, and E. Penz. 1984. Manipulation of the pelagic food web by stocking with predacious fishes. *Internationale Revue Der Gesamten Hydrobiologie* 69(3):407-428.
- Benndorf, J. 1990. Conditions for effective biomanipulation - conclusions derived from whole-lake experiments in Europe. *Hydrobiologia* 200:187-203.
- Benndorf, J. 1995. Possibilities and limits for controlling eutrophication by biomanipulation. *Int. Rev. Ges. Hydrobiol.* 85: 519–534.
- Berg, S., E. Jeppesen, and M. Søndergaard. 1997. Pike (*Esox lucius L.*) stocking as a biomanipulation tool. 1. Effects on the fish population in Lake Lyng, Denmark. *Hydrobiologia* 342/343:311–318.
- Brabrand, A. and B. Faafeng. 1993. Habitat shift in roach (*Rutilus rutilus*) induced by pikeperch (*Stizostedion lucioperca*) introduction: predation risk versus pelagic behavior. *Oecologia* 95:38–46.
- Brooks, J. L., and S. I. Dodson. 1965. Predation, body size, and composition of plankton. *Science* 150(3692):28-35.
- Carline, R. F., B. L. Johnson, and T. J. Hall. 1984. Estimation and Interpretation of proportional stock density for fish populations in Ohio impoundments. *North American Journal of Fisheries Management* 4(2):139-154.
- Carpenter, S. R., D. L. Christensen, J. J. Cole, K. L. Cottingham, X. He, J. R. Hodgson, J. F. Kitchell, S. E. Knight, M. L. Pace, D.M. Post, D. E. Schindler, and N. Voichick. 1995. Biological control of eutrophication in lakes. *Environmental Science & Technology* 29(3):784-786.
- Carpenter, S. R., and J. F. Kitchell. 1988. Consumer control of lake productivity. *BioScience* 38(11):764-769.

- Carpenter, S. R., and J. F. Kitchell. 1992. Trophic cascade and biomanipulation – interface of research and management - reply. *Limnology and Oceanography* 37(1):208-213.
- Carpenter, S. R., J. F. Kitchell, and J. R. Hodgson. 1985. Cascading trophic interactions and lake productivity. *BioScience* 35(10):634-639.
- Carpenter, S. R. Replication and treatment strength in whole-lake experiments. *Ecology* 70:453-463.
- Cyterski, M. J., and J. J. Ney. 2005. Availability of clupeid prey to primary piscivores in Smith Mountain Lake, Virginia. *Transactions of the American Fisheries Society* 134(5):1410-1421.
- Demelo, R., R. France, and D. J. McQueen. 1992. Biomanipulation - hit or myth. *Limnology and Oceanography* 37(1):192-207.
- Dettmers, J. M, D. R. Devries and R. A. Stein. 1996. Quantifying responses to hybrid striped bass predation across multiple trophic levels: Implications for reservoir biomanipulation. *Transactions of the American Fisheries Society* 125:491-504.
- Dettmers, J. M., R. A. Stein, and E. M. Lewis. 1998. Potential regulation of age-0 gizzard shad by hybrid striped bass in Ohio reservoirs. *Transactions of the American Fisheries Society* 127(1):84-94.
- Dettmers, J. M., and R. A. Stein. 1992. Food-consumption by larval gizzard shad – zooplankton effects and implications for reservoir communities. *Transactions of the American Fisheries Society* 121(4):494-507.
- Dewey, M. R., W. B. Richardson, and S. J. Zigler. 1997. Patterns of foraging and distribution of bluegill sunfish in a Mississippi River backwater: influence of macrophytes and predation. *Ecology of Freshwater Fish* 6:8-15.
- Downes, B. J., L. A. Barmuta, P. G. Fairweather, D. P. Faith, M. J. Keough, P. S. Lake, B. D. Mapstone, and G. P. Quinn. 2002. *Monitoring ecological impacts: concepts and practice in flowing waters*. Cambridge University Press, Cambridge.
- Drenner, R. W., R. M. Baca, J. S. Gilroy, M. R. Ernst, D. J. Jensen, and D. H. Marshall. 2002. Community responses to piscivorous largemouth bass: A biomanipulation experiment. *Lake and Reservoir Management* 18(1):44-51.
- Drenner, R. W., J. D. Smith, and S. T. Threlkeld. 1996. Lake trophic state and the effects of omnivorous fish. *Hydrobiologia* 319:213-223.
- Drenner, R. W., and K. D. Hambright. 2002. Piscivores, trophic cascades, and lake management. *The Scientific World Journal* 2:284-307.

- Du, J. 2002. Combined algorithms for constrained estimation of finite mixture distributions with grouped data and conditional data. McMaster University, Hamilton.
- Elser, J. J., and C. R. Goldman. 1991. Zooplankton effects on phytoplankton in lakes of contrasting trophic status. *Limnology and Oceanography* 36(1):64-90.
- Findlay, C. S., D. G. Bert, and L. G. Zheng. 2000. Effect of introduced piscivores on native minnow communities in Adirondack lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 57(3):570-580.
- Findlay, D. L., M. J. Vanni, M. Paterson, K. H. Mills, S. E. M. Kasian, W. J. Findlay and A. G. Salki. 2005. Dynamics of a boreal lake ecosystem during a long-term manipulation of top predators. *Ecosystems* 8:603-618.
- Garvey, J., and R. Stein. 1998a. Linking bluegill and gizzard shad prey assemblages to growth of age-0 largemouth bass in reservoirs. *Transactions of the American Fisheries Society* 127(1):70-83.
- Garvey, J. E., and R. A. Stein. 1998b. Competition between larval fishes in reservoirs: the role of relative timing of appearance. *Transactions of the American Fisheries Society* 127(6):1021-1039.
- Haberman, J., R. Laugaste, and T. Noges. 2007. The role of cladocerans reflecting the trophic status of two large and shallow Estonian lakes. *Hydrobiologia* 584:157-166.
- Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community structure, population control, and competition. *American Naturalist* 94(879):421-425.
- Hambright, K. D. 1994. Morphological constraints in the piscivore-planktivore interaction - implications for the trophic cascade hypothesis. *Limnology and Oceanography* 39(4):897-912.
- Hambright, K. D., R. J. Trebatoski, R. Drenner and D. Kettle. 1986. Experimental study of the impacts of bluegill (*Lepomis macrochirus*) and largemouth bass (*Micropterus salmoides*) on pond community structure. *Canadian Journal of Fisheries and Aquatic Sciences* 43:1171-1176.
- Hambright, K. D., R. W. Drenner, S. R. McComas, and N. G. Hairston. 1991. Gape limited piscivores, planktivore size refuges, and the trophic cascade hypothesis. *Archiv Für Hydrobiologie* 121(4):389-404.
- Hansson, L. A., H. Annadoter, E. Bergman, S. F. Hamrin, E. Jeppesen, T. Kairesalo, E. Luokkanen, P. Nilsson, M. Søndergaard and J. Strand. 1998. Biomanipulation as an application of food-chain theory: Constraints, synthesis, and recommendations for temperate lakes. *Ecosystems* 1(6):558-574.

- Herbst, D. B., E. L. Silldorff, S. D. Cooper. 2009. The influence of introduced trout on the benthic communities of paired headwater streams in the Sierra Nevada of California. *Freshwater Biology* 54:1324-1342.
- Higgins, K. A., M. J. Vanni, and M. J. González. 2006. Detritivory and the stoichiometry of nutrient cycling by a dominant fish species in lakes of varying productivity. *Oikos* 114: 419-430.
- Howick, G. L., and W. J. Obrien. 1983. Piscivorous feeding-behavior of largemouth bass - an experimental-analysis. *Transactions of the American Fisheries Society* 112(4):508-516.
- Hrbáček, J., O. Albertova, B. Desortova, V. Gottwaldova, and J. Popovsky. 1986. Relation of the zooplankton biomass and share of large cladocerans to the concentration of total phosphorus, chlorophyll-a and transparency in Hubenov and Vrchlice Reservoirs. *Limnologica* 17:301-308.
- Hrbáček, J., D. Dvorakova, V. Korinek, and L. Prochazkova. 1961. Demonstration of the effect of the fish stock on the species composition of the zooplankton and the intensity of metabolism of the whole plankton association. *Verh. Int. Verein. Limnol.* 14:192-195.
- Hunter, M. D., and P. W. Price. 1992. Playing chutes and ladders - heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology* 73(3):724-732.
- Jeppesen, E., J. P. Jensen, C. Jensen, B. Faafeng, D. O. Hessen, M. Søndergaard, T. Lauridsen, P. Brettum, and K. Christoffersen. 2003. The impact of nutrient state and lake depth on top down control in the pelagic zone of lakes: A study of 466 lakes from the temperate zone to the arctic. *Ecosystems* 6(4):313-325.
- Johnson, B. M., R. A. Stein, and R. F. Carline. 1988. Use of a quadrat rotenone technique and bioenergetics modeling to evaluate prey availability to stocked piscivores. *Transactions of the American Fisheries Society* 117(2):127-141.
- Keough, M. J., and B. D. Mapstone. 1995. Protocols for designing marine ecological monitoring programs associated with BEK Mills. National Pulp Mills Research Program, Technical Report no. 11, Canberra, ACT: CSIRO.
- Kramer, R. H. and L. L. Smith Jr. 1962. Formation of year classes in largemouth bass. *Transactions of the American Fisheries Society* 91(1):29-41.
- Lawrence, J. M. 1957. Estimated sizes of various forage fishes largemouth bass can swallow. *Proc. Annu. Conf. Southeast. Assoc. Game Fish Comm.* 11:220-225.

- Leibold, M. A. 1989. Resource edibility and the effects of predators and productivity on the outcome of trophic interactions. *American Naturalist* 134(6):922-949.
- Leppa, M., H. Hamalainen, and J. Karjalainen. 2003. The response of benthic macroinvertebrates to whole-lake biomanipulation. *Hydrobiologia* 498(1-3):97-105.
- Littell, R. C., G. A. Milliken, W. W. Stroup, R. D. Wolfinger and O. Schabenberger. 2006. SAS[®] for Mixed Models. Second Ed. SAS Institute Inc. Cary, North Carolina, USA.
- Lodge, D. M., S. C. Blumenshine, and Y. Vadeboncoeur. 1998. Insights and application of large scale, long-term ecological observations and experiments. Pages 202-235 *in* W. J. Resetarits and J. Bernardo, editors. *Experimental Ecology: Issues and Perspectives*. Oxford University Press, Oxford, UK.
- Lowe, R. L. 1996. Periphyton patterns in lakes. Pages. 57–76. *in* R. J. Stevenson, M. L. Bothwell, R. L. Lowe, editors. *Algal Ecology: Freshwater Benthic Ecosystems* Academic Press, San Diego, California.
- Macdonald, P. D. M., and P. E. J. Green. 1988. User's guide to program MIX: an interactive program for fitting mixtures of distributions. Release 2.3, January 1988. Ichthus Data Systems, Hamilton, Ontario. iv+60 pp.
- Macdonald, P. D. M., and T. J. Pitcher. 1979. Age-groups from size-frequency data – versatile and efficient method of analyzing distribution mixtures. *Journal of the Fisheries Research Board of Canada* 36(8):987-1001.
- Mazumder, A. 1994. Patterns of algal biomass in dominant odd-link vs. even-link lake ecosystems. *Ecology* 75(4):1141-1149.
- McQueen, D. J., M. R. S. Johannes, J. R. Post, T. J. Stewart, and D. R. S. Lean. 1989. Bottom-up and top-down impacts on freshwater pelagic community structure. *Ecological Monographs* 59(3):289-309.
- McQueen, D. J., J. R. Post, and E. L. Mills. 1986. Trophic relationships in freshwater pelagic ecosystems. *Canadian Journal of Fisheries and Aquatic Sciences* 43(8):1571-1581.
- McQueen, D. J. 1990. OPINION Manipulating lake community structure: where do we go from here? *Freshwater Biology* 23(3):613-620.
- Mehner, T. 2010. No empirical evidence for community-wide top-down control of prey fish density and size by fish predators in lakes. *Limnology and Oceanography* 55(1):203-213.
- Merritt, R. W., and K. W. Cummins. 1996. An introduction to the aquatic insects of North America. Kendall/Hunt Publishing, Dubuque, Iowa.

- Mittelbach, G. G., A. M. Turner, D. J. Hall, J. E. Rettig, and C. W. Osenberg. 1995. Perturbation and resilience— a long term, whole-lake study of predator extinction and reintroduction. *Ecology* 76:2347-2360.
- Nowlin, W. H., R. W. Drenner, K. R. Guckenberger, M. A. Laudén, G. T. Alonso, J. E. Fennell, and J. L. Smith. 2006. Gape limitation, prey size refuges and the top-down impacts of piscivorous largemouth bass in shallow pond ecosystems. *Hydrobiologia* 563:357-369.
- O'Brien, W. J. 1990. Perspectives on fish in reservoir ecosystems. Pages 209-225 in K. W. Thornton, B. L. Kimmel, and F. E. Payne, editors. *Reservoir Limnology: Ecological Perspectives*. John Wiley & Sons Inc., New York.
- Olson, N. W., C. P. Paukert, D. W. Willis, and J. A. Klammer. 2003. Prey selection and diets of bluegill *Lepomis macrochirus* with differing population characteristics in two Nebraska natural lakes. *Fisheries Management and Ecology* 10:31-41.
- Pace, M. L., J. J. Cole, S. R. Carpenter, and J. F. Kitchell. 1999. Trophic cascades revealed in diverse ecosystems. *Trends in Ecology & Evolution* 14(12):483-488.
- Paukert, C. P., and D. W. Willis. 2002. Seasonal and diel habitat selection by bluegills in A shallow natural lake. *Transactions of the American Fisheries Society* 131(6):1131-1139.
- Parkos, J. J. and D. H. Wahl. 2010. Intra- and inter system variation in largemouth bass recruitment: Reproduction, prey availability, and the timing of year class establishment. *Transactions of the American Fisheries Society* 139(5):1372-1385.
- Parrack, M. L. and N. J. Cummings. 2003. Errors in transforming length samples to age frequencies without age samples. *Fisheries Research* 63:235-243.
- Parrish, D. L., and B. Vondracek. 1989. Population dynamics and ecology of Lake Erie gizzard shad. Ohio Department of Natural Resources, Project No. F-61-R-2 Annual Performance Report, Columbus, Ohio.
- Persson, L. 1999. Trophic cascades: Abiding heterogeneity and the trophic level concept at the end of the road. *Oikos* 85(3):385-397.
- Pierce, C. L., and B. D. Hinrichs. 1997. Response of littoral invertebrates to reduction of fish density: Simultaneous experiments in ponds with different fish assemblages. *Freshwater Biology* 37(2):397-408.
- Pimm, S. L., and R. L. Kitching. 1988. Food web patterns - trivial flaws or the basis of an active research-program. *Ecology* 69(6):1669-1672.
- Polis, G. A., A. L. W. Sears, G. R. Huxel, D. R. Strong, and J. Maron. 2000. When is a trophic cascade a trophic cascade? *Trends in Ecology & Evolution* 15(11):473-475.

- Polis, G. A., and D. R. Strong. 1996. Food web complexity and community dynamics. *American Naturalist* 147(5):813.
- Potthoff, A. J., B. R. Herwig, M. A. Hanson, K. D. Zimmer, M. G. Butler, J. R. Reed, B. G. Parsons, and M. C. Ward. 2008. Cascading food-web effects of piscivore introductions in shallow lakes. *Journal of Applied Ecology* 45(4):1170-1179.
- Power, M. E. 1990. Effects of fish in river food webs. *Science* 250(4982):811-814.
- Ramcharan, C. W., D. J. McQueen, E. Demers, S. A. Popiel, A. M. Rocchi, N. D. Yan, A. H. Wong, and K. D. Hughes. 1995. A comparative approach to determining the role of fish predation in structuring limnetic ecosystems. *Archiv Fur Hydrobiologie* 133(4):389-416.
- Reynolds, C. S. 1994. The ecological basis for the successful biomanipulation of aquatic communities. *Archiv Fur Hydrobiologie* 130(1):1-33.
- Rudstam, L. G., R. C. Lathrop, and S. R. Carpenter. 1993. The rise and fall of a dominant planktivore - direct and indirect effects on zooplankton. *Ecology* 74(2):303-319.
- Schaus, M. H., M. J. Vanni, and T. E. Wissing. 2002. Biomass-dependent diet shifts in omnivorous gizzard shad: Implications for growth, food web, and ecosystem effects. *Transactions of the American Fisheries Society* 131:40-54.
- Schindler, D. W. 1998. Replication versus realism: The need for ecosystem-scale experiments. *Ecosystems* 1(4):323-334.
- Schramm, H. L. and K. L. Jirka. 1989. Epiphytic macroinvertebrates as a food resource for bluegills in Florida lakes. *Transactions of the American Fisheries Society* 118:416-426.
- Seda J, J. Hejzlar, and J. Kubecka. 2000. Trophic structure of nine Czech reservoirs regularly stocked with piscivorous fish. *Hydrobiologia* 429:141-149
- Shapiro, J. and D. I. Wright. 1984. Lake restoration by biomanipulation – Round Lake, Minnesota the 1st 2years. *Freshwater Biology* 14: 371-383.
- Shapiro, J., V. Lamarra, and M. Lynch. 1975. Biomanipulation: an ecosystem approach to lake restoration. Pages 85-96 in P. L. Brezonik, and J. L. Fox, editors. *Water Quality Management through Biological Control*. University of Florida, Gainesville.
- Shurin, J. B., E. T. Borer, E. W. Seabloom, K. A. Anderson, C. A. Blanchette, B. Broitman, S. D. Cooper, and B. S. Halpern. 2002. A cross-ecosystem comparison of the strength of trophic cascades. *Ecology Letters* 5(6):785-791.

- Sierp, M. T., J. G. Qin, and F. Recknagel. 2009. Biomanipulation: a review of biological control measures in eutrophic waters and the potential for Murray cod *Maccullochella peelii peelii* to promote water quality in temperate Australia. *Reviews in Fish Biology and Fisheries* 19(2):143-165.
- Smoot, J. C. and R. H. Findlay. 2010. Nutrient requirements of detritivorous gizzard shad *Dorosoma cepedianum* are met with sediment bacterial and algal biomass. *Aquatic Biology* 8:105-114.
- Steinman, A. D. 1996. Effects of grazers on freshwater benthic algae. Pages 341-373 in Stevenson, R. J. Bothwell, M. L. and Lowe, R. L. editors, *Algal Ecology: Freshwater Benthic Ecosystems*. Academic Press
- Stein, R. A., D. R. DeVries, and J. M. Dettmers. 1995. Food-web regulation by a planktivore: Exploring the generality of the trophic cascade hypothesis. *Canadian Journal of Fisheries and Aquatic Sciences* 52(11):2518-2526.
- Svensson, J. M., E. Bergman, and G. Andersson. 1999. Impact of cyprinid reduction on the benthic macroinvertebrate community and implications for increased nitrogen retention. *Hydrobiologia* 404:99-112.
- Thornton, K. W. 1990. Perspectives on reservoir limnology. Pages 1-13 in K. W. Thornton, B. L. Kimmel, and F. E. Payne, editors. *Reservoir Limnology: Ecological Perspectives*. John Wiley & Sons Inc.
- Tonn, W. M., C. A. Paszkowski, and I. J. Holopainen. 1992. Piscivory and recruitment – Mechanisms structuring prey populations in small lakes. *Ecology* 73(3):951-958.
- Underwood, A. J. 1994. On Beyond Baci - Sampling designs that might reliably detect environmental disturbances. *Ecological Applications* 4(1):3-15.
- Vadeboncoeur, Y. D. M. Lodge, and S. R. Carpenter. 2001. Whole-lake fertilization effects on distribution of primary production between benthic and pelagic habitats. *Ecology* 82:1065-1077.
- Vadeboncoeur, Y., M. J. Vander Zanden, and D. M. Lodge. 2002. Putting the lake back together: reintegrating benthic pathways into lake food web models. *Bioscience* 52:44-54.
- Vander Zanden, M. J., and Y. Vadeboncoeur. 2002. Fishes as integrators of benthic and pelagic food webs in lakes. *Ecology* 83:2152-2161.
- Vanni, M. J., C. Luecke, J. F. Kitchell, and J. J. Magnuson. 1990. Effects of planktivorous fish mass mortality on the plankton community of Lake Mendota, Wisconsin - implications for biomanipulation. *Hydrobiologia* 200:329-336.

- Vanni M. J., and J. L. Headworth. 2004. Cross-habitat transport of nutrients by omnivorous fish along a productivity gradient: Integrating watersheds and reservoir food webs. Pages 43–61 in G. A. Polis, M. E. Power, and G. R. Huxel, editors. *Food Webs at the Landscape Level*. Chicago: University of Chicago Press.
- Vanni, M. J., K. K. Arend, M. T. Bremigan, D. B. Bunnell, J. E. Garvey, M. J. González, W. H. Renwick, P. A. Sorrano and R. A. Stein. 2005. Linking landscapes and food webs: Effects of omnivorous fish and watersheds on reservoir ecosystems. *Bioscience* 55: 155-167.
- Welker, M. T., C. L. Pierce, and D. H. Wahl. 1994. Growth and survival of larval fishes - roles of competition and zooplankton abundance. *Transactions of the American Fisheries Society* 123(5):703-717.
- Welschmeyer, N. A. 1994. Fluorometric analysis of chlorophyll-a in the presence of chlorophyll-B and pheopigments. *Limnology and Oceanography* 39(8):1985-1992.
- Werner, E. E., and D. J. Hall. 1988. Ontogenetic habitat shifts in bluegill - the foraging rate predation risk trade-off. *Ecology* 69(5):1352-1366.
- Werner, E. E., G. G. Mittelbach, and D. J. Hall. 1981. The role of foraging profitability and experience in habitat use by the bluegill sunfish. *Ecology* 62:1 116-125.
- Werner, E. E., J. F. Gilliam, D. J. Hall, and G. G. Mittelbach. 1983. An experimental test of the effects of predation risk on habitat use in fish. *Ecology* 64(6):1540-1548.
- Wetzel, R. G., and G. E. Likens. 1991. *Limnological Analyses*, 2nd edition. Springer Verlag Inc., New York.
- Wetzel, R. G. 2001. *Limnology: Lake and River Ecosystems*, Third edition. Academic Press.

Table 2.1. Select characteristics of 13 Illinois lakes monitored annually from 1998-2005 to test for the effects of supplemental largemouth bass (*Micropterus salmoides*) introductions (stocked) and controls (reference). Information for most parameters taken from Douglas et al. (1993) with the exception of Total Phosphorous (TP) which represents seasonal means (June-August), from data collected during 1998 sampling.

Waterbody	Treatment	Max Depth (m)	Surface Area (ha)	Watershed Area (ha)	Residence Time (yrs)	Conductivity (umhos)	TP(ug/L)
Gizzard Shad Absent							
Sterling	Reference	4.37	28.6	72	8.5	625	45
Lincoln Trail	Reference	10.67	56.9	850	0.9	225	95
Walnut Point	Reference	9.75	21.8	103	0.3	383	147
Murphysboro	Stocked	9.75	58.1	697	1.0	192	93
Le-aqua-na	Stocked	6.71	17.3	1012	0.3	467	157
Kakusha	Stocked	3.66	22.9	550	0.3	426	200
Gizzard Shad Present							
Dolan	Reference	5.18	70.0	431	0.5	265	463
Paradise	Reference	4.88	57.6	4686	0.1	454	181
Lake of the Woods	Reference	6.70	10.5	206	0.6	481	105
Wood	Stocked	5.79	11.2	465	0.2	420	166
Charleston	Stocked	4.88	132.2	560	0.002	362	150
Homer	Stocked	7.32	32.7	3755	0.1	N/A	384
Pierce	Stocked	10.06	61.2	8150	0.4	462	243

Table 2.2. Proportional species composition of electrofishing samples from 13 Illinois lakes from pre-manipulation sampling during fall of 1998. Numbers in parenthesis represent raw counts for each species. Species codes are as follows: LMB—largemouth bass (*Micropterus salmoides*), BLG—bluegill (*Lepomis macrochirus*), GZS—gizzard shad (*Dorosoma cepedianum*), SMB—smallmouth bass (*Micropterus dolomieu*), BLC—black crappie (*Pomoxis nigromaculatus*), RSF—reardear sunfish (*Lepomis microlophus*), GSF—green sunfish (*Lepomis cyanellus*), WAM—warmouth sunfish (*Lepomis gulosus*), CAP—common carp (*Cyprinus carpio*).

Lake	Proportion of Total Catch								
	LMB	BLG	GZS	SMB	BLC	RSF	GSF	WAM	CAP
Sterling	0.42(8)	0.32(6)	-	0.26(5)	-	-	-	-	-
Lincoln Trail	0.31(57)	0.57(106)	-	-	0.02(4)	0.04(8)	-	0.06(11)	-
Walnut Point	0.12(23)	0.80(150)	-	-	-	0.04(7)	0.04(7)	-	-
Murphysboro	0.27(56)	0.73(153)	-	-	-	-	-	-	-
Le-aqua-na	0.12(41)	0.88(310)	-	-	-	-	-	-	-
Kakusha	0.24(92)	0.76(293)	-	-	-	-	-	-	-
Dolan	0.09(46)	0.68(340)	0.23(116)	-	-	-	-	-	-
Paradise	0.03(20)	0.30(240)	0.67(534)	-	-	-	-	-	<0.01(6)
Lake of the Woods	0.01(4)	0.76(233)	0.23(69)	-	-	-	-	-	-
Wood	0.16(46)	0.75(221)	0.09(27)	-	-	-	-	-	-
Charleston	0.07(51)	0.48(354)	0.42(309)	-	-	-	-	-	0.03(18)
Homer	0.20(28)	0.68(97)	0.12(17)	-	-	-	-	-	-
Pierce	0.12(24)	0.65(130)	0.11(22)	0.12(24)	-	-	-	-	-

Table 2.3. Multiple Before-After, Control-Impact (MBACI) analysis to test for changes in water quality variables following supplemental introduction of largemouth bass. Mean difference for each parameter between treatment and control lakes are shown before and after introduction. P-values are for the Trt x Period term from the repeated measures ANOVA.

Parameter	Impact - Control Difference Before	Impact - Control Difference After	df	F	P
Gizzard Shad Not Present					
Chlorophyll a (ug/L)	9.78(±11.41)	15.56(±9.49)	1,4	0.28	0.63
Secchi Depth (m)	-1.12(±0.39)	-0.91(±0.33)	1,4	0.84	0.41
Total P (ug/L)	70.09(±132.31)	172.53(±118.67)	1,4	0.36	0.58
Gizzard Shad Present					
Chlorophyll a (ug/L)	-11.79(±10.62)	-6.78(±8.29)	1,5	0.49	0.52
Secchi Depth (m)	0.02(±0.19)	0.04(±0.17)	1,5	0.04	0.84
Total P (ug/L)	-41.88(±47.84)	-14.26(±37.59)	1,5	0.36	0.57

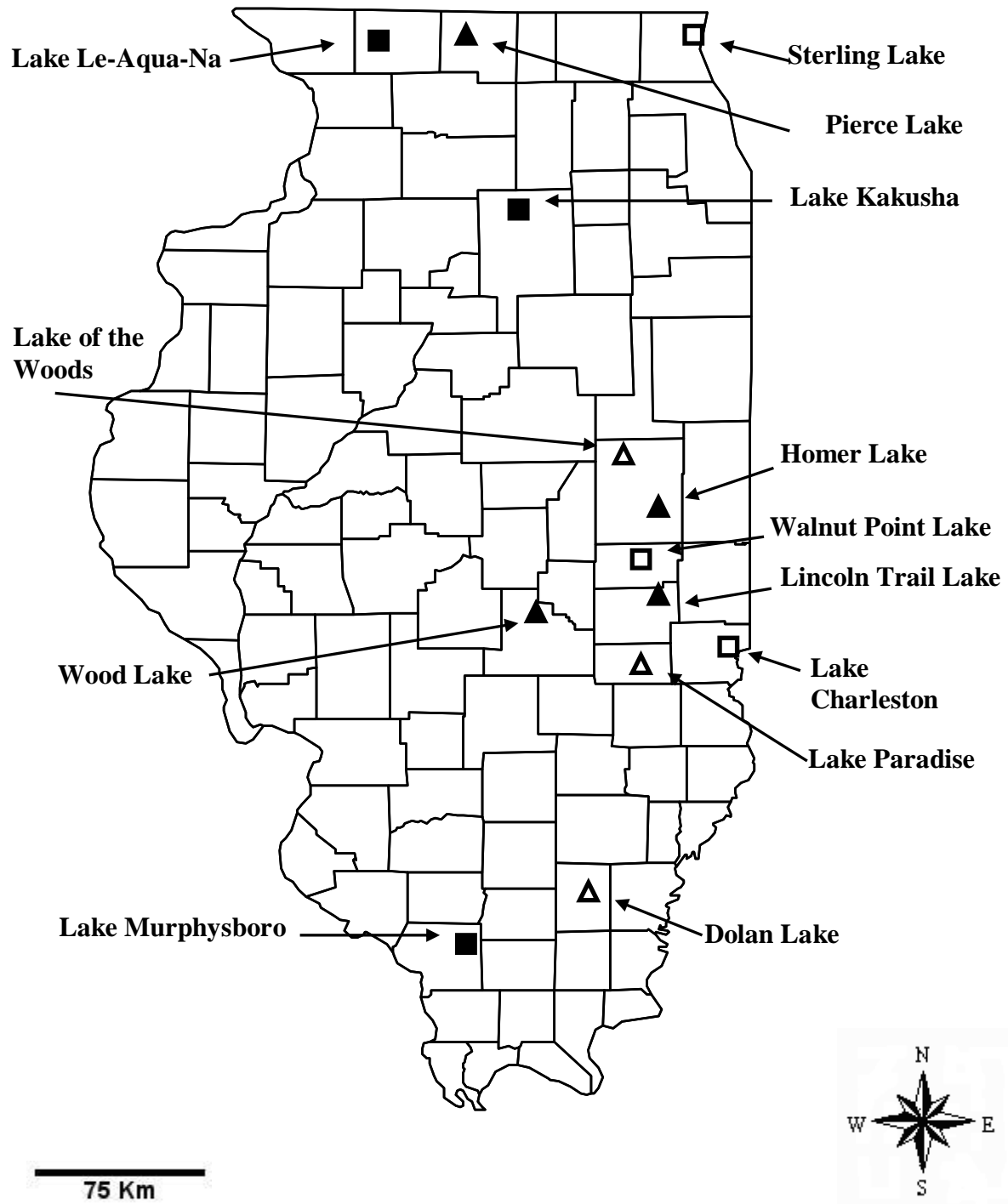


Figure 2.1. Locations of 13 Illinois lakes monitored from 1998-2005. Systems where gizzard shad (*Dorosoma cepedianum*) were absent are represented by squares and systems where this species was present are represented by triangles. Lakes where supplemental largemouth bass were introduced are represented by solid symbols and controls by open symbols.

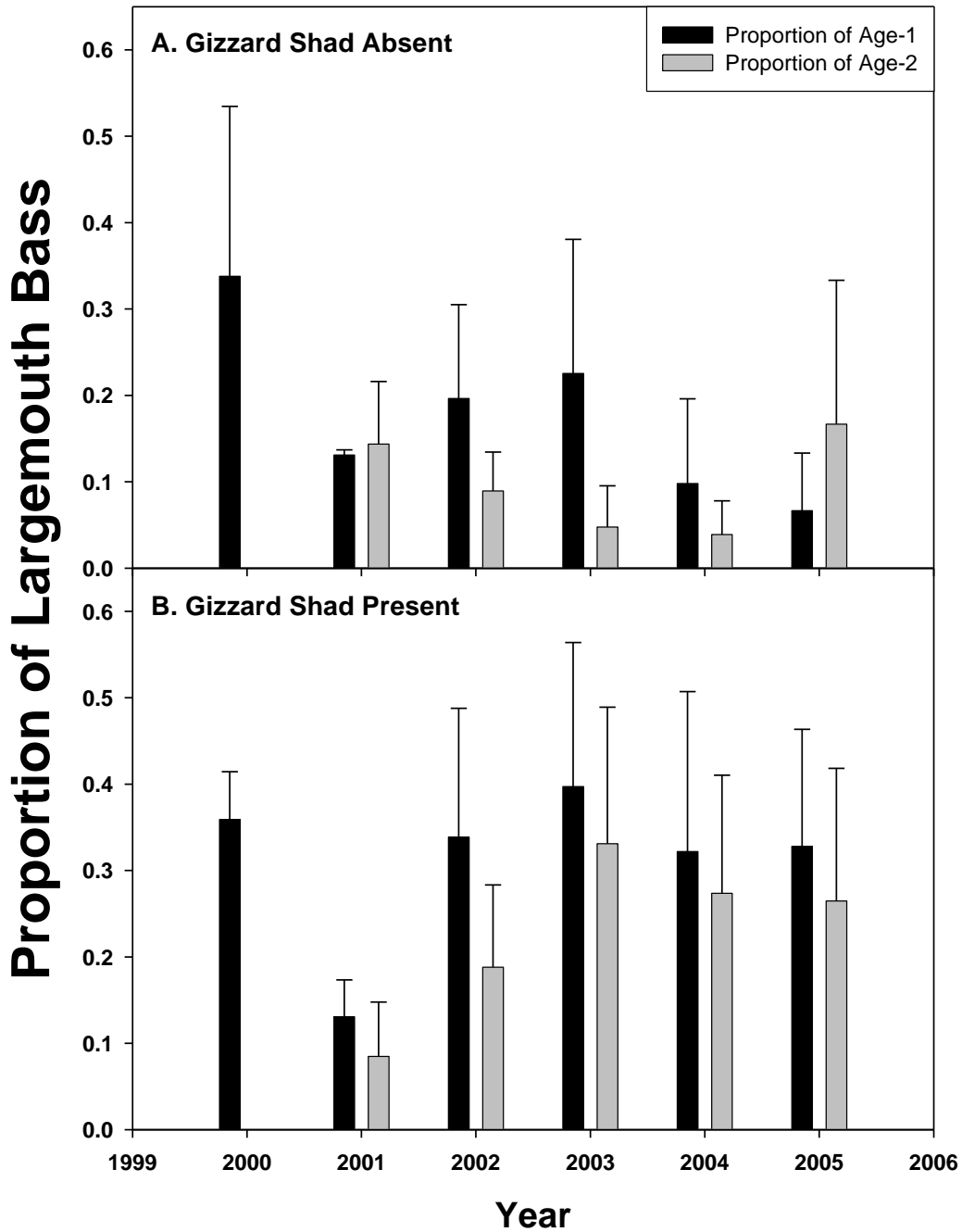


Figure 2.2. Mean proportion of total collected largemouth bass (*Micropterus salmoides*) by year and age group comprised of introduced fish for impoundments where gizzard shad (*Dorosoma cepedianum*) were absent (A) and present (B). Fish were collected from standardized fall electrofishing (see methods for description) conducted during 2000-2005. Error bars represent ± 1 standard error.

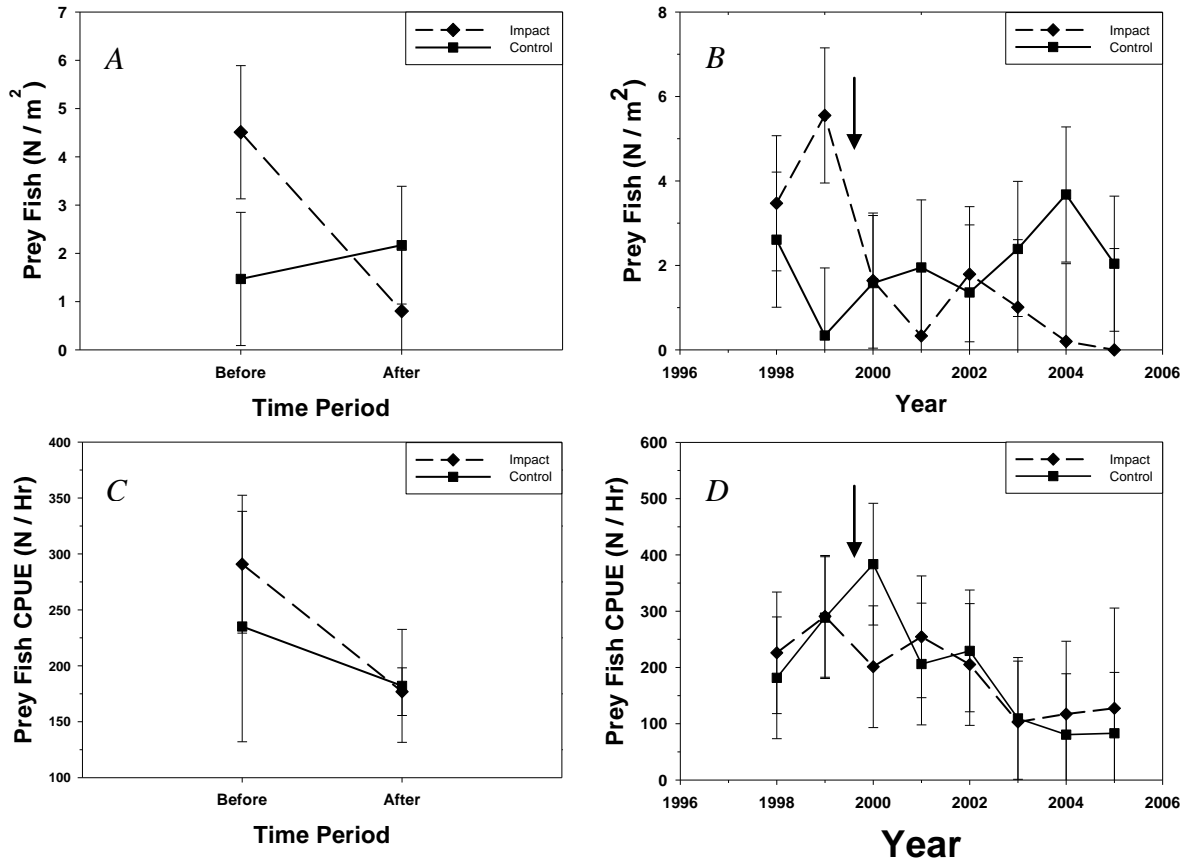


Figure 2.3. Mean density of littoral (A) and catch-per-effort of adult (C) planktivorous and benthivorous fish before and after initiation of supplemental largemouth bass (*Micropterus salmoides*) introductions and annual time series (littoral density B, catch-per-effort D) for lakes where gizzard shad (*Dorosoma cepedianum*) were absent (arrows represent time of initial supplemental largemouth bass introductions). Error bars represent ± 1 standard error.

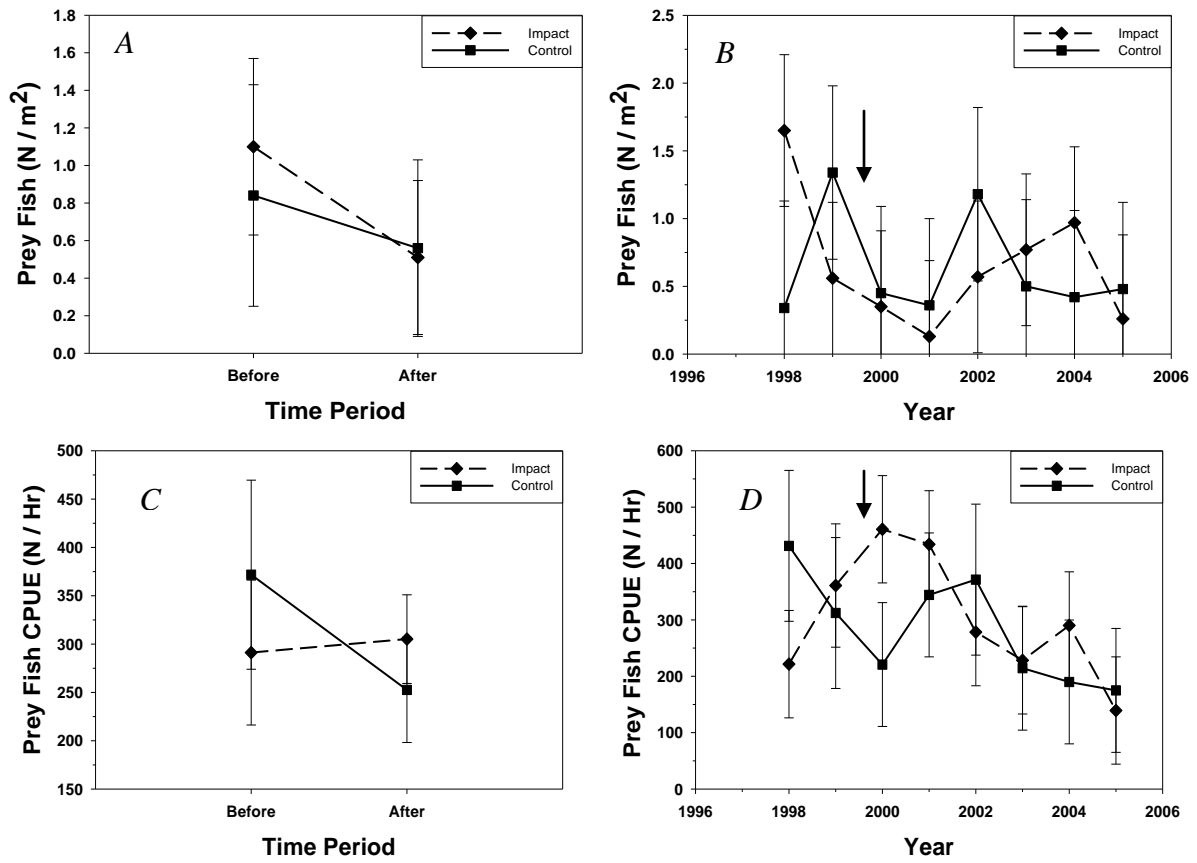


Figure 2.4. Mean density of littoral (A) and catch-per-effort of adult (C) planktivorous and benthivorous fish before and after initiation of supplemental largemouth bass (*Micropterus salmoides*) introductions and annual time series (littoral density B, catch-per-effort D) for lakes where gizzard shad (*Dorosoma cepedianum*) were present (arrows represent time of initial supplemental largemouth bass introductions). Error bars represent ± 1 standard error.

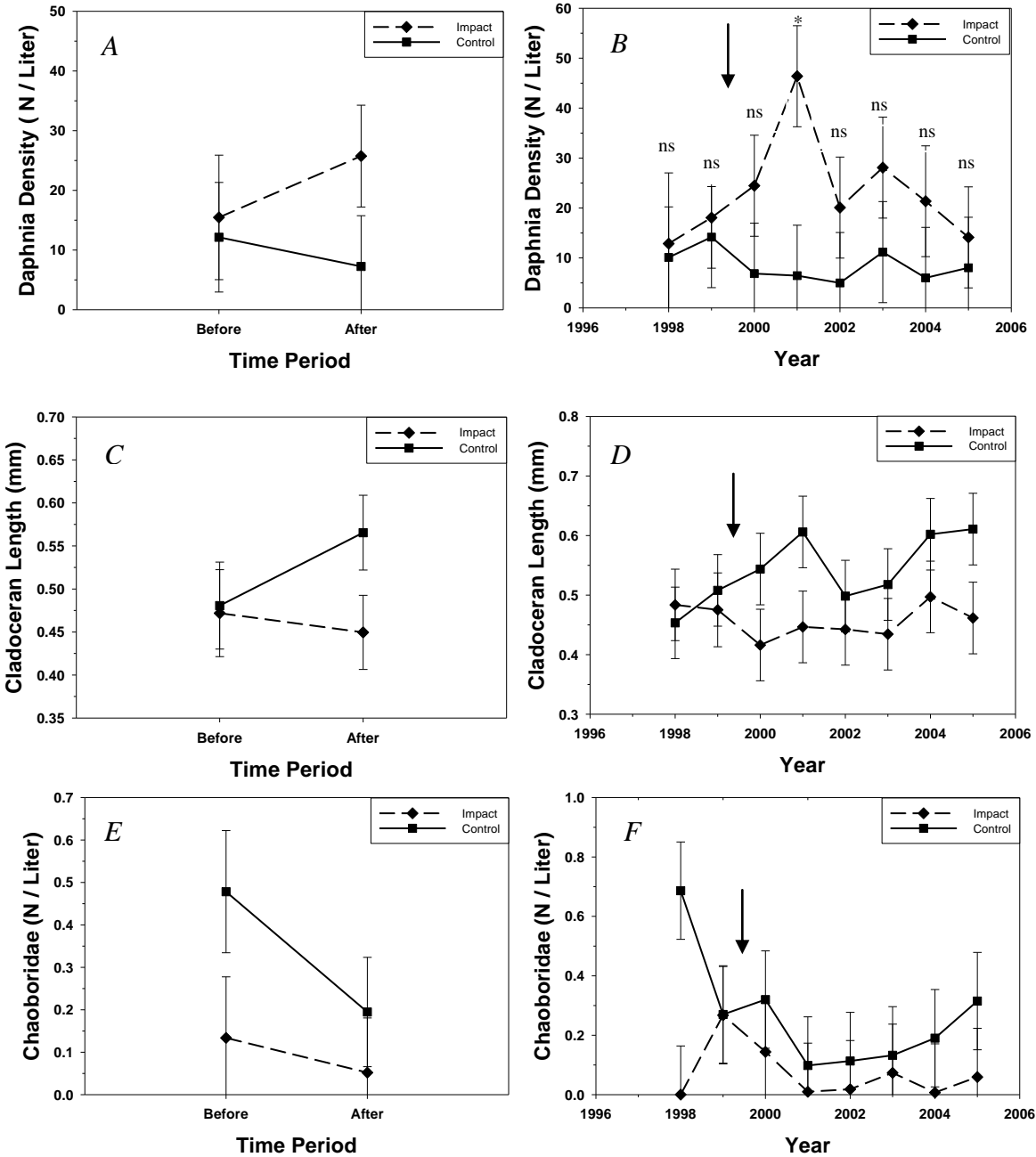


Figure 2.5. Mean concentration of *Daphnia* spp. (top), average length of cladoceran zooplankton (middle) and mean concentration of Chaoboridae (bottom) before and after initiation of supplemental largemouth bass (*Micropterus salmoides*) introductions (left panel, A,C,E) and annual time series (right panel, B,D,F) for lakes where gizzard shad (*Dorosoma cepedianum*) were absent (arrows represent time of initial supplemental largemouth bass introductions). In cases of significant Year(BA) x Trt interactions significant differences between treatments within years are denoted by asterisks and non-significant differences are also noted (ns). Error bars represent ± 1 standard error.

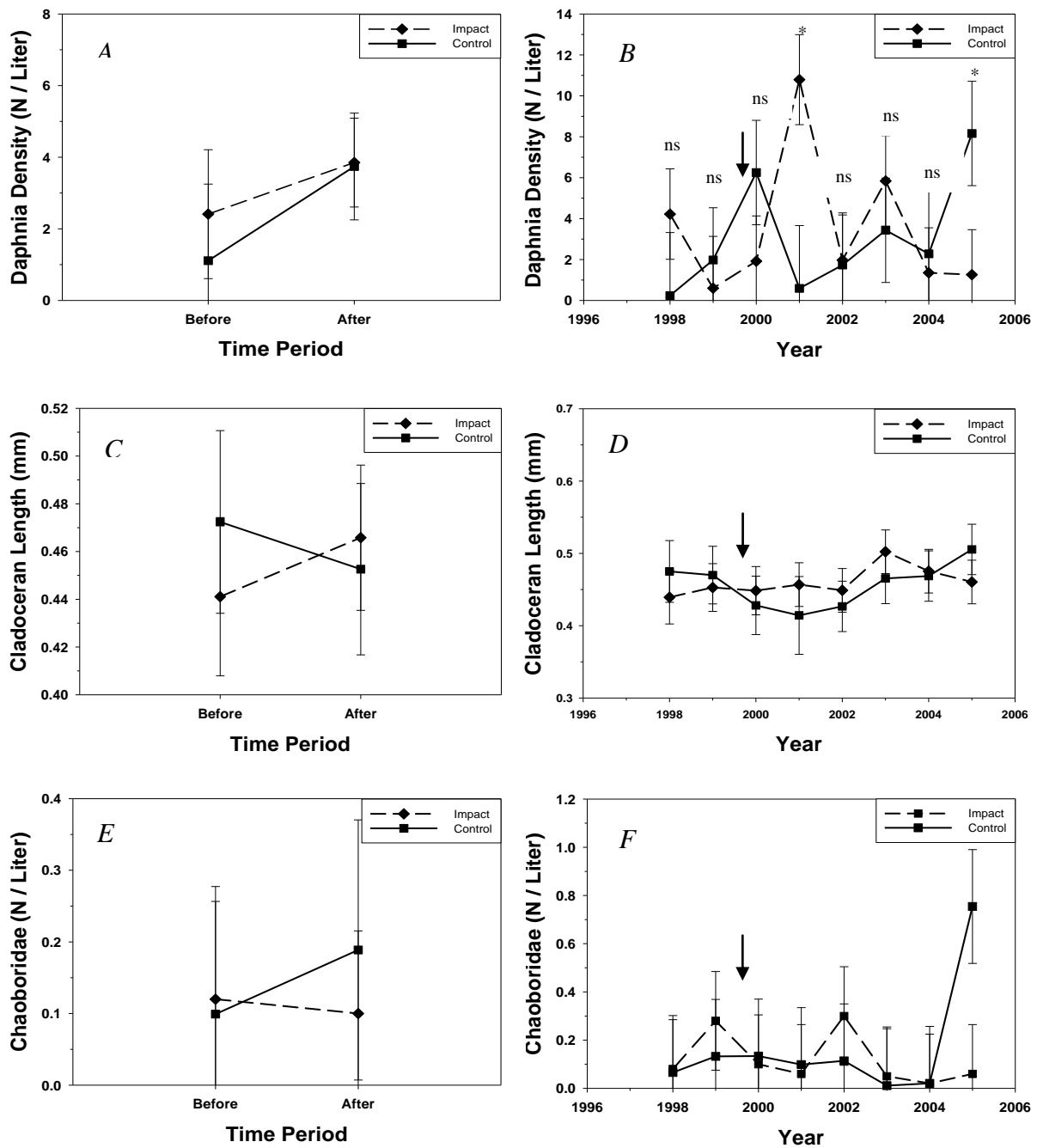


Figure 2.6. Mean concentration of *Daphnia* spp.(top), average length of cladoceran zooplankton (middle) and mean concentration of Chaoboridae (bottom) before and after initiation of supplemental largemouth bass (*Micropterus salmoides*) introductions (left panel, A,C,E) and annual time series (right panel, B,D,F) for lakes where gizzard shad (*Dorosoma cepedianum*) were present (arrows represent time of initial supplemental largemouth bass introductions). In cases of significant Year(BA) x Trt interactions, significant differences between treatments within years are denoted by asterisks and non-significant differences are also noted (ns). Error bars represent ± 1 standard error.

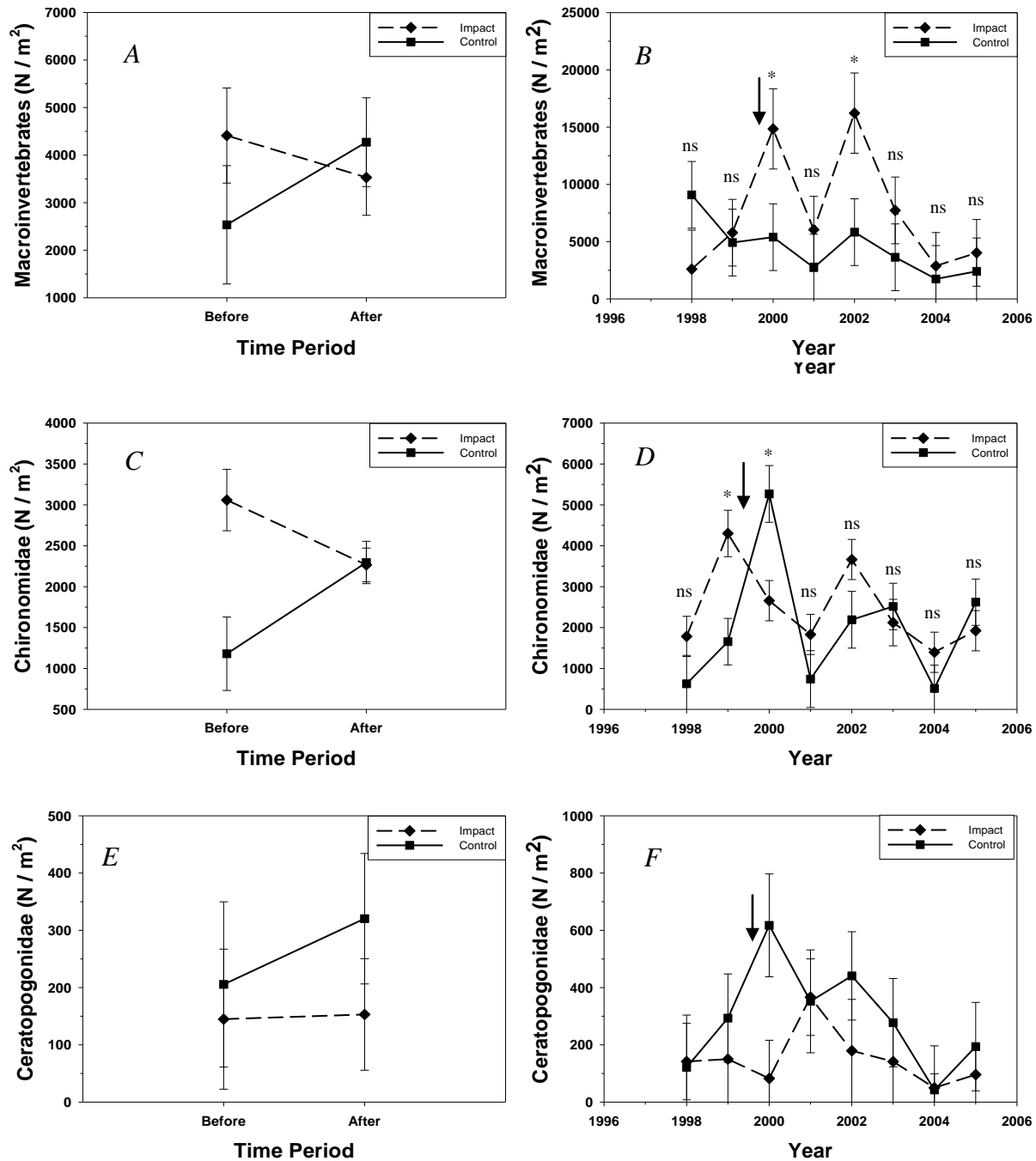


Figure 2.7. Mean density of total macroinvertebrates (top), Chironomidae (middle) and Ceratopogonidae (bottom) before and after initiation of supplemental largemouth bass (*Micropterus salmoides*) introductions (left panel, A,C,E) and annual time series (right panel, B,D,F) for lakes where gizzard shad (*Dorosoma cepedianum*) were absent (arrows represent time of initial supplemental largemouth bass introductions). In cases of significant Year(BA) x Trt interactions significant differences between treatments within years are denoted by asterisks and non-significant differences are also noted (ns). Error bars represent ± 1 standard error

**CHAPTER 3: EFFECTS OF MUSKELLUNGE (ESOX MASQUINONGY)
INTRODUCTION ON POPULATION CHARACTERISTICS OF
RESIDENT FISH SPECIES IN ILLINOIS LAKES**

ABSTRACT

Due to the desire to produce new sport fisheries, the introduction of muskellunge (*Esox masquinongy*) outside its native range has become increasingly common in the U.S. Despite this trend, there is little information on the effects of muskellunge introductions on lake ecosystems and existing fisheries. In this study, I analyzed time series data from 16 Illinois lakes to test for trends in population characteristics of several ecologically and recreationally important fish species in response to the introduction of muskellunge. Standardized electrofishing samples from a set of lakes receiving introductions (n = 8) were compared to spatially paired controls (n = 8) spanning time periods ranging from 5 – 10 years after initial introduction. Metrics of relative abundance, condition, and size structure for each species were evaluated via paired before-after-control-impact (BACI) analysis. These paired analyses were then used to generate measures of effect size and a global analysis performed via a “meta-BACI” approach. Individual lake pairs were highly variable; however, meta-analysis indicated a significant increases in largemouth bass relative abundance (measured as catch-per-hour), increases in black crappie size structure (RSDP), and decreases in white crappie relative abundance in response to muskellunge introduction. Results for bluegills, common carp, gizzard shad, and redear sunfish were not consistent indicating little influence of muskellunge introduction on these species. My results represent a first step toward an understanding of the effects of muskellunge introduction into Illinois lakes.

INTRODUCTION

Fish species introductions (both intentional and unintentional) have been a consequence of human cultural and economic activity for over 2,000 years (Balon 1974). Despite this long history of species introduction, ecologists and fisheries biologists have only recently begun to study their effects on recipient aquatic communities. Interest in ecological effects of fish species introductions has been spurred by costly effects of introduced fishes on economically important fisheries and the structure of entire aquatic ecosystems (Fuller et al. 1999; Vitule et al. 2009). Although species invasions are widely considered among the leading threats to global biodiversity (Pelicice et al. 2009; Gozlan et al. 2010), introducing new fish species remains a common practice in fisheries management and aquaculture (Rahel 1997; Gozlan 2008). Fishes are commonly introduced to increase aquaculture production, enhance local recreational or commercial fisheries, or in efforts to influence water quality; these actions can enhance ecosystem services and benefit local economies (Hiram and Moyle 1999). Some species introductions can have positive effects on local fisheries; however, there remains a considerable amount of scientific uncertainty concerning the effects of introducing many species and the ability to predict potential effects in a given ecological context remains elusive (Leprieur et al. 2009). Because the unintended consequences of species introductions can be costly (and possibly irreversible; Lodge et al. 1998), any species introduction without prior research carries considerable risk. There exists a great need for research to inform management decisions regarding species introductions (García-Berthou et al. 2005; Keller et al. 2007).

In inland freshwater environments, apex piscivorous species are among the most commonly introduced fishes due to demand generated by recreational angling with potential positive, negative, or neutral effects on resident fish communities (Eby et al. 2006; Goodenough

2010). Among the most obvious potential effects of introduced piscivores on resident fish populations are direct effects of predation on resident species and/or competition with native piscivores (Goldschmidt et al. 1993; Huckins et al. 2000). In addition to direct effects of predation and competition, introduced predators can drive a nearly limitless range of both positive and negative indirect effects with predator facilitation or interference, trophic cascades, altered food web linkages, changes in nutrient dynamics, changes in habitat coupling, and changes in species richness being just a subset of observed effects (Pace 1999; Vander Zanden et al. 1999; Koel et al. 2005; Schulze et al. 2006). The intensity of interactions between resident populations and introduced predators depends on availability of prey refuges, behavior, diet, temporal overlap between introduced and resident species, as well as, the potential for resource limitation (Schoener 1974; Eby et al. 2006). While the myriad of potential effects of predator introductions argues for caution in management actions; such actions coupled with adequate monitoring can provide useful tests of ecological theory and add to case studies which may aid in forecasting effects of future introductions (Lodge 1993).

In this study, I test for the effects of introduced muskellunge (*Esox masquinongy*) on resident fish populations of eight Illinois lakes. Responses were evaluated for a piscivore (largemouth bass (*Micropterus salmoides*)), four invertivores (bluegill (*Lepomis macrochirus*), redear sunfish (*Lepomis microlophus*), black crappie (*Pomoxis nigromaculatus*), white crappie (*Pomoxis annularis*)) a benthivore (common carp (*Cyprinus carpio*)) and an omnivorous planktivore/detritivore (gizzard shad (*Dorosoma cepedianum*)). With the exception of the invasive common carp, these species are native to the majority of the central, southern, and eastern United States (Smith 1997). The native range of the muskellunge overlaps considerably with these species, but is smaller being nested in the northeast and central areas of North

America and parts of central and eastern Canada (Crossman 1978). Due to their popularity as a sportfish, muskellunge have increasingly been introduced into natural and man-made waters outside of their native range. For example, since their initial introduction in 1979, the number of Illinois lakes with muskellunge introductions has risen each year and now includes over 34 water bodies. Intentional and unintended introductions have occurred in over 12 U.S states in recent decades (Fuller 2011). Although muskellunge introductions have led to the development of successful fisheries, it has sparked considerable controversy among angling groups over fears that they will compete with and/or prey upon resident species and impact alternative existing fisheries.

Recent published studies on muskellunge introduction have mainly examined food habits and modeled potential influences in river systems (Brenden et al 2004, Curry et al 2007). Outside of grey literature, only one published study to my knowledge has tested for the effects of muskellunge introduction into a lake. In this study, muskellunge introduction was associated with declines in black crappie and white sucker populations in a Michigan lake (Siler and Bayerle 1986). Although these studies provide some understanding of the effects of muskellunge introduction, they were either lacking in key experimental elements or were conducted on systems very different from those in Illinois. A particular problem in previous work has been a lack of controls, which complicates the separation of trends due to natural variation and muskellunge introduction (Underwood 1994). In addition, the previous studies of muskellunge introduction have been conducted in northern, native lake systems (Siler and Bayerle 1986) that have many ecological and fish community differences from the reservoirs in the lower Midwest (Thornton 1990) where many introductions are occurring. My objective was to test for the responses of several ecologically and recreationally important fish species to

muskellunge introduction in a set of Illinois lakes, while incorporating adequate control systems to allow for the separation of effects on introduction from other natural variation.

MATERIALS AND METHODS

Muskellunge Introductions

All muskellunge introductions used fish cultured at the Jake Wolf Memorial Fish Hatchery, Illinois Department of Natural Resources (IDNR) and were conducted by personnel of the IDNR or Illinois Natural History Survey (INHS). Fish were produced using wild caught gametes from parents netted from North Spring Lake, Illinois during early spring (early-mid March). Immediately after hatching, and for a period of about two weeks, fish were fed an artificial diet and held in raceways before being moved to a series of outdoor ponds where they were fed fathead minnows (*Pimephales promelas*) until mid-August. Muskellunge were stocked into receiving waters at an average total length of 200-280 mm and densities ranging from 1 – 12 per hectare (Table 3.1).

Data collection and site selection

To test for the effects of muskellunge introduction in Illinois lakes, I analyzed time series data of various fisheries metrics for 16 Illinois lakes collected as part of standardized sampling conducted by the IDNR and the INHS. The set of 16 lakes chosen for analysis (Figure 3.1; Table 3.2) included lakes with muskellunge introductions (N = 8) and nearby reference waters without stockings (N = 8). Data for each lake was acquired and compiled from two sources including the Illinois Fisheries Analysis System (FAS; Bayley et al. 1990) and data collected by INHS as part of ongoing or previous research projects. Standardized sampling protocol (both IDNR and INHS) consisted of daytime three-phase AC boat mounted electrofishing (3,000 W, 230V AC,

and 50 Hz; see Bayley and Austin 2002 for a detailed description) conducted on three one-half hour fixed shoreline transects sampled on 1-3 dates in the fall of each year (October – November). During each sampling run, all fish were netted, identified to species, counted, and a subsample of each species (up to 50 individuals) was measured for total length and weight.

Lakes were selected for analysis based on data availability and verifiable development of adult muskellunge populations. Lakes were selected for analysis if a minimum of four years of pre- and post-muskellunge introduction electrofishing data existed. Evidence that significant adult populations of muskellunge had developed was based on electrofishing as well as targeted modified fyke-net catches (3.8 cm bar mesh, 1.2 X 1.8 m frames with six 0.75 m hoops; Table 3.1). Lakes were selected if within the post introduction period (4-7 years), the average catch rate of stock length muskellunge exceeded 0.5 or greater fish per net per night (50% of the IDNR management goal for muskellunge lakes). In one instance (Mill Creek Lake), fyke net data were not available to verify adult muskellunge populations; however, this lake had electrofishing catch rates of stock length and greater muskellunge comparable to other lakes with known established adult populations (Table 3.1). Each selected muskellunge lake was paired with a nearby control lake that was not stocked. After identifying qualifying muskellunge lakes, a list of potential control lakes was generated based on lakes with concurrent annual electrofishing time series. This list was then trimmed to a set of lakes or lake with the closest geographic distance and fish community (presence or absence of gizzard shad). In cases where muskellunge lakes overlapped in their prospective controls due to close proximity (Wheel, Johnson and Shovel Lakes) or where candidate controls were within 10km of each other, lakes were paired based on size (e.g. Lakes Shovel – Lou Yeager and Johnson-Springfield respectively).

Although muskellunge populations in lakes selected for analysis were verified by modified fyke net sampling, only AC electrofishing data was available from control systems; therefore, my analysis of effects of muskellunge introduction was restricted to electrofishing data. Boat electrofishing is a seasonally and compositionally selective gear that is most suited to indexing abundance and size structure of nearshore species (Bonar et al. 2010). In order to control for season and to ensure adequate indexing of relative abundance, I restricted my analysis to fall samples of species known to have high vulnerability to electrofishing gear (Bayley and Austen 2002). These species included largemouth bass, bluegill, redear sunfish (*Lepomis microlophus*), gizzard shad (*Dorosoma cepedianum*), common carp (*Cyprinus carpio*), black crappie (*Pomoxis nigromaculatus*) and white crappie (*P. annularis*). All species did not occur in all lakes, which limited the number of lake pairs included in some cases. My analysis focused on comparing the relative changes (before vs after) in several common fisheries management metrics including relative abundance (CPUE; number per hour), size structure (proportional size distribution; PSD), preferred length relative size distribution (RSD-P), and condition (relative weight; W_r) in lakes where muskellunge were introduced relative to control systems for each species.

Statistical Analyses

Individual lakes selected for analysis varied in the timing of initial muskellunge introduction from 1996-2005 as well as the years in which they were sampled. In order to minimize the effects of temporal differences in data collection, each stocked and reference lake combination was treated as an independent experiment and analyzed using paired before-after control-impact analysis (BACIP, Underwood 1994). Paired analysis using waters from the same

geographic region is a commonly used approach as a control for regional climate related variation in whole lake studies (Carpenter 1989). Each paired time series was matched by year and only years in which both lakes were sampled were used in analysis. Paired time series were analyzed using a linear mixed model with fixed effects of before or after muskellunge introduction (BA) and control or introduced lakes (CI) and their interaction (BA*CI). Two random terms were included to account for variation within sites across time. One term for year nested within before-after periods (Y(BA)) and one term for the interaction of control or introduced lakes and year within the before or after period CI*Y(BA) (see Downes et al 2002 for a formal description of this model). The final linear mixed model was then as follows:

$$Y_{ijk} = \mu + CI_{i\dots} + BA_{\dots k} + Y(BA)_{jk} + BA*CI_{i.k} + CI*Y(BA)_{ijk}$$

The BA*CI term tests for any changes in average values of the parameter of interest coincident with the effect in question (muskellunge introduction) and is tested with the CI*Y(BA) term (Downes et al. 2002). Serial correlation among years (nonzero covariance) due to repeated measurements was accounted for by fitting various covariance structures to the data (SAS[®]; PROC MIXED) and choosing the structure that generated the best model based on the corrected Akaike's information criterion (AICC; Littell et al. 2000). I used the null hypothesis of no change in the response variable between introduced muskellunge lakes and non-introduced muskellunge lakes. To control for experiment wise type-1 errors I adjusted my alpha from an original value of 0.05 to a bonferroni adjusted value of 0.006. This adjustment was made by dividing alpha by 8 which was a maximum number of tests performed across lake pairs for any individual variable.

In order to draw more general conclusions concerning the effects of muskellunge introduction, I also used a recently described “meta-BACI” approach to conduct a meta-analysis of each metric across lake pairs following the general approach described by Gurevitch and Hedges (1993) and modified for BACI designs by Conner et al (2007). For each metric of interest, meta-analysis was conducted by comparing the change in the least squares means for control and reference systems from before and after muskellunge introduction (estimated from the above linear mixed model). The difference in mean values before and after muskellunge introduction was used to calculate an effect size (d) using the formula:

$$d_i = (M_{ia} - M_{ib}) - (M_{ca} - M_{cb})$$

and

$$SE(d_i) = \sqrt{\text{var}(M_{ia}) + \text{var}(M_{ib}) + \text{var}(M_{ca}) + \text{var}(M_{cb})}$$

Where d_i = relative effect in lake i , M = least squares mean of parameter of interest with subscripts: ia , M of lakes receiving muskellunge after introduction; ib , M of lakes receiving muskellunge before introduction; ca , M of control lakes after introduction; cb M of control lakes before introduction. In this BACI approach, changes are considered relative because the value of the effect size does not necessarily represent a true change in the mean of the lake receiving muskellunge. Rather, it is possible that the mean value changed relatively less than its paired control and this situation would still be considered a measurable effect (Connor et al. 2007). Each of the paired effect sizes was weighted by the reciprocal of its respective variance to account for differences in sample sizes and variability and evaluated with a paired t-test (Gurevitch and Hedges 1993). I was also interested in the potential importance of muskellunge

density in determining effect sizes, therefore I conducted pairwise Pearson correlations between effect sizes and average catch-per-effort (electrofishing number per hour) muskellunge in the post-introduction period for each variable. These techniques allowed us to test for the generality of effects of muskellunge introduction across all lake pairs and to test for potential effects of varying muskellunge density. Significance was declared at an alpha less than or equal to $P = 0.05$.

RESULTS

Significant changes in population characteristics were observed for largemouth bass and *Pomoxis* spp. following introduction of muskellunge. On the individual lake scale, largemouth bass populations showed significant changes in relative abundance in one lake and a significant change in size structure in one lake. Largemouth bass relative abundance increased relative to controls in Wheel Lake after muskellunge introduction while largemouth bass RSDP increased relative to controls Shovel Lake (Table 3.3). Meta-analysis of largemouth bass population parameters indicated an overall significant effect size for relative abundance across eight lake pairs (Table 3.4). Effect sizes for largemouth bass relative abundance were positive for 7 of 8 lake pairs resulting in a positive mean effect size of 23.21 (95% CI \pm 20.2) largemouth bass per hour of electrofishing (Figure 3.2). No significant overall effects were detected across lake pairs for size structure or condition (Table 3.4). There were no significant relationships between relative muskellunge density and effect sizes for any of the measured largemouth bass population characteristics (Table 3.4).

Paired analysis of bluegill population parameters in individual lakes indicated significant changes in relative abundance in one lake, significant changes in size structure in three lakes

(Table 3.3). Relative abundance increased relative to the control by 14 bluegills per hour of electrofishing in Mill Creek Lake. Size structure increased in two lakes relative to controls (Argyle Lake and Mill Creek Lake) and declined in one (Johnson Lake) after muskellunge introduction. Despite changes in some parameters in individual lakes, there was no overall effect detected across lake pairs in the meta-analysis for any of the measured bluegill population characteristics (all $P > 0.05$; Table 3.4). Furthermore, there were no significant relationships between relative muskellunge density and effect sizes for any of the measured bluegill population characteristics (Table 3.4).

Redear sunfish relative abundance and condition (W_r) data were available from three lake pairs (Table 3.3) and size structure from one lake pair. There were no statistically significant changes in any of the parameters at the individual lake scale (Table 3.3). Meta-analysis across three lake pairs indicated no consistent changes in redear sunfish relative abundance or condition after muskellunge introduction relative to controls (all $P > 0.05$; Table 3.4).

There were no significant changes in population characteristics of black crappie when analyzed at the scale of individual lake pairs (table 2.2) however meta-analysis of effect sizes indicated a significant average increase in RSD-P relative to controls (Table 3.4). All four lakes examined showed positive effect sizes relative to controls for RSDP ranging from an increase of 2.5 to 19.1 (Figure 3.3). There were no significant relationships between relative muskellunge density and effects sizes for any of the measured black crappie population characteristics (Table 3.4).

Effects on white crappie populations were assessed in two lake pairs (Argyle Lake and Wheel Lake) and included relative abundance, size structure (PSD and RSDP) and condition (W_r). There were no significant changes in population characteristics of white crappie following

muskellunge introduction for either lake when analyzed on the basis of individual lake pairs (Table 3.3). Effect sizes for relative abundance in both lakes were negative due to increases in controls that were not present in lakes receiving muskellunge (Figure 3.4). This difference in changes resulted in an overall significant negative effect of muskellunge introduction and a negative average effect size relative to controls of 7.3 white crappie per hour of electrofishing (Table 3.4).

Unlike largemouth bass and *Pomoxis* populations, I observed no effects of muskellunge introduction on raw effect sizes for gizzard shad and common carp population characteristics (all $P > 0.05$; Table 3.3). There was also no significant correlation between relative muskellunge density and effect sizes for population characteristics for these two species after muskellunge introduction (Table 3.4).

DISCUSSION

This study represents the first to my knowledge with adequate controls to evaluate the effects of muskellunge introduction on resident fish communities. I found that muskellunge introduction had few negative effects and some positive effects on population characteristics of a number of resident fish species on a time scale of four to seven years after introduction. The lack of negative effects of muskellunge introduction is not likely due to low densities of muskellunge as nearly all of these lakes (7 of 8; measured as trap-net catch per effort) met or exceeded the IDNR management goal of 1 fish per net per night during the post introduction period. Furthermore, the average catch rates in these lakes were similar to or greater than the 75th percentile (0.8 per net per night) for densities in native muskellunge lakes in Wisconsin averaged across 188 lakes sampled from 2000-2008 (Simonson 2010). Therefore muskellunge densities in

these lakes exceeded average densities northern native populations. These findings should however not be construed to mean that there is no relationship between muskellunge density and effects on recipient populations. While I found no significant relationship between muskellunge density and effect sizes in receiving lake fish populations this may be due to the small number of lakes for some of these tests or to the range of densities examined. While I cannot make inferences to cases where muskellunge may be present in even greater densities I can say that in a series of lakes with significant adult populations, where densities often exceeded management goals and rivaled or exceeded densities of muskellunge found in their native range, I found no strong negative effects on the species examined.

The positive responses in largemouth bass relative abundance to muskellunge introduction were among the strongest of my results with catch-per-hour effect sizes positive for seven of the eight cases. I cannot evaluate the mechanisms responsible for the increases in largemouth bass catch rates, but recent research provides two plausible causes for these observations. The presence of muskellunge leads to increased growth of largemouth bass in ponds when controlling for piscivore densities and biomass (Carey and Wahl 2010). Laboratory observations indicated that this effect was likely due to a facilitative interaction between largemouth bass and muskellunge when foraging on shared prey (Carey and Wahl *in press*). Such facilitative interactions have been documented among other piscivores and are known to increase population growth rates of the benefiting piscivore (Eklov and VanKooten 2001; Schulze et al. 2006). These behavioral interactions may offer an explanation for the numerical response of largemouth bass to muskellunge introduction. Alternatively, the introduction of new predator types often results in shifts in habitat use of resident predators (Werner and Hall 1977) that could affect capture rates. For example, the introduction of pikeperch (*Sander lucioperca*)

to a European lake resulted in increased use of the littoral zone by resident piscivorous perch (*Perca fluviatilis*). A similar effect might occur for largemouth bass as they reach smaller adult sizes than muskellunge and body size is a known determinant of intra-guild competitive interactions (Fedriani et al. 2000). If competition with adult muskellunge caused largemouth bass to increase their use of littoral areas, would expect electrofishing catch rates to increase as this gear primarily indexes the littoral zone. A growing body of research supports a need to further explore interactions between piscivorous fishes at the lake scale to test for mechanisms by which species such as largemouth bass and muskellunge interact.

Although there were some significant effects observed for *Lepomis* populations at the scale of individual lakes, these responses were not consistent and my global analysis across lakes indicated a lack of consistent responses. Several previous studies have shown influences of other resident and introduced piscivores on population characteristics of *Lepomis* species (Belk and Hales 1993; Schneider and Lockwood 2002; Tomcko and Pierce 2005). There are several factors that may limit the likelihood for muskellunge to influence *Lepomis* populations. Laboratory studies have shown that esocids have difficulty capturing sunfish relative to other potential prey species due to their anti-predatory defenses (Tomcko et al. 1984; Wahl and Stein 1988), which may limit their ability to influence *Lepomis* populations. The presence of alternative prey, especially gizzard shad, in a majority of my lakes may also limit the responses of sunfish populations to muskellunge introduction. Although sunfish are a primary prey species for piscivores in many lower midwestern lakes, muskellunge select soft-rayed fishes such as gizzard shad over sunfishes in systems where they are present (Wahl and Stein 1988). Gizzard shad were present in five of the eight lakes receiving muskellunge introductions and the presence of gizzard shad may buffer sunfish populations from predation and reduce effects of muskellunge

on these species. There is a need to evaluate potential effects of muskellunge introduction on *Lepomis* species in systems without gizzard shad and I would caution against extrapolating my results to these systems.

Along with largemouth bass, the only other species showing consistent responses to muskellunge introduction were black and white crappie. These results are consistent with one of the few previous studies testing for responses of lake fish communities to muskellunge introduction, which implicated effects on crappie populations (Siler and Bayerle 1986). Responses of crappie population characteristics including increased size structure and decreased relative abundance are consistent with predictions of increased piscivory. Several previous studies have implicated a role of piscivores including largemouth bass, northern pike (*Esox lucius*) and saugeye (*Sander vitreus x Sander canadensis*) in regulating crappie abundance and size structure (Gabelhouse 1984; Willis et al. 1984; Boxrucker 2002; Galinet et al. 2002). The responses of crappie populations to muskellunge introduction are in contrast to those of the other sunfishes. Differences in habitat selection and diel movements between crappie and other sympatric sunfishes (Keast et al. 1992), may alter the likelihood of interactions with muskellunge. Regardless of the potential causes of differing responses among species, my results may be valuable for crappie management of Illinois lakes where the development of high density, slow growing populations comprised of smaller individuals is a common problem (Mitzner 1984). My results suggest muskellunge may influence abundance and size structure of crappie populations.

Gizzard shad are known to be a preferred prey of muskellunge in Midwestern lakes where they often dominate fish community biomass (Johnson et al. 1988; Wahl and Stein 1991; Wahl and Stein 1993). Despite the preference, I found no evidence that muskellunge

introduction affected gizzard shad population characteristics. These findings are consistent with several previous studies with other species on lower latitude lake ecosystems suggesting an inability of piscivores to influence gizzard shad population dynamics (Johnson et al. 1988; Stein et al. 1995; Dettmers et al. 1998). Several unique aspects of gizzard shad biology have been identified including high fecundity, rapid growth, and omnivorous feeding behavior, which may limit the ability of piscivores to control populations of this species (see Stein et al. 1995 and references therein). In addition, gizzard shad populations may be disproportionately subsidized relative to other species by watershed derived nutrients and detritus, which may further contribute to their high productivity and insensitivity to piscivores in these systems (Bremigan 2001; Vanni et al. 2005; Pilati et al. 2009). My results for Illinois lakes suggest that this important prey may not be a limiting factor for muskellunge.

I also found no evidence for an influence of muskellunge introduction on relative abundance, size structure or condition of common carp. Control of common carp populations is important due to their negative effects on aquatic ecosystems and sport fisheries in North America (Parkos et al. 2003). Only a few studies have suggested that piscivores may influence common carp recruitment (Weber and Brown 2009). High common carp recruitment events may be linked to winterkill induced release from larval predators (Bajer et al 2010) and predators may be responsible for sporadic recruitment and relatively low densities of common carp in Nebraska's sandhill lakes (Paukert et al.2003; Coulter et al. 2008). Alternatively, limited foraging on introduced common carp by resident predators was found in France (Criveli 1981). My results suggest that common carp populations may be resistant to the predatory effects of introduced muskellunge. These results may be due to specific characteristics of my systems including availability of alternative prey, predator densities, and habitat characteristics.

There are several limitations of the data and approach that I used. The empirical nature of the available data and analysis precludes definitive inferences concerning the specific mechanisms by which muskellunge might be affecting fish species in these lakes. The strength of my analyses is highest for the subset of the species examined with more lake pairs (primarily largemouth bass and bluegill). Inferences for other species such as black crappie, white crappie, gizzard shad, common carp, and redear sunfish are based on a smaller number of available lake pairs, which makes the interpretation of findings for these species less robust. A limitation of a study such as ours is that no two lakes or populations are ever identical and thus their treatment as true replicates is not without issue. These problems in evaluating effects of management actions in natural systems have been the impetus for the development of the methods such as the BACI design and met-analysis approaches used here (Downes et al. 2002). In an attempt to address the inherent variation associated with my lakes, I evaluated effects of muskellunge introduction in a spatially paired manner and then used a more global analysis of independent effect sizes to make final inferences. This approach is more powerful and less sensitive to inherent variation among individual sites (Connor et al. 2007).

My results suggest that muskellunge introductions have minimal negative effects on several ecologically and recreationally important fish species in Illinois lakes. I found evidence for a strong positive interaction between introduced muskellunge and largemouth bass populations when generalizing across eight Illinois lakes. In addition, I found evidence that muskellunge may influence the size structure and/or abundance of crappie populations although these findings are from a smaller number of lake systems. With the exception of crappie populations, I found little evidence for influences of introduced muskellunge on important prey species in these systems including bluegill, redear sunfish and gizzard shad. Although I feel this

study represents a valuable first step in exploring fish community responses to muskellunge introduction, I urge that more research will be necessary to validate the generality of these findings. As the introduction of muskellunge into systems outside its native range continues, there is a particular need for long-term assessments of the effects of this introduced piscivore and a need to evaluate responses of other potentially important fishes not evaluated here.

LITERATURE CITED

- Ahrens, R. N., C. J. Walters and V. Christensen. 2012. Foraging arena theory. *Fish and Fisheries* 13:41-59.
- Arthington, A. H. 1991. Ecological and genetic impacts of introduced and translocated freshwater fishes in Australia. *Canadian Journal of Fisheries and Aquatic Sciences* 48:33-43.
- Becker, G. C. 1983. *Fishes of Wisconsin*. University of Wisconsin Press, Madison, Wisconsin.
- Bajer, P. G., and P. W. Sorensen. 2010. Recruitment and abundance of an invasive fish, the common carp, is driven by its propensity to invade and reproduce in basins that experience winter-time hypoxia in interconnected lakes. *Biological Invasions* 12:1101-1112.
- Bayley, P. B., and D. J. Austen. 2002. Capture efficiency of a boat electrofisher. *Transactions of the American Fisheries Society*. 131:435-451.
- Bayley, P. B., S. T. Sobaski, and D. J. Austen. 1990. The fishery analysis system (FAS): creel survey and lake analyses. INHS Center for Aquatic Ecology. Aquatic Ecology Technical Report 90/12.
- Belk, M. C., and L. S. Hales. 1993. Predation induced differences in growth and reproduction of bluegills (*Lepomis macrochirus*). *Copeia* 4: 1034-1044.
- Bonar, S. A., W. A. Hubert, and D. W. Willis. Editors. 2010. *Standard Methods for Sampling North American Freshwater Fishes*. American Fisheries Society, Bethesda, Maryland.

- Boxrucker, J. 2002. Improved growth of a white crappie population following stocking of saugeyes (sauger × walleye): a top-down, density-dependent growth response. *North American Journal of Fisheries Management* 22:1425-1437.
- Bremigan, M. T., and R. A. Stein. 2001. Variable gizzard shad recruitment with reservoir productivity. *Ecological Applications* 11:1425-1437.
- Brenden, T. O., E. M. Hallerman, and B. R. Murphy. 2004. Predatory impact of muskellunge on New River, Virginia, smallmouth bass. *Proceedings of the Southeastern Association of Fish and Wildlife Agencies* 58:12-22.
- Brown, G. E., D. P. Chivers, and J. F. Smith. 1997. Differential learning rates of chemical versus visual cues of a northern pike by fathead minnows in a natural habitat. *Environmental Biology of Fishes* 49:89-96.
- Carey, M. P. and D. H. Wahl. 2010. Interactions of multiple predators with different foraging modes in an aquatic food web. *Oecologia* 162:443-452.
- Carey, M. P. and D. H. Wahl. 2011. Foraging modes of predators and behaviors of prey determine the outcome of multiple predator interactions. *Transactions of the American Fisheries Society* *In Press*.
- Carpenter, S. R. 1989. Replication and treatment strength in whole-lake experiments. *Ecology* 70:453-463.
- Conner, M. M., M. W. Miller, M. R. Ebinger, K. P. Burnham. 2007. A meta-BACI approach for evaluating management intervention in chronic wasting disease in mule deer. *Ecological Applications* 17:140-153.
- Copp, G. H., and coauthors. 2005. To be, or not to be, a non-native freshwater fish? *Journal of Applied Ichthyology* 21(4):242-262.
- Coulter, D. P., J. C. Jolley, K. R. Edwards and D. W. Willis. 2008. Common carp (*Cyprinus carpio*) population characteristics and recruitment in two Nebraska sandhill lakes. *Transactions of the Nebraska Academy of Sciences* 31:35-41.
- Criveli, A. J. 1981. The biology of the common carp, *Cyprinus carpio* L. in the Camargue, southern France. *Journal of Fish Biology* 18:271-290.
- Crossman, E. J. 1978. Taxonomy and distribution of North American esocids. Pages 13-26 *in*: R. L. Kendall, editor. *Selected coolwater fishes of North America*. American Fisheries Society, Special Publication 11, Bethesda, Maryland.
- Curry, A. R. 2007. Using movements and diet analyses to assess effects of introduced muskellunge (*Esox masquinongy*) on Atlantic salmon (*Salmo salar*) in the Saint John River, New Brunswick. *Environmental Biology of Fish* 79:49-60.

- Dettmers, J. M., R. A. Stein, and E. M. Lewis. 1998. Potential regulation of age-0 gizzard shad by hybrid striped bass in Ohio reservoirs. *Transactions of the American Fisheries Society* 127:84-94.
- Downes, B. J., L. A. Barmuta, P. G. Fairweather, D. P. Faith, M. J. Keough, P. S. Lake, B. D. Mapstone, and G. P. Quinn. 2002. *Monitoring Ecological Impacts Concepts and Practice in Flowing Waters*. Cambridge University Press, Cambridge, UK.
- Eby, L. A., W. J. Roach, L. B. Crowder, and J. A. Stanford. 2006. Effects of stocking up freshwater food webs. *Trends in Ecology and Evolution* 21:576-584.
- Eklov, P., and T. VanKooten. 2001. Facilitation among piscivorous predators: Effects of prey habitat use. *Ecology* 82(9):2486-2494.
- Fedriani, J. M., Fuller, T. K., Sauvajot, R. M., and York, E. C. 2000. Competition and intraguild predation among three sympatric carnivores. *Oecologia*, 125: 258–270.
- Fuller, P. L., L. G. Nico, and J. D. Williams. 1999. Nonindigenous fishes introduced into inland waters of the United States. American Fisheries Society, Bethesda, Maryland.
- Fuller, P. L. 2011. *Esox masquinongy*. USGS Nonindigenous Aquatic Species Database, Gainesville, FL. Available: <http://nas.er.usgs.gov> (January 2011).
- Gabelhouse, D. W. 1984. An assessment of crappie stocks in small Midwestern private impoundments. *North American Journal of Fisheries Management* 4:371-384.
- Galinet, G. F., D. W. Willis, B. G. Blackwell, and M. J. Hubers. 2002. Influence of a saugeye (sauger x walleye) introduction program on the black crappie population in Richmond Lake, South Dakota. *North American Journal of Fisheries Management* 22:1416-1424.
- Gammon, J. R., and A. D. Hasler. 1965. Predation by introduced muskellunge on perch and bass 1 - 1-5. *Transactions of the Wisconsin Academy Sciences Arts and Letters* 54:249-&.
- García-Berthou, E., C. Alcaraz, Q. Pou-Rovira, L. Zamora, G. Coenders, C. Feo. 2005. Introduction pathways and establishment rates of invasive aquatic species in Europe. *Canadian Journal of Fisheries and Aquatic Sciences* 62: 453-463.
- Godard, R. D., B. B. Bowers, C. Wannamaker. 1998. Responses of golden shiner minnows to chemical cues from snake predators. *Behavior* 135: 1213-1228.
- Goldschmidt, T., F. Witte, and J. Wanink. 1993. Cascading effects of the introduced Nile perch on the detritivorous phytoplanktivorous species in the sublittoral areas of Lake Victoria. *Conservation Biology* 7:686-700.

- Goodenough, A. E., 2010. Are the ecological impacts of alien species misrepresented? A review of the “native good, alien bad” philosophy. *Community Ecology* 11:13-21.
- Goren, M., and B. S. Galil. 2005. A review of changes in the fish assemblages of Levantine inland and marine ecosystems following the introduction of non-native fishes. *Journal of Applied Ichthyology* 21(4):364-370.
- Gozlan, R. E., J. R. Britton, I. Cowx, and G. H. Copp. 2010. Current knowledge on non-native freshwater fish introductions. *Journal of Fish Biology* 76(4):751-786.
- Gozlan, R. E. 2008. Introduction of non-native freshwater fish: is it all bad? *Fish and Fisheries* 9:106–115.
- Gurevitch, J, and L. V. Hedges. 1993. Meta-analysis: combining the results of independent experiments. Pages 378-398 *in* S. M. Scheiner and J. Gurevitch, editors. *Design and Analysis of Ecological Experiments*. Chapman and Hall, NY.
- Holker, F., H. Doerner, T. Schulze, S. S. Haertel-Borer, S. D. Peacor, and T. Mehner. 2007. Species-specific responses of planktivorous fish to the introduction of a new piscivore: implications for prey fitness. *Freshwater Biology* 52(9):1793-1806.
- Huckins, C. J. F., C. W. Osenberg, and G. G. Mittelbach. 2000. Species introductions and their ecological consequences: An example with congeneric sunfish. *Ecological Applications* 10(2):612-625.
- Johnson, B. M., R. A. Stein, and R. F. Carline. 1988. Use of a quadrat rotenone technique and bioenergetics modeling to evaluate prey availability to stocked piscivores. *Transactions of the American Fisheries Society* 117:127-141.
- Hiram, L.W. and P. B. Moyle. 1999. Management of introduced fishes. Pages 345-369 *in* C. C. Kohler and W. A. Hubert, editors. *Inland Fisheries management in North America*, 2nd edition. American Fisheries Society, Bethesda, Maryland.
- Keast, A. and M. G. Fox. 1992. Space use and feeding patterns in an offshore fish assemblage in A shallow mesotrophic lake. *Environmental Biology of Fishes* 34:159-170.
- Keller, R. P., D. M. Lodge, and D. C. Finnoff. 2007. Risk assessment for invasive species produces net bioeconomic benefits. *Proceedings of the National Academy of Sciences of the United States of America* 104(1):203-207.
- Koel, T. M., P. E. Bigelow, P. D. Doepke, B. D. Ertel, and D. L. Mahony. 2005. Nonnative lake trout result in yellowstone cutthroat trout decline and impacts to bears and anglers. *Fisheries* 30:10-19.

- Leprieur, F., S. Brosse, E. Garcia-Berthou, T. Oberdorff, J. D. Olden, and C. R. Townsend. 2009. Scientific uncertainty and the assessment of risks posed by non-native freshwater fishes. *Fish and Fisheries* 10(1):88-97.
- Lodge, D. M., R. A. Stein, K. M. Brown, A. P. Covich, C. Bronmark, J. E. Garvey, and S. P. Klosiewski. 1998. Predicting impacts of freshwater exotic species on native biodiversity: challenges in spatial scaling. *Australian Journal of Ecology* 23:53-67.
- Mirza, R. S. and D. P. Chivers. 2000. Predator-recognition training enhances survival of brook trout: evidence from laboratory and field-enclosure studies. *Canadian Journal of Zoology* 78:2198-2208.
- Mitzner, L. M. 1984. Crappie management: problems and solutions. *North American Journal of Fisheries Management* 4:339-340.
- Olson, J. A., J. M. Olson, R. E. Walsh, and B. D. Wisenden. 2012. A method to train groups of predator naïve fish to recognize and respond to predators when released into the natural environment. *North American Journal of Fisheries Management* 32: 77-81.
- Parkos, J. J., V. J. Santucci and D. H. Wahl. 2003. Effects of adult common carp (*Cyprinus carpio*) on multiple trophic levels in shallow mesocosms. *Canadian Journal of Fisheries and Aquatic Sciences* 60:182-192.
- Pace, M. L., J. J. Cole, S. R. Carpenter, and J. F. Kitchell. 1999. Trophic cascades revealed in diverse ecosystems. *Trends in Ecology & Evolution* 14(12):483-488.
- Paukert, C. P., W. Stancill, T. J. Debates, and D. W. Willis. 2003. Predatory effects of northern pike and largemouth bass: Bioenergetic modeling and ten years of fish community sampling. *Ecology of Freshwater Fish* 18:13-24.
- Pelicice, F. M., and A. A. Agostinho. 2009. Fish fauna destruction after the introduction of a non-native predator (*Cichla kelberi*) in a Neotropical reservoir. *Biological Invasions* 11(8):1789-1801.
- Pilati, A., M. J. Vanni, M. J. Gonzalez and A. K. Gaulke. 2009. Effects of agricultural subsidies of nutrients and detritus on fish and plankton of shallow- reservoir ecosystems.
- Smith, P. and W. L. Pflieger. 1997. *The fishes of Missouri, Revised Edition*. Missouri Department of Conservation. Jefferson City, Missouri.
- Rahel, F. J. 1997. From Johnny Appleseed to Dr. Frankenstein: changing values and the legacy of fisheries management. *Fisheries* 22: 8-9.

- Savino, J. F., M. G. Henry, and H. L. Kincaid. 1993. Factors affecting feeding-behavior and survival of juvenile lake trout in the great lakes. *Transactions of the American Fisheries Society* 122:366-377.
- Schmitz, W. R., and R. E. Hetfeld. 1965. Predation by introduced muskellunge on perch and bass 2 - Years 8-9. *Transactions of the Wisconsin Academy Sciences Arts and Letters* 54:273-282.
- Schneider, J. C. and L. N. Lockwood. 2002. Use of walleye stocking, antimycin treatments, and catch-and-release angling regulations to increase growth and length of stunted bluegill populations in Michigan lakes. *North American Journal of Fisheries Management* 3:1041-1052.
- Schoener, T. W. 1974. Resource partitioning in ecological communities. *Science* 185:27-39.
- Schulze, T., U. Baade, H. Dorner, R. Eckmann, S. Haertel-Borer, F. Hölker, and T. Mehner. 2006. Response of the residential piscivorous fish community to introduction of a new predator type in a mesotrophic lake. *Canadian Journal of Fisheries and Aquatic Sciences* 63(10):2202-2212.
- Siler, D. H. and G. B. Beyerle. 1986. Introduction and management of northern muskellunge in Iron Lake, Michigan. *American Fisheries Society Special Publication* 15: 257-262.
- Simonson, T. 2010. Muskellunge management update. Publication FH-508-2010. Wisconsin Department of Natural Resources. Bureau of Fisheries Management. Madison, Wi.
- Stein, R. A., D. R. DeVries, and J. M. Dettmers. 1995. Food web regulation by a planktivore: Exploring the generality of the trophic cascade hypothesis. *Canadian Journal of Fisheries and Aquatic Sciences* 52:2518-2526.
- Tomcko, C. M. and R. B. Pierce. 2005. Bluegill recruitment, growth, population size structure, and associated factors in Minnesota lakes. *North American Journal of Fisheries Management* 25:171-179.
- Tomcko, C. M., R. A. Stein, and R. F. Carline. 1984. Predation by tiger muskellunge on bluegill-effects of predator experience, vegetation and prey density 113:588-594.
- Thornton, K. W. 1990. Perspectives on reservoir limnology. Pages 1-13 *in* K. W. Thornton, B. L. Kimmel, and F. E. Payne, editors. *Reservoir Limnology: Ecological Perspectives*. John Wiley & Sons Inc.
- Underwood, A. J. 1994. On beyond baci - sampling designs that might reliably detect environmental disturbances. *Ecological Applications* 4(1):3-15.

- Vander Zanden, M. J., J. M. Casselman, and J. B. Rasmussen, 1999. Stable isotope evidence for the food web consequences of species invasions in lakes. *Nature* 401: 464–467.
- Vanni, M. J., K. K. Arend, M. T. Bremigan, D. B. Bunnell, J. E. Garvey, M. J. Gonzalez, W. H. Renwick, P. A. Soranno and R. A. Stein. 2005. Linking landscapes and food webs: effects of omnivorous fish and watersheds on reservoir ecosystems. *Bioscience* 55:155-167.
- Vitule, J. R. S., C. A. Freire, and D. Simberloff. 2009. Introduction of non-native freshwater fish can certainly be bad. *Fish and Fisheries* 10(1):98-108.
- Wahl, D. H. and R. A. Stein. 1993. Comparative population characteristics of muskellunge (*Esox masquinongy*), northern pike (*Esox lucius*) and their hybrid (*E-masquinongy x E-lucius*). *Canadian Journal of Fisheries and Aquatic Sciences* 50:1961-1968.
- Wahl, D. H. and R. A. Stein. 1991. Food-consumption and growth of three esocids: field tests of a bioenergetic model. *Transactions of the American Fisheries Society* 120:230-246.
- Wahl, D. H. and R. A. Stein. 1988. Selective predation by three esocids: the role of prey behavior and morphology. *Transactions of the American Fisheries Society* 117:142-151.
- Walters, C. J. and F. Juanes. 1993. Recruitment limitation as a consequence of natural-selection for use of restricted feeding habitats and predation risk-taking by juvenile fishes. *Canadian Journal of Fisheries and Aquatic Sciences* 50:2058–2070.
- Weber, M. J. and M. L. Brown. 2009. Effects of common carp on aquatic ecosystems 80 years after ‘Carp as a dominant’: ecological insights for fisheries management. *Reviews in Fisheries Science* 17:524–537.
- Werner, E. E., and Hall, D. J. 1977. Habitat partitioning in a freshwater fish community. *Journal of the Fisheries Research Board of Canada* 34:360–370.
- Willis, D. W., J. F. Smeltzer, and S. A. Flickinger. 1984. Characteristics of a crappie population in an unfished small impoundment containing northern pike. *North American Journal of Fisheries Management* 4:385-389.

Table 3.1. Treatment and control lakes as well as muskellunge (*Esox masquinongy*) (MUE) stocking information and characteristics of resulting populations for 16 Illinois lakes used to evaluate effects of introduction. Muskellunge were sampled by fall AC electrofishing (EF) whereas PSD and number per net-night were calculated using fish collected from springtime modified fyke net sampling. Values represent means whereas values in parentheses represent the range of values from all post-introduction sampling. Cases where only one sampling event was available are represented by single values.

Treatment Lake	Argyle Lake	Johnson Lake	Mill Creek Lake	Lake Mingo	Ridge Lake	Sauk Trail Lake	Shovel Lake	Wheel Lake
Control Lake	Lake Jacksonville	Lake Springfield	Lincoln Trail Lake	Homer Lake	Walnut Point Lake	Lake Le-aqua-na	Lake Lou Yeager	Schuy - Rush Lake
Years Before	1991,1995,1997 1998, 2000	1994-1997 1999-2001	1983-1992	1998-2002	1998,1999 2001-2005	1988,1989 1991-2000	1996-1999	1993-1996, 1998
Years After	2002, 2005-2007	2003-2007	1997,2001 2005,2007	2003-2008	2006-2011	2001-2007	2000,2002 2003,2006	2000,2003 2004,2006
Years Stocked	2000,2002-2003 2006-2007	2001-2003 2005-2007	1999-2003 2005-2007	2002-2008	2005-2011	2000-2002 2006-2007	1999,2000,2001-2003 2005-2007	1999,2000,2002-2003 2005-2007
MUE Stocking Density	6.15 (2.85-9.20)	4.16 (2.47-9.05)	1.11 (1.11-1.12)	7.20 (2.47-14.06)	12.11 (7.27-14.53)	3.11 (2.47-4.94)	2.50 (2.47-2.69)	2.55 (2.47-3.18)
Mean MUE EF CPUE	1	1.06(0.85-1.4)	1.11(0.35-2)	2.85(2.00-4.00)	1.95(1.28-2.86)	3.03	1.63(0.74-5.2)	1.66(0.71-4.51)
Mean MUE PSD	83	39.55 (9.5-69.6)	no data	64.5 (56-77)	100	83.33 (50-100)	57.67 (35-74)	54.43 (0-80)
Mean MUE Per Net Night	1.29	1.11 (0.81-1.38)	no data	1.33 (0.75-1.77)	0.78	1.03 (0.25-2.00)	1.77 (0.5-4.25)	1.73 (0.27-4.2)

Table 3.2. Select characteristics of 16 Illinois lakes monitored to test for the effects of muskellunge (*Esox masquinongy*) introduction on resident fish population characteristics. Data are from Douglas et al. (1993).

Lake Pair	Area (Ha)	Maximum Depth (m)	Mean Depth (m)	Mean Secchi Depth (m)	Mean Conductivity
Argyle	32.6	11.27	4.88	1.13	312
Jacksonville	184.2	9.45	3.79	0.71	495
Johnson	272.7	12.1	5.32	1.58	529
Springfield	1582.1	7.92	4.01	0.43	539
Mill Creek	305.4	18.29	6.61	1.87	242
Lincoln Trail	56.9	10.67	4.84	1.38	225
Mingo	71.7	10.06	3.68	1.37	338
Homer	32.7	7.32	2.46	2.6	390
Ridge	5.5	3.30	2.15	1.21	.
Walnut Point	11.2	5.79	3.82	0.62	444
Sauk Trail	21	6.1	2.33	0.53	361
Le-aqua-na	17.3	6.71	3.19	0.54	467
Shovel	90.9	18.00	5.87	1.52	244
Lou-Yeager	540.2	9.45	3.02	0.50	391
Wheel	159.1	16.70	4.31	1.29	404
Schuy-Rush	101.5	11.89	3.77	0.46	298

Table 3.3. Species, population parameters, differences (after-before), calculated relative effect sizes and results of paired before-after control-impact (BACIP) analysis, for each of 8 Illinois lake pairs evaluated for effects of muskellunge (*Esox masquinongy*) introduction. Results are presented from the BA*CI term of the linear mixed model analysis. See methods section calculation of relative effect sizes and linear mixed model analysis. Significance was determined by a bonferroni adjusted alpha of $P < 0.006$ and are bolded.

Lake Pair	Parameter	M _{ib}	M _{ia}	M _{cb}	M _{ca}	Effect Size (<i>d</i>)	SE (<i>d</i>)	F	Num DF	Den DF	<i>P</i>
Johnson - Springfield	BLCCPUE	5.07	2.65	7.04	5.03	-0.41	2.10	0.03	1.00	9.00	0.877
Mill Creek - Lincoln Trail	BLCCPUE	6.82	9.37	6.72	6.54	2.74	3.42	0.77	1.00	12.00	0.398
Suak Trail - Leaquana	BLCCPUE	13.11	17.79	5.54	8.08	2.15	5.78	0.03	1.00	13.00	0.859
Wheel - Schuy Rush	BLCCPUE	6.67	3.89	27.20	7.33	17.09	6.08	13.28	1.00	6.00	0.011
Johnson - Springfield	BLCPSD	67.25	80.62	78.24	82.71	8.90	17.87	0.62	1.00	9.00	0.450
Mill Creek - Lincoln Trail	BLCPSD	50.97	57.24	61.51	40.61	27.16	30.40	0.48	1.00	11.00	0.504
Suak Trail - Leaquana	BLCPSD	48.28	55.64	24.80	42.70	-10.54	19.17	0.15	1.00	13.00	0.701
Wheel - Schuy Rush	BLCPSD	34.25	83.36	45.49	28.63	65.97	20.33	18.25	1.00	5.00	0.008
Johnson - Springfield	BLCRSDP	23.19	44.32	38.30	41.37	18.05	14.67	4.75	1.00	9.00	0.057
Mill Creek - Lincoln Trail	BLCRSDP	10.19	24.82	24.69	31.71	7.62	20.43	0.17	1.00	11.00	0.688
Suak Trail - Leaquana	BLCRSDP	4.02	9.25	0.00	2.52	2.70	7.52	0.12	1.00	13.00	0.738
Wheel - Schuy Rush	BLCRSDP	1.32	3.36	11.15	0.00	13.18	4.56	8.63	1.00	5.00	0.032
Johnson - Springfield	BLCWR	92.64	97.47	104.72	107.16	2.39	4.04	0.39	1.00	9.00	0.547
Mill Creek - Lincoln Trail	BLCWR	93.70	86.84	99.20	93.42	-1.08	4.71	0.07	1.00	12.00	0.798
Suak Trail - Leaquana	BLCWR	92.37	89.13	94.32	95.88	-4.80	5.81	0.98	1.00	13.00	0.341
Wheel - Schuy Rush	BLCWR	90.67	90.14	97.64	81.44	15.66	4.96	16.32	1.00	6.00	0.007
Argyle - Jacksonville	BLGCPUE	34.23	19.00	13.15	7.48	-9.55	6.65	1.12	1.00	7.00	0.135
Johnson - Springfield	BLGCPUE	13.66	10.01	12.69	11.53	-2.49	3.96	1.13	1.00	8.00	0.319
Mill Creek - Lincoln Trail	BLGCPUE	29.59	19.03	38.72	13.41	14.75	6.00	16.33	1.00	12.00	0.002
Mingo - Homer	BLGCPUE	198.36	63.63	164.65	87.18	-57.27	192.42	0.63	1.00	6.00	0.456
Ridge - Walnut Point	BLGCPUE	191.42	110.06	121.44	115.44	-75.36	134.85	0.21	1.00	7.00	0.662
Suak Trail - Leaquana	BLGCPUE	68.53	56.45	27.23	34.41	-19.25	13.96	1.73	1.00	14.00	0.209
Shovel - Lou Yeager	BLGCPUE	21.00	12.67	18.03	17.55	-7.84	5.02	3.47	1.00	3.00	0.160
Wheel - Schuy Rush	BLGCPUE	16.61	14.40	24.36	24.23	-2.07	5.42	0.06	1.00	6.00	0.810
Argyle - Jacksonville	BLGPSD	32.75	53.11	14.58	3.54	31.39	8.32	15.08	1.00	7.00	0.006
Johnson - Springfield	BLGPSD	16.12	0.21	41.90	52.75	-26.76	6.46	16.14	1.00	8.00	0.004

Table 3.3 Continued	Parameter	M _{ib}	M _{ia}	M _{cb}	M _{ca}	Effect Size (<i>d</i>)	SE (<i>d</i>)	F	Num DF	Den DF	<i>P</i>
Mill Creek - Lincoln Trail	BLGPSD	20.91	18.68	32.22	6.09	23.90	7.87	13.01	1.00	12.00	0.004
Mingo - Homer	BLGPSD	11.52	9.92	24.23	19.60	3.02	14.96	0.07	1.00	6.00	0.800
Ridge - Walnut Point	BLGPSD	46.42	23.97	37.20	49.65	-34.91	16.47	3.41	1.00	8.00	0.102
Suak Trail - Leaquana	BLGPSD	28.44	24.78	30.20	30.55	-4.01	6.83	0.07	1.00	14.00	0.792
Shovel - Lou Yeager	BLGPSD	29.61	32.58	56.92	44.71	15.18	14.73	0.12	1.00	3.00	0.748
Wheel - Schuy Rush	BLGPSD	20.20	9.68	20.70	8.96	1.23	9.90	0.02	1.00	5.00	0.890
Argyle - Jacksonville	BLGWR	88.98	93.92	87.40	80.76	11.57	2.00	1.04	1.00	7.00	0.854
Johnson - Springfield	BLGWR	94.21	78.64	93.90	95.10	-16.77	9.98	1.81	1.00	8.00	0.216
Mill Creek - Lincoln Trail	BLGWR	88.32	82.12	93.45	83.95	3.29	5.03	0.29	1.00	12.00	0.600
Mingo - Homer	BLGWR	96.69	104.90	90.84	103.81	-4.75	1.72	6.87	1.00	5.00	0.047
Suak Trail - Leaquana	BLGWR	99.52	96.05	93.14	98.87	-9.21	7.63	1.42	1.00	14.00	0.253
Shovel - Lou Yeager	BLGWR	98.85	91.65	105.60	113.26	-14.85	9.54	2.06	1.00	3.00	0.247
Wheel - Schuy Rush	BLGWR	96.79	76.73	94.13	90.65	-16.58	12.99	0.07	1.00	5.00	0.804
Argyle - Jacksonville	CAPCPUE	13.51	4.22	8.53	8.92	-9.68	8.96	0.56	1.00	3.00	0.879
Suak Trail - Leaquana	CAPCPUE	4.37	5.21	3.40	5.71	-1.46	3.46	0.29	1.00	9.00	0.602
Argyle - Jacksonville	CAPPSD	60.67	97.18	77.65	67.73	46.43	24.86	2.95	1.00	3.00	0.790
Suak Trail - Leaquana	CAPPSD	71.43	71.43	100.00	100.00	0.00	24.45	0.02	1.00	9.00	0.887
Argyle - Jacksonville	CAPRSDP	49.24	77.14	10.40	25.73	12.57	17.89	0.26	1.00	3.00	0.172
Argyle - Jacksonville	CAPWR	113.25	103.64	101.16	93.95	-2.40	6.84	0.03	1.00	3.00	0.068
Suak Trail - Leaquana	CAPWR	92.90	112.28	97.57	119.09	-2.14	15.98	0.03	1.00	9.00	0.866
Argyle - Jacksonville	GZSCPUE	66.25	20.17	21.58	8.40	-32.90	24.19	1.44	1.00	5.00	0.106
Johnson - Springfield	GZSCPUE	15.28	6.44	12.74	8.71	-4.82	7.04	1.04	1.00	8.00	0.337
Mingo - Homer	GZSCPUE	41.18	56.30	54.46	77.66	-8.07	27.71	0.06	1.00	4.00	0.813
Shovel - Lou Yeager	GZSCPUE	9.96	5.40	28.60	29.74	-5.71	8.40	0.40	1.00	2.00	0.592
Wheel - Schuy Rush	GZSCPUE	24.39	25.77	23.15	18.82	5.71	10.21	0.84	1.00	4.00	0.412
Argyle - Jacksonville	GZSPSD	9.30	8.00	2.58	14.59	-13.31	15.93	0.40	1.00	5.00	0.721
Johnson - Springfield	GZSPSD	63.31	41.35	9.04	16.38	-29.31	21.07	1.94	1.00	8.00	0.255
Mingo - Homer	GZSPSD	0.00	5.64	16.51	9.53	12.62	23.23	0.53	1.00	4.00	0.507
Shovel - Lou Yeager	GZSPSD	49.62	100.00	2.82	17.32	35.88	28.11	0.06	1.00	2.00	0.828
Wheel - Schuy Rush	GZSPSD	4.00	6.82	0.74	0.00	3.55	4.38	0.60	1.00	4.00	0.481

Table 3.3 Continued	Parameter	M _{ib}	M _{ia}	M _{cb}	M _{ca}	Effect Size (<i>d</i>)	SE (<i>d</i>)	F	Num DF	Den DF	<i>P</i>
Argyle - Jacksonville	GZSWR	98.52	97.25	85.89	85.97	-1.35	5.11	0.05	1.00	5.00	0.691
Johnson - Springfield	GZSWR	94.92	101.37	87.63	84.13	9.95	7.61	0.99	1.00	8.00	0.348
Mingo - Homer	GZSWR	84.80	80.89	89.00	80.93	4.16	7.52	0.54	1.00	5.00	0.495
Shovel - Lou Yeager	GZSWR	92.90	88.16	74.45	91.26	-21.55	8.42	2.16	1.00	2.00	0.279
Wheel - Schuy Rush	GZSWR	96.53	96.18	95.25	90.12	4.78	8.23	0.78	1.00	4.00	0.427
Argyle - Jacksonville	LMBCPUE	61.19	70.51	50.79	48.96	11.16	13.80	0.41	1.00	7.00	0.531
Johnson - Springfield	LMBCPUE	36.74	51.66	52.68	45.66	21.94	9.30	6.89	1.00	10.00	0.025
Mill Creek - Lincoln Trail	LMBCPUE	43.56	26.33	50.96	21.34	12.40	8.29	3.07	1.00	12.00	0.162
Mingo - Homer	LMBCPUE	87.35	65.09	47.74	52.62	-27.14	27.73	1.00	1.00	9.00	0.344
Ridge - Walnut Point	LMBCPUE	53.77	194.92	62.26	139.06	64.36	41.54	3.17	1.00	8.00	0.113
Suak Trail - Leaquana	LMBCPUE	93.52	140.16	40.46	55.27	31.83	27.82	1.47	1.00	15.00	0.244
Shovel - Lou Yeager	LMBCPUE	51.39	67.52	25.94	25.48	16.59	10.90	7.20	1.00	5.00	0.044
Wheel - Schuy Rush	LMBCPUE	28.98	65.48	55.17	30.28	61.39	11.11	24.59	1.00	7.00	0.002
Argyle - Jacksonville	LMBPSD	56.02	59.55	64.38	66.68	1.24	7.85	0.01	1.00	7.00	0.989
Johnson - Springfield	LMBPSD	64.15	73.90	61.78	59.78	11.75	7.48	2.36	1.00	10.00	0.086
Mill Creek - Lincoln Trail	LMBPSD	72.14	60.88	50.92	57.82	-18.16	18.17	1.31	1.00	12.00	0.274
Mingo - Homer	LMBPSD	36.83	24.49	43.86	53.78	-22.27	10.31	4.66	1.00	9.00	0.059
Ridge - Walnut Point	LMBPSD	35.97	46.37	34.98	27.35	18.03	10.60	5.44	1.00	8.00	0.048
Suak Trail - Leaquana	LMBPSD	55.47	58.86	63.91	66.00	1.31	9.57	0.06	1.00	15.00	0.814
Shovel - Lou Yeager	LMBPSD	51.23	66.21	66.44	66.15	15.27	9.59	5.25	1.00	5.00	0.071
Wheel - Schuy Rush	LMBPSD	59.91	58.76	52.17	77.66	-26.64	7.99	7.97	1.00	6.00	0.030
Argyle - Jacksonville	LMBRSDP	25.64	22.99	30.62	35.58	-7.61	7.80	0.63	1.00	7.00	0.332
Johnson - Springfield	LMBRSDP	26.82	39.99	23.19	26.67	9.70	4.72	6.40	1.00	10.00	0.030
Mill Creek - Lincoln Trail	LMBRSDP	28.36	11.87	18.56	3.88	-1.81	8.81	0.06	1.00	12.00	0.814
Mingo - Homer	LMBRSDP	22.63	3.92	23.78	17.85	-12.78	7.54	2.87	1.00	9.00	0.124
Ridge - Walnut Point	LMBRSDP	7.35	2.11	10.43	8.31	-3.12	7.47	0.18	1.00	8.00	0.680
Suak Trail - Leaquana	LMBRSDP	21.60	25.18	30.57	31.08	3.06	9.57	0.06	1.00	15.00	0.806

Table 3.3 Continued	Parameter	M _{ib}	M _{ia}	M _{cb}	M _{ca}	Effect Size (<i>d</i>)	SE (<i>d</i>)	F	Num DF	Den DF	<i>P</i>
Shovel - Lou Yeager	LMBRSDP	14.17	30.71	33.44	18.38	31.60	5.32	46.52	1.00	5.00	0.001
Wheel - Schuy Rush	LMBRSDP	26.69	32.07	25.98	62.21	-30.86	8.00	6.88	1.00	6.00	0.039
Argyle - Jacksonville	LMBWR	95.86	96.82	98.66	98.53	1.08	2.88	0.10	1.00	7.00	0.773
Johnson - Springfield	LMBWR	95.37	99.11	104.63	105.84	2.54	2.31	0.27	1.00	10.00	0.613
Mill Creek - Lincoln Trail	LMBWR	90.17	89.99	85.37	82.61	2.58	2.06	1.69	1.00	12.00	0.218
Mingo - Homer	LMBWR	96.67	91.19	95.96	99.75	-9.27	3.73	6.12	1.00	5.00	0.056
Suak Trail - Leaquana	LMBWR	101.94	102.07	102.07	105.76	-3.55	2.81	1.10	1.00	15.00	0.311
Shovel - Lou Yeager	LMBWR	97.96	95.03	100.73	102.63	-4.83	3.61	2.11	1.00	5.00	0.207
Wheel - Schuy Rush	LMBWR	94.08	95.90	99.53	100.55	0.79	2.80	0.16	1.00	7.00	0.702
Argyle - Jacksonville	RSFCPUE	13.17	8.83	9.13	7.39	-2.60	4.41	0.29	1.00	7.00	0.401
Johnson - Springfield	RSFCPUE	3.47	1.25	0.87	3.01	-4.37	1.10	8.83	1.00	4.00	0.041
Mill Creek - Lincoln Trail	RSFCPUE	17.41	13.37	21.84	10.99	6.81	6.18	1.18	1.00	12.00	0.299
Mill Creek - Lincoln Trail	RSFPSD	43.51	70.50	29.04	23.66	32.36	10.95	9.96	1.00	12.00	0.008
Argyle - Jacksonville	RSFWR	102.37	103.98	87.97	89.34	0.24	8.39	0.04	1.00	7.00	0.840
Johnson - Springfield	RSFWR	86.51	103.31	91.17	90.89	17.08	6.83	1.01	1.00	3.00	0.600
Mill Creek - Lincoln Trail	RSFWR	91.10	97.06	99.41	100.52	4.85	7.45	0.25	1.00	12.00	0.623
Argyle - Jacksonville	WHCCPUE	7.33	5.83	10.16	16.53	-7.86	4.84	1.61	1.00	4.00	0.256
Wheel - Schuy Rush	WHCCPUE	4.55	3.04	6.49	11.99	-7.01	2.88	5.22	1.00	3.00	0.107
Argyle - Jacksonville	WHCPSD	63.33	88.89	66.11	79.56	12.10	16.30	0.25	1.00	4.00	0.324
Wheel - Schuy Rush	WHCPSD	62.22	90.63	85.71	64.63	49.49	30.31	2.70	1.00	3.00	0.199
Argyle - Jacksonville	WHCRSDP	5.27	34.35	21.44	35.46	15.06	10.45	1.46	1.00	4.00	0.046
Wheel - Schuy Rush	WHCRSDP	5.00	37.08	38.36	30.37	40.07	33.25	1.28	1.00	3.00	0.340
Argyle - Jacksonville	WHCWR	93.57	101.98	78.81	84.89	2.33	6.91	0.05	1.00	4.00	0.441
Wheel - Schuy Rush	WHCWR	90.29	94.66	95.60	93.20	6.77	6.07	2.57	1.00	3.00	0.207

Table 3.4. Species population metrics, mean relative effect sizes, standard errors and results of meta-analysis across 8 Illinois lake pairs evaluated for effects of muskellunge (*Esox masquinongy*) introduction. Significant comparisons ($P < 0.05$) are in bold. Abbreviations as follows: largemouth bass (*Micropterus salmoides*) (LMB), bluegill (*Lepomis macrochirus*) (BLG), gizzard shad (*Dorosoma cepedianum*) (GZS), common carp (*Cyprinus carpio*) (CAP), redear sunfish (*Lepomis microlophus*) (RSF), black crappie (*Pomoxis nigromaculatus*) (BLC), and white crappie (*Pomoxis annularis*) (WHC).

Parameter	Mean Effect Size (SE)	DF	Paired t	P	r	P
LMB CPUE	23.21(8.53)	7	2.72	0.03	-0.27	0.58
LMB PSD	-1.59(6.20)	7	-0.26	0.81	-0.27	0.51
LMB RSDP	1.02(6.70)	7	0.15	0.88	-0.34	0.41
LMB WR	-0.83(1.60)	7	-0.52	0.62	-0.73	0.06
BLG CPUE	-3.65(4.33)	7	-0.84	0.43	-0.63	0.10
BLG PSD	1.56(8.15)	7	0.19	0.81	0.01	0.98
BLG WR	-1.21(4.01)	6	-0.30	0.77	-0.07	0.87
GZS CPUE	-5.63(5.00)	4	-1.13	0.32	-0.17	0.78
GZS PSD	0.97(8.01)	4	0.12	0.59	0.32	0.60
GZS WR	-0.54(5.12)	4	-0.11	0.54	0.20	0.75
CAP CPUE	-3.75(3.68)	1	-1.02	0.42	No Test	.
CAP PSD	23.02(23.22)	1	0.99	0.8	No Test	.
CAP WR	-6.19(1.53)	1	-3.49	0.16	No Test	.
RSF CPUE	-2.67(2.57)	2	-1.04	0.41	No Test	.
RSF WR	7.95(5.07)	2	1.57	0.26	No Test	.
BLC CPUE	3.42(3.39)	3	1.01	0.39	-0.02	0.98
BLC PSD	21.49(16.78)	3	1.28	0.29	-0.33	0.67
BLC RSDP	10.34(3.15)	3	3.29	0.05	-0.62	0.38
BLC WR	3.24(4.31)	3	0.75	0.51	-0.32	0.68
WHC CPUE	-7.33(0.41)	1	-17.69	0.04	No Test	.
WHC PSD	25.18(17.83)	1	1.41	0.39	No Test	.
WHC RSDP	21.04(10.67)	1	1.97	0.30	No Test	.
WHC WR	4.69(2.22)	1	2.12	0.28	No Test	.

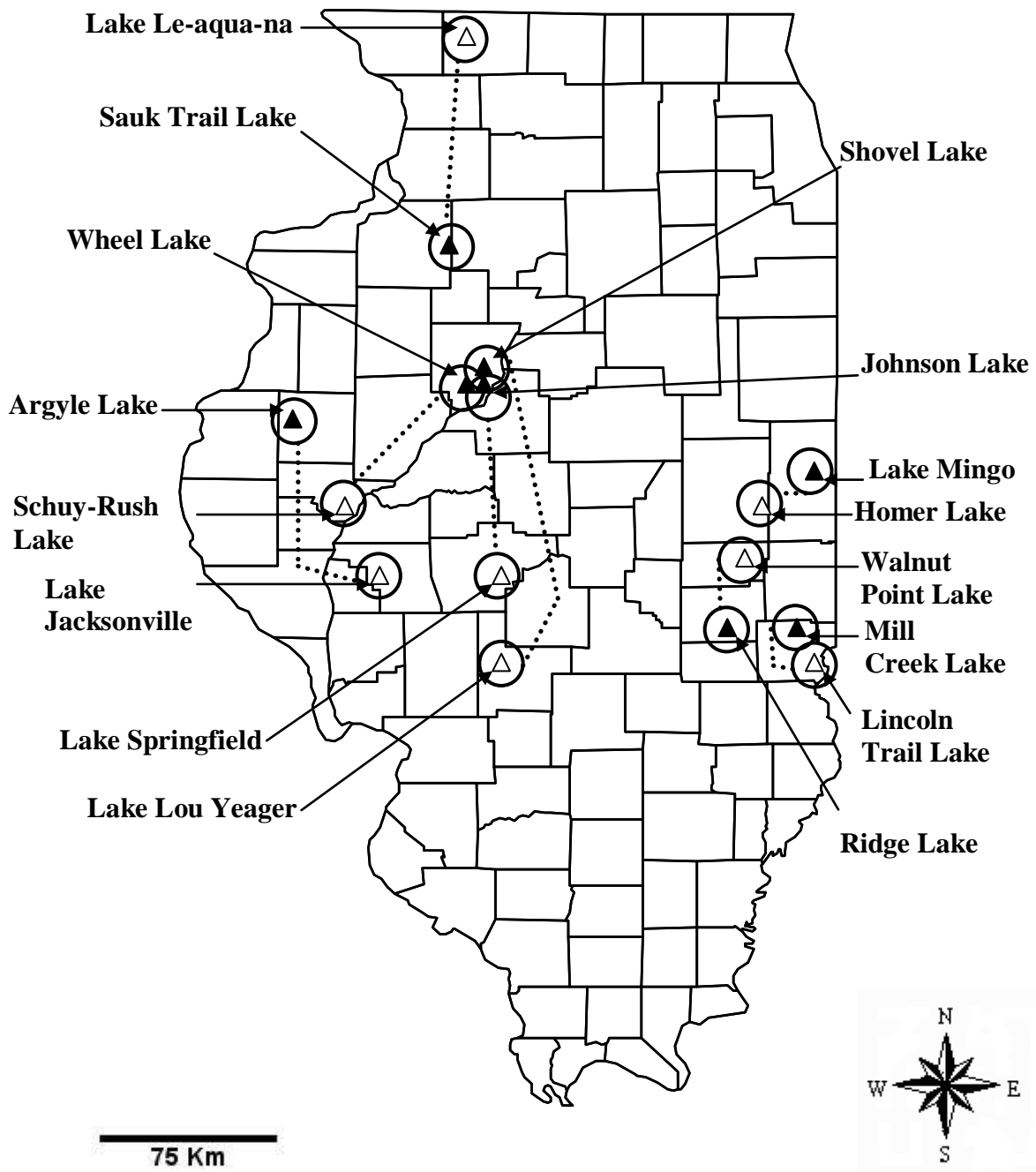


Figure 3.1. Locations of 16 spatially paired Illinois lakes used to evaluate effects of muskellunge (*Esox masquinongy*) introduction on population characteristics of resident fishes. Filled symbols were lakes stocked with muskellunge whereas open symbols were controls. Circles connected by dashed lines indicate specific lake pairings.

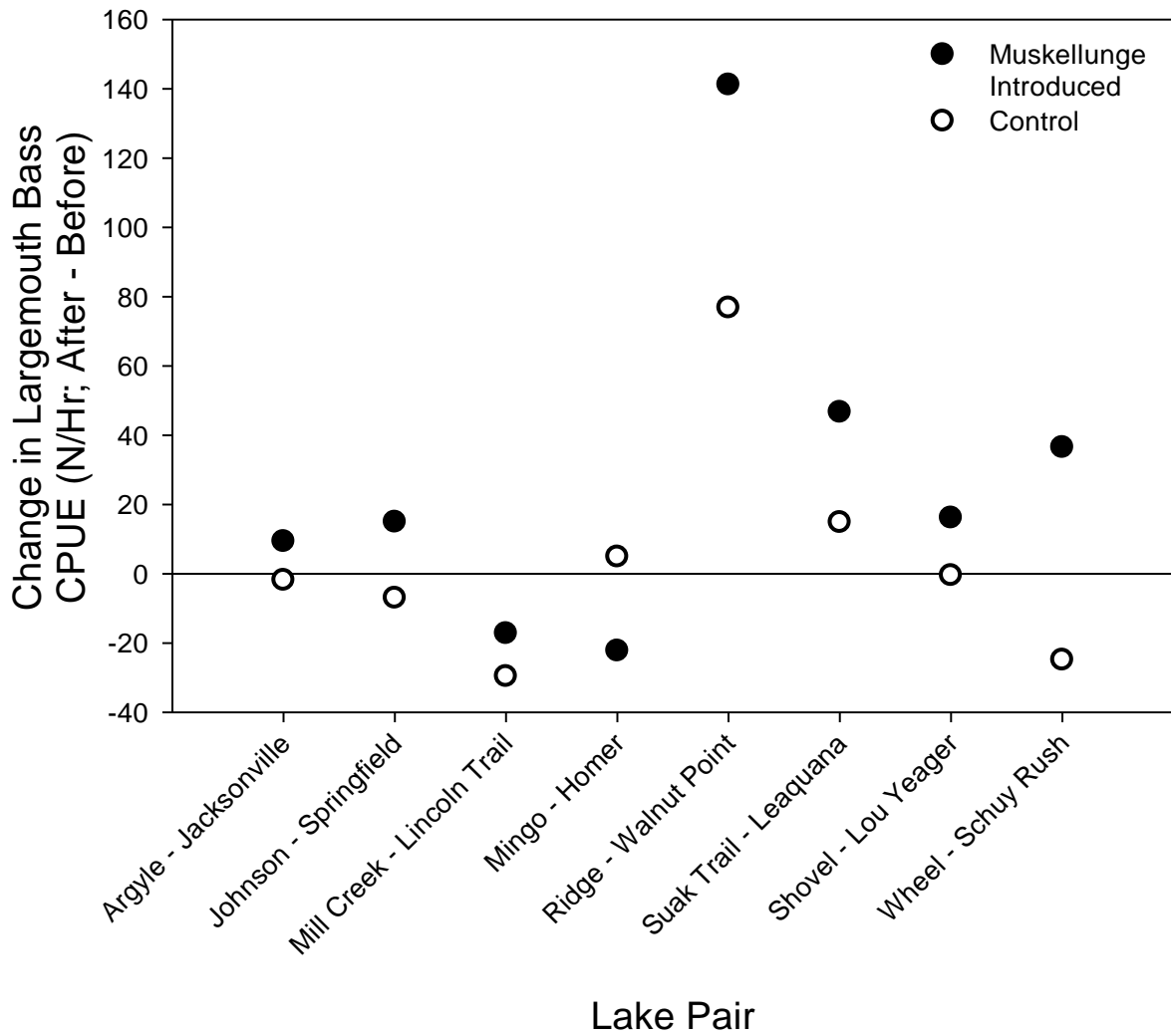


Figure 3.2. Change (after – before) in number of largemouth bass (*Micropterus salmoides*) collected per hour during standardized fall electrofishing sampling in Illinois lakes receiving muskellunge (*Esox masquinongy*) introductions (N = 8) and their spatially paired control lakes (N = 8) after muskellunge introduction.

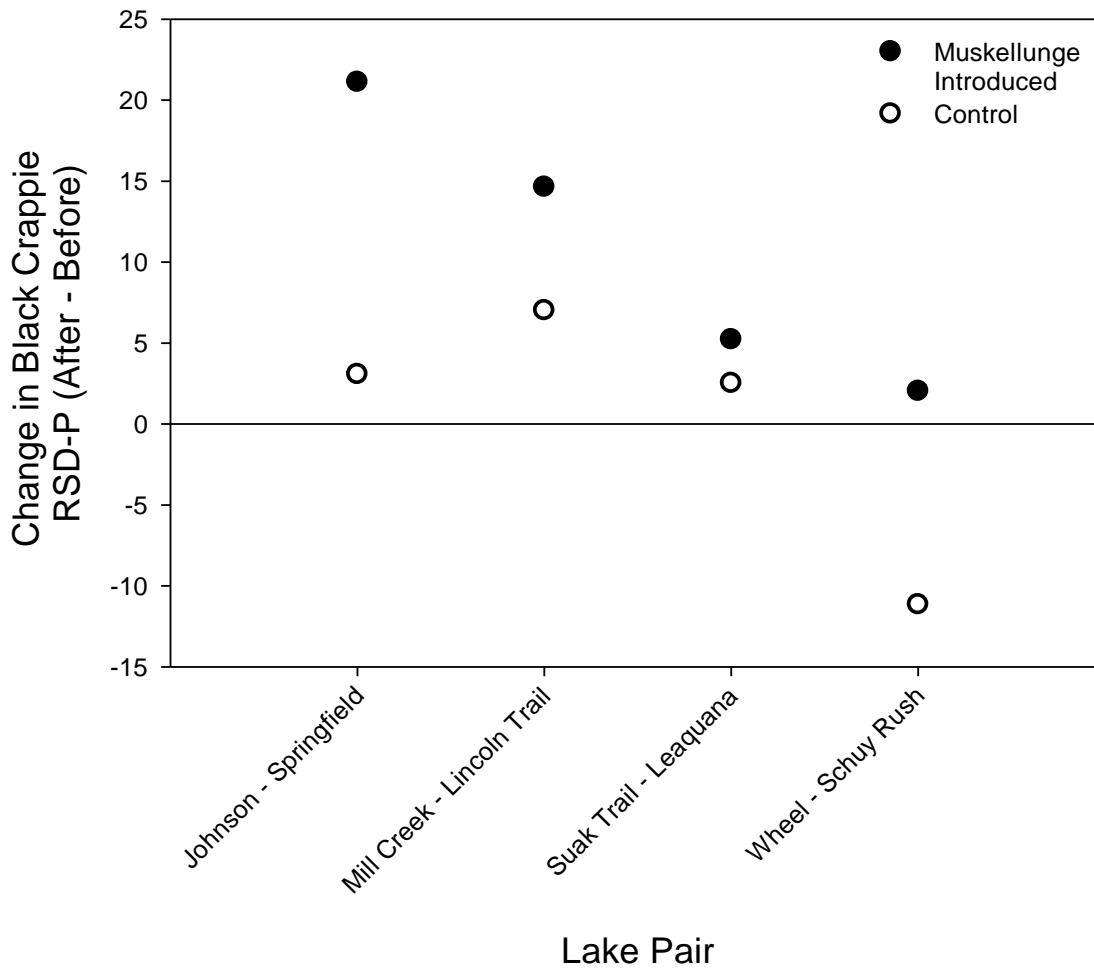


Figure 3.3. Change (after – before) in relative size distribution of preferred length black crappie (*Pomoxis nigromaculatus*) collected during standardized fall electrofishing sampling in Illinois lakes receiving muskellunge (*Esox masquinongy*) introductions (N = 4) and their spatially paired control lakes (N = 4) after muskellunge introduction.

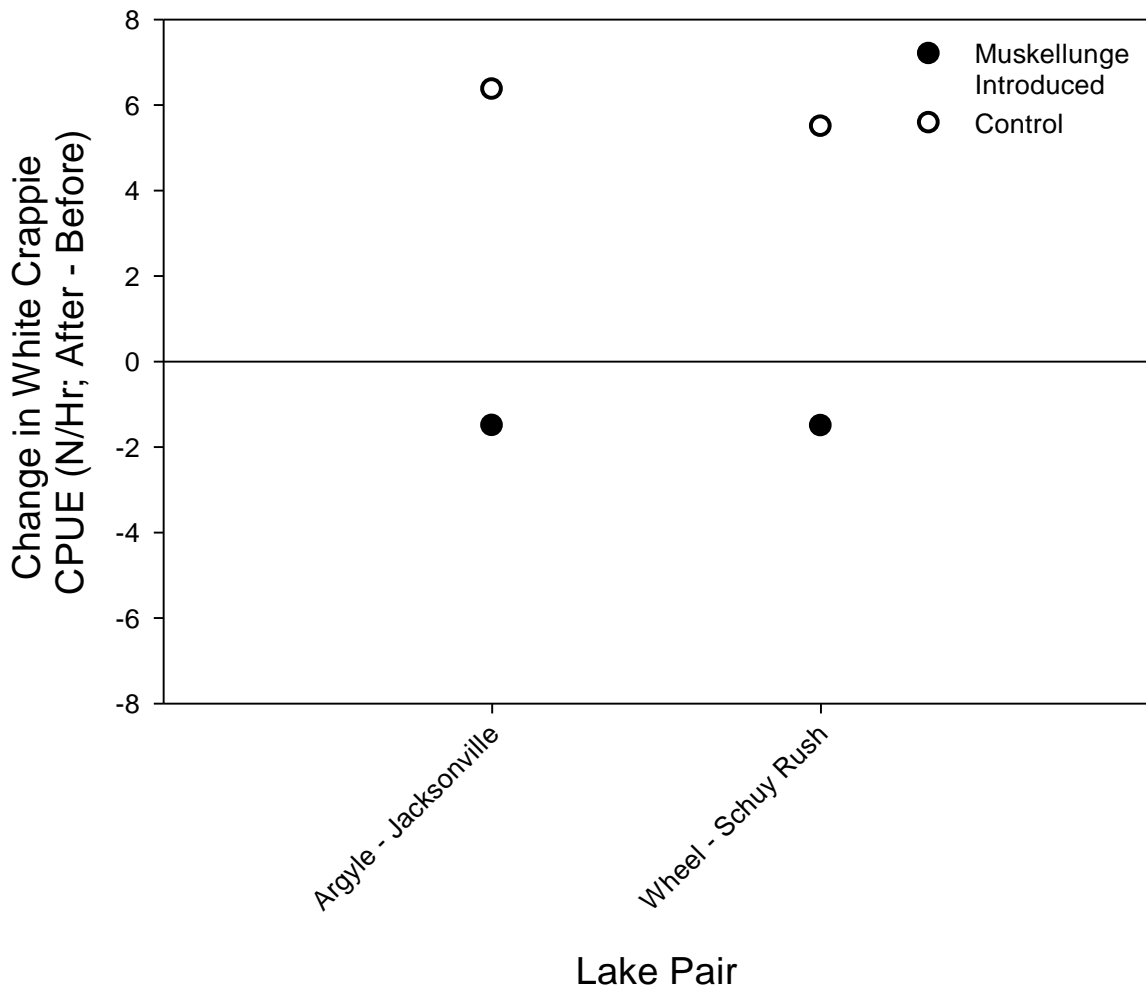


Figure 3.4. Change (after – before) in number of white crappie (*Pomoxis annularis*) collected per hour during standardized fall electrofishing surveys in Illinois lakes receiving muskellunge (*Esox masquinongy*) introductions (N = 2) and their spatially paired control lakes (N = 2) after muskellunge introduction.

CHAPTER 4: EFFECTS OF COARSE WOODY HABITAT COMPLEXITY AND SPECIES SPECIFIC BEHAVIORS ON PISCIVORE-PREY INTERACTIONS OF FOUR FRESHWATER FISH SPECIES

ABSTRACT

Prey refuges represent an important mechanism by which habitat structure affects ecological communities. In freshwater fish communities, most research has focused on aquatic vegetation and neglected alternative habitats. I tested for the interactions between predator foraging modes of two common littoral piscivores (muskellunge *Esox masquinongy* and largemouth bass *Micropterus salmoides*), and anti-predator behavior of two common prey species (golden shiner *Notemigonus crysoleucas* and bluegill *Lepomis macrochirus* across a gradient of coarse woody habitat complexity in a mesocosm setting. I hypothesized that experiments using a habitat generalist (largemouth bass) and behaviorally flexible prey (bluegill) would show the strongest refuging effect of coarse woody habitat. Piscivore-prey interactions were observed in laboratory pools with coniferous deadfalls. A refuging effect of coarse wood was not supported under my experimental conditions. Golden shiner experienced an increase in mortality rate with increasing coarse wood complexity when preyed upon by largemouth bass. Both prey species reduced activity rates with increasing complexity, but exhibited differing patterns for shoal size, number of isolated individuals, and proximity to piscivores that may explain differences in vulnerability across the habitat gradient. Increasing CWH complexity was associated with changes in largemouth bass behavior including reductions in activity rates and reduced capture efficiency at intermediate complexities. Habitat complexity did not strongly affect foraging success or behavior of muskellunge. My results reinforce the importance of

species-specific behavioral traits in determining influences of physical habitat on piscivore-prey relationships in freshwater fish communities.

INTRODUCTION

Refuge habitats are a well-established mechanism known to affect the strength and dynamics of predation in natural communities. These habitats are either inaccessible to predators or otherwise reduce predation risk relative to surrounding habitats (Sih 1987). Depending upon specific behaviors, refuges can cause both stabilizing and destabilizing effects on predator-prey dynamics and therefore are important in understanding population dynamics (Krivan 1998). The ability of refuge habitats to alter the ecological dynamics of predator-prey interactions is a major mechanism by which habitat structure can influence natural communities. Delineating the habitats that serve as refuges and the species that are able to use them is important to understand the role of physical habitat in natural populations.

In lentic freshwater environments, complex structural habitat in the littoral zone serves as an important refuge for many species of small fish and invertebrates (reviewed by Smokorowski et al. 2007). These studies have focused mainly on aquatic vegetation that at high densities has been shown to reduce predator foraging success (e.g. Savino and Stein 1982; Goetceitas and Colgan 1989; Swisher et al. 1998). Although high-density submerged vegetation can serve as a refuge from predation for small freshwater fish, other common littoral habitats have received less attention (Mallory et al 2000; Sass et al. 2006a), but comprise a diverse group of natural and artificial structures.

Several properties of coarse woody habitat (CWH) including potentially large size, complex branching, temporal stability, and a high potential density make it a likely candidate as

an important refuge habitat (Guyette and Cole 1999; Christensen et al. 1996; Mallory et al. 2000; Newbrey et al. 2005). In addition, aquatic vegetation is unable to grow in some lake ecosystems due to nutrient or light limitation, inappropriate substrates or steepness of shorelines, which may further increase the importance of CWH in some ecosystems. Field patterns have shown that use of CWH by several common temperate freshwater piscivore and prey fishes increases with branching complexity suggesting increased refuge for prey and subsequent attraction of predators (Newbrey et al. 2005; Sass et al. 2011). Recent work investigating the role of CWH as a driver of prey fish population dynamics has however been equivocal. Coarse wood removal from a northern Wisconsin lake was followed by an abrupt decline in prey fish (yellow perch; *Perca flavescens*) abundance due to increased largemouth bass predation and loss of spawning habitat directly implicating this habitat as a refuge from predation (Sass et al. 2006a; Helmus and Sass 2008). In contrast, a recent study focusing on responses of prey fish (bluegill; *Lepomis macrochirus*) to woody habitat addition found no effects on prey fish population dynamics (Sass et al. 2011). Brush addition in small ponds increased the over-winter survival of small age-0 largemouth bass (Miranda et al 1994). Although some previous studies suggest a role of CWH in affecting prey fish survival, mechanistic understanding has been difficult due to equivocal results and the fact that CWH can support higher densities of macroinvertebrates than adjacent sediments (Smokorowski et al. 2006) and is positively correlated with fish growth rates (Schindler et al. 2000) that may increase fish survival (Houde 1997). The observed effects of increased food availability and potential effects on survival are confounded with potential refuge from predation and the interactions between these factors. Furthermore, it is unclear whether equivocal results from wood removal and wood addition experiments represent differences in traits of the prey species involved or a poorly understood form of ecological hysteresis. A test of

the refuge value in a controlled setting is needed to explicitly assess the ability of CWH to affect piscivore success in capturing prey.

Responses of predators and prey to habitat change are often species specific (Savino and Stein 1989a; Christensen and Persson 1993; Eklöv and Diehl 1994; Greenberg et al 1995; Flynn and Ritz 1999). The ability of prey species to use potential refuge habitat is dependent on traits of species, which may interact with changes in habitat in complex ways (Michel and Adams 2009). For example, ambush predators may not be as sensitive to the presence of complex structure as more active cruising/lunging predators (Savino and Stein 1989; Eklöv and VanKooten 2001). Furthermore, behaviorally inflexible prey that rely on swarming or shoaling as a defense may be unaffected or suffer increased mortality in the presence of more complex structure (Savino and Stein 1989; Flynn and Ritz 1999; Laurel and Brown 2006). Information on how species with differing foraging modes and anti-predator behaviors may interact with refuge habitat is needed to gain a more holistic understanding of the influence on predator-prey interactions.

I tested for the interactions of four freshwater fish species (two piscivores and two prey) with increasing complexity of CWH to examine the role on piscivore-prey interactions. Two common freshwater piscivores, the largemouth bass (*Micropterus salmoides*) and the muskellunge (*Esox masquinongy*), and two common prey species, the golden shiner (*Notemigonus crysoleucas*) and bluegill (*Lepomis macrochirus*), were chosen based on their mutual coexistence in many Midwestern and northern lake ecosystems in North America and their contrasting predatory and anti-predatory behaviors. Largemouth bass rely predominantly on a cruising attack strategy in relatively open habitats and switch to a sit-and wait or ambush strategy with high habitat complexity (Savino and Stein 1982, Ahrenstorff et al. 2009). The

body form of the largemouth bass is characteristic of a habitat and feeding generalist (Webb 1984). In contrast, muskellunge are obligate ambush piscivores that maintain a sit-and wait strategy regardless of habitat context (Eklöv 1992; Savino and Stein 1989a). Bluegill possess a laterally compressed body and long pectoral fins characteristic of adaptation to maneuvering in and around objects (Webb 1986). In addition, bluegill display an adaptive shift in behavior with changing habitat complexity from forming loose shoals at low habitat complexity to concentrating within high complexity habitat when available (Savino and Stein 1989b). Golden shiner are a common lentic prey fish known to inhabit littoral and pelagic areas spending the majority of its time shoaling regardless of the surrounding habitat (Faber 1980). The cyprinid body form of golden shiners is more generalized and less adapted to maneuvering in and around objects as compared to the bluegill (Webb 1984).

Given the contrasting morphologies and behaviors among the species, I hypothesized that if CWH functions as an effective refuge from predation, then I would expect the combination of a generalist piscivore (largemouth bass) and laterally compressed maneuvering prey species (bluegill) most likely to show a strong refuge effect. I further hypothesized that if species-specific behaviors are important in determining the refuge value of CWH, then combinations of both generalist piscivores with swarming/shoaling prey (golden shiner) and ambush piscivores (muskellunge) with either prey species would be less likely to result in decreased foraging success and increased prey survival with increasing habitat complexity. My objectives were to examine the piscivore-prey interactions of species with contrasting predatory styles and anti-predatory behavior to test for the contexts under which CWH may be considered a predation refuge. I tested for the effects of CWH complexity on specific predatory and anti-predatory behaviors known to influence piscivore foraging success and prey vulnerability. In this way, I

tested for potential mechanistic explanations for any effects of CWH complexity on the outcomes of piscivore-prey interactions among these species in my experimental unit.

MATERIALS AND METHODS

Fish Collection and Care

Largemouth bass (N = 65; MeanTL \pm SE = 122 \pm 15 mm) and bluegill sunfish (N = 2,356; MeanTL \pm SE = 45 \pm 6 mm) were collected from local lake populations via seining and electrofishing. Muskellunge (N = 76; MeanTL \pm SE = 170 \pm 18 mm) were obtained from the Jake Wolfe Memorial Fish Hatchery, Illinois Department of Natural Resources, Manito, Illinois. Golden shiners (N = 2,531; MeanTL \pm SE = 51 \pm 7 mm) were obtained from local bait dealers. Piscivore species were held separately in two identical fiberglass rectangular tanks (2.13m L X 0.61m W X 0.56m D; 530 L total volume; Living Stream System; Frigid Units Inc., Toledo, OH), while prey species were also held separately, but spread among four identical square fiberglass tanks (1.1 m W X 0.67m D; 550 L total volume). All tanks were fitted with plastic mesh covers, a self-contained charcoal recirculating filtration system, and continuous aeration. Piscivores were maintained by feeding them fathead minnows (*Pimephales promelas*) obtained from local bait dealers, while prey fish were maintained on a diet of commercial fish food (Tetrafin flakes[®]). In order to expose naïve prey to predation, a single muskellunge and largemouth bass were held in each prey holding tank before and during the experiment. In this way, I sought to minimize any differences in experience with piscivores between prey species. Only healthy individuals, with no visible disease or malformations, and observed to have normal swimming and feeding behavior were used in the experiment.

Habitat Treatments

In order to create natural CWH treatments, I selected three naturally fallen red pine (*Pinus resinosa*) logs from the forest floor surrounding the Kaskaskia Biological station. Complexity of deadfalls was assessed using an adaptation of the qualitative system of Mallory et al. (2000) as modified by Wagner and Wahl (2007). The scoring system ranked deadfalls from 0 – 5 with 0 representing the least and 5 the most complex (Table 4.1). Individual branches were sought which represented scores of 0, 3, and 5 hereafter referred to as low, moderate, and high complexity. In addition to choice based on complexity, each log was selected to be roughly 15 cm in diameter and 1 – 1.5 m in total length in order to standardize as much as possible for these additional structural properties (see Table 4.2 for physical habitat dimensions). Target diameter was based on average measurements of CWH from published field surveys, and previous experiments evaluating refuge value of CWH (Everett and Ruiz 1993; Mallory et al. 2000; Newbrey et al. 2006); however, field estimates of median lengths of CWH were slightly greater (range 2.5-4.5m) than the structure used in my study. I were constrained by the dimensions of the experimental arena and therefore used the longest pieces of CWH that would fit within the pools. Each log was secured to a standard masonry brick (9.5 X 6.4 X 20.3 cm; 1.3 kg) with small diameter twine in order to sink the structure and hold it in place. A brick was also placed in the tank center of the no habitat control to control for any effect of the presence of the brick on results.

Experimental Setup and Protocol

Treatments consisting of individual piscivores (largemouth bass or muskellunge) crossed with each prey species (ten individual prey of either golden shiners or bluegill) were replicated (N = 11) across 3 levels of CWH complexity and a no habitat control (sixteen total treatment

combinations) in circular laboratory pools (Figure 4.1). Prey densities (3.9 per meter squared) were selected to lie within the range found in littoral zones of natural systems (range 1-12 per meter squared; Wahl and Stein 1988). Pools were 1.8 m diameter tanks with a white bottom and sides and filled to a depth of 0.67 m with aerated filtered water (1600 L total volume). Piscivore-prey interactions were videotaped under controlled indoor conditions in the wet laboratory at the Kaskaskia Biological Station, INHS, Sullivan, IL, USA. Water temperature was held between 16 and 18 C, and photoperiod was set at 12 h light: 12 h dark.

All experiments were conducted in one of four identical tanks described previously. Prior to beginning trials, a randomization scheme was generated using statistical software (PROC PLAN; SAS[®] Version 8) to ensure that each treatment combination was randomly assigned. Each 16-treatment replicate was divided into groups of 4 for each individual trial. Each complete replicate trial was conducted over a one-week period and consisted of four trials (four tanks per trial and 16 total experiments per replicate). Woody habitat was reassigned to a new tank after each trial. Preliminary trials with a subset of treatments indicated no effect of trial (day) on results so I considered the completion of each set of 4 trials as a single block. Week was used as a blocking factor in final analyses to control for any long term temporal variation within the experiment.

Piscivores were acclimated to prey free tanks for 24 hrs prior to the start of a trial to reduce the effect of handling stress and to standardize hunger levels. Prey fish were introduced 10 minutes prior to the start of a trial and were spatially separated from the piscivores in a clear plastic holding chamber that allowed exchange of both visual and chemosensory piscivore cues to reach the prey and prevented any bias due to prey being naïve of piscivore presence. Trials were begun by gently releasing prey from the holding chamber in the area of the tank farthest

from the piscivore. To minimize disturbance and assist with behavioral measurements, a suspended opaque curtain surrounded all four tanks and the experimental trials were recorded on videocassette by suspending a camera (AUC-75, Atlantis Camera, Englewood, New Jersey, USA) 2 m above each tank with a complete view of the tank circumference (see Cooke and Bunt 2004 for a description). Piscivore behaviors were recorded for the first hour of the experiment (Savino and Stein 1982; Savino and Stein 1989a). After the completion of behavioral recordings, each experiment was allowed to run for a total of 24 hours upon which all piscivores were removed and all surviving prey fish counted.

In order to avoid confounding prey size preferences with effects of habitat complexity, I scaled prey sizes to published optimal sizes for each piscivore. Bluegills were 25-32% of largemouth total length (TL) and 20-25% of muskellunge TL and (Hoyle and Keast 1987). golden shiners were 20-30% of largemouth bass TL and 25-30% of muskellunge (Gillen et al. 1981; Reid et al. 1999; Winemiller and Taylor 1987). In this way, I minimized the influence of piscivore body size and size selection on comparisons of survival rates between prey species. Individuals of prey species were used only once over the course of the study. The large number of treatments and replicates required multiple uses of piscivores. To avoid any bias, piscivores with the same level of experience were used in each block of the experiment. After completing a trial, previously used fish were segregated to another holding tank (identical to the original) until all fish had been used once (blocks 1-9). Randomly selected subsets of piscivores were then reused to complete the last two blocks of the experiment to control for variation due to learning.

Behavioral Measurements

Quantified behaviors of piscivores included measures of frequency of occurrence and duration of several key components of the predation sequence including searching/swimming, follows, pursuits, attacks, and captures (Savino and Stein 1982). An index of piscivore activity rates was calculated as the sum of time spent swimming, pursuing, attacking and capturing prey over 1hr observations. In addition, I recorded distances of all strikes and captures and calculated strike and capture efficiencies as the ratio of strikes to follows and captures to strikes, respectively. Recordings were digitally recorded using a video capture device and associated software (Grabbee X 2.0; Videohome Technology Corporation; Taipei, Taiwan) and behaviors were quantified using the professional version of the BEAST software package (Windward Technology; Kaneohe, Hawaii). Piscivore strike distances were calculated with ImageJ[®] software (Rasband 2011) from still images using the single camera method (Laurel et al. 2005), which uses the relative distance between an individual fishes' 2-dimensional (x,y) position and its shadow on the tank bottom to calculate its height in the water column (z).

Behaviors of prey were collected by sampling 18 evenly distributed points (every 200 s) throughout each one-hour video segment. Measures of prey behavior included the number of independent shoals, the number of isolated individual prey, the average distance between the piscivore and the nearest prey fish, and a measure of prey activity. A shoal was considered any group of 2 or more individuals moving in relative unison around the tank or if stationary maintaining a linear distance of less than 3 body lengths from any other individual. An independent school was any group of two or more individuals moving independently from any other group and at least 3 body lengths apart. The criterion of three body lengths was chosen based on previous research, which showed that nearest neighbor distances between shoaling

individuals averages around 0.7 body lengths and that fish outside this distance are not likely to be actively shoaling (Pitcher 1983). Randomly following two prey fish from each point sampling time and recording the proportion of a 60 second period each individual spent swimming indexed prey activity. If non-shoaling individuals were present, one of the two observations included a non-shoaling individual in order to estimate an average activity rate for the entire prey assemblage. Distances between piscivores and the nearest prey were calculated using the methods outlined previously for piscivore strike distances. Means were calculated from all 18 measurements for each variable across each 1-hour segment to produce a single value for each replicate.

Statistical analyses

All analyses were performed using a linear mixed model incorporating fixed effects of prey species, CWH complexity, interactions between these factors, and a random blocking factor (week). Data for each piscivore species were analyzed separately to avoid confounding piscivore energetic requirements with responses to habitat complexity. All errors were tested for assumptions of normality using a Shapiro-Wilk's test and homogenous variances using Levene's test. In cases where model residuals did not conform to a normal distribution, a square root transformation was used (proportion data). When significant main effects were found for the fixed factor of CWH complexity *post hoc* comparisons between levels were assessed using Tukey tests. To test for potential CWH by prey species interactions, pre-planned linear contrasts were used to make pairwise comparisons within each level of CWH between prey species. When prey species by CWH interactions were significant, comparisons between levels of CWH within prey species were made using linear contrasts using a Tukey modification to control family-wise

error rates. All analyses were performed using the SAS[®] system version 8 and all tests were considered significant at an alpha of 0.05.

RESULTS

Piscivore Foraging Success and Behavior

The number of follows by largemouth bass was significantly affected by an interaction between prey species and CWH complexity ($df = 3, 79; F = 3.40; P = 0.02$). Bluegills were followed more at no ($P < 0.01$) and low ($P < 0.01$) CWH complexity than golden shiners, whereas the two species experienced similar numbers of follows at moderate and high levels of CWH (all $P > 0.05$; Figure 4.2A). The interaction was driven by changes in the frequency with which largemouth bass followed bluegills, whereas follows of golden shiners was unchanged across CWH complexity (all $P > 0.05$). Largemouth bass followed significantly fewer bluegills at moderate CWH complexity than at zero or low complexity (all $P < 0.05$), while high CWH complexity was intermediate (Figure 2A). In contrast, the number of follows performed by muskellunge was not significantly affected by any of the measured factors (all $P > 0.05$; Figure 4.2B)).

The number of attacks by largemouth bass mirrored those for the number of captures over the same 1-hr period. The number of attacks was significantly affected by prey species ($df = 1, 79; F = 9.95; P < 0.01$). Across all levels of CWH, largemouth bass attacked golden shiner prey (Mean \pm SE = 8.37 ± 1.18) an average of 2.87 times more often than bluegills (Mean \pm SE = 2.99 ± 1.21 ; Linear contrast; all $P < 0.05$; Figure 4.2C). In contrast, the number of attacks performed by muskellunge was not affected by any of the measured factors (all $P > 0.20$; Figure 4.2D).

The number of prey captured by largemouth bass during 1-hr was significantly affected by prey species ($df = 1, 79; F = 21.28; P < 0.01$). Averaged across all CWH treatments, largemouth bass captured over three times more golden shiners (Mean \pm SE = 2.17 ± 0.24) than bluegills (Mean \pm SE = 0.71 ± 0.25) and this difference was significant at all levels of CWH (Linear contrasts; all $P < 0.05$; Figure 4.2E). In contrast, the number of prey captured by muskellunge during the 1-hr period was significantly affected by the main effect of CWH complexity ($df = 3, 79; F = 3.39; P < 0.03$), but not the interaction with prey species. Muskellunge captured a greater number of prey fish at low CWH complexity as compared to the other levels or the structure free treatments (Tukey tests; all $P < 0.03$). The number of bluegills and golden shiners consumed by muskellunge did not differ at any level of CWH (all $P > 0.12$; Figure 4.2F).

The number of prey captured over 24-hr by largemouth bass was similarly affected by prey species ($df = 1, 79; F = 10.87; P < 0.01$); however, over this longer time period there was also a significant interaction between prey species and CWH complexity ($df = 3, 79; F = 3.10; P = 0.03$). The number of golden shiners captured was similar to the number of bluegills captured in the zero complexity treatment (Linear Contrast; $P = 0.63$); however, the number of shiners captured was significantly higher at all of the treatments containing CWH (Linear Contrasts; all $P < 0.05$; Figure 4.2G). The number of golden shiner prey consumed by largemouth bass increased with increasing CWH complexity, while the number of bluegills consumed was unchanged across the habitat complexity gradient. The number of golden shiners captured was significantly greater (approximately 35% higher) at the highest level of CWH complexity than in the zero structure treatment (Tukey; $P < 0.02$); but no significant differences existed between CWH levels for bluegill prey (Tukey tests, all $P > 0.20$). For muskellunge, the number of prey

captured was significantly affected only by the main effect of prey species ($df = 1, 79; F = 21.74; P < 0.01$). Muskellunge captured significantly higher numbers of golden shiners (1.8 times more) than bluegills across all habitat complexity treatments (all $P < 0.04$; Figure 4.2H) over the 24-hr period.

The proportion of largemouth bass follows resulting in attacks on prey fish (square root transformed) was significantly affected by prey species ($df = 1, 79; F = 26.15; P < 0.01$; Figure 4.3A). Across all levels of CWH, the proportion of largemouth bass follows resulting in an attack was more than twice as high for golden shiner prey (Mean \pm SE = 0.37 ± 0.03) than for bluegills (Mean \pm SE = 0.18 ± 0.03) that was significant at all levels of CWH (Linear contrasts; all $P < 0.04$) with the exception of the moderate complexity treatment where the two species did not differ ($P = 0.29$; Figure 4.3A). Similarly, the proportion of muskellunge follows that resulted in strikes (square root transformed) was affected by prey species ($df = 1, 79; F = 4.01; P = 0.05$). For muskellunge, the difference between prey species was driven by a significant difference in the number of follows resulting in attacks for golden shiners than for bluegills in the no structure control (Linear Contrast; $P < 0.05$; Figure 4.3B) with no significant differences between prey species in all treatments containing CWH (Linear contrasts all $P > 0.20$).

The rate at which largemouth bass strikes resulted in captures (capture efficiency; square root transformed) was significantly affected by the main effects of prey species ($df = 1, 79; F = 4.27; P = 0.04$) and CWH complexity ($df = 3, 79; F = 4.03; P = 0.01$). Across all levels of CWH, largemouth bass capture efficiency was 17% greater for golden shiners (untransformed mean \pm SE = 0.47) than for bluegills (untransformed mean \pm SE = 0.30). The effect of prey species was due to the cumulative effects of subtle differences across CWH complexity as there were no significant differences between prey species within any level of CWH (all $P > 0.09$; Figure

4.3C). The proportion of largemouth bass strikes resulting in captures was significantly lower at moderate CWH complexity than at either zero or high complexity (Tukey tests; all $P < 0.05$) with low habitat complexity being intermediate. For muskellunge, the proportion of attacks that resulted in captures (square root transformed) was significantly affected by prey species ($df = 1, 79$ $F = 6.93$; $P = 0.01$), CWH complexity ($df = 3, 79$; $F = 3.00$; $P = 0.04$) and the interaction between these two factors ($df = 3, 79$; $F = 2.50$; $P = 0.05$). The proportion of muskellunge follows resulting in attacks was similar in the structure less and the moderate complexity treatment (Linear Contrasts; all $P > 0.24$), whereas a significantly higher proportion of attacks resulted in captures for golden shiners than for bluegills at low and high CWH complexity (Linear Contrasts; all $P < 0.05$; Figure 4.3D). Changes existed in the proportion of muskellunge strikes resulting in captures for golden shiners whereas there were no significant changes across CWH complexities for bluegills (Tukey tests; all $P > 0.09$). When preying on golden shiners, a greater proportion of muskellunge attacks resulted in more captures at low and high CWH complexity than in the structure less environment (all $P < 0.08$), whereas moderate CWH complexity was intermediate (Figure 4.3D).

Largemouth bass activity rates were significantly affected by the main effects of prey species ($df = 1, 79$; $F = 11.29$; $P < 0.01$) and CWH complexity ($df = 3, 79$; $F = 3.13$; $P = 0.03$) as well as the interaction between these two factors ($df = 3, 79$; $F = 3.65$; $P = 0.02$). The number of seconds largemouth bass spent active was significantly higher for bluegill than golden shiners at zero and low, CWH complexity (Linear Contrasts; all $P < 0.01$) whereas there was no difference between prey species at moderate or high CWH complexity (all $P > 0.10$; Figure 4.4A). There were changes in largemouth bass activity levels with bluegills across CWH complexities that were not present across golden shiner treatments (Figure 4.4A). With bluegill prey largemouth

bass activity was significantly lower at moderate and high CWH complexities as compared to the zero structure treatment (Tukey tests; all $P < 0.04$) while the low complexity treatment was intermediate. There were however no significant differences in largemouth bass activity levels across CWH complexities in treatments with golden shiners (Figure 4.4A). In contrast to largemouth bass, muskellunge activity levels were not affected by any of the measured factors (all $P > 0.47$; Figure 4.4B).

Largemouth bass strike distance was not affected by prey species, CWH complexity, or their interaction (all $P > 0.14$; Table 4.4). Similarly muskellunge strike distance was not affected by any of the measured factors (all $P > 0.10$; Table 4.4).

Prey Behavior

With largemouth bass, the average number of independent prey shoals was significantly affected by the main effect of prey species ($df = 1, 79$; $F = 22.39$; $P < 0.01$) and the interaction between prey species and CWH complexity ($df = 3, 79$; $F = 4.48$; $P < 0.01$). Bluegills formed a significantly greater number of independent shoals than golden shiners across zero, low, and moderate CWH complexities (Linear Contrasts; all $P < 0.01$) while the two species showed no significant differences at the highest level ($P = 0.44$; Table 4.3). The interaction between species and CWH complexity was driven by opposing patterns of response in shoaling behavior between the two prey species. The number of independent bluegill shoals decreased with increasing CWH complexity with the number of shoals being significantly lower at moderate and high CWH complexity than either zero or low complexities (Tukey tests; all $P < 0.03$). In contrast, the number of independent golden shiner shoals increased at the highest level of CWH complexity being significantly greater than all of the other treatments (Tukey tests; all $P < 0.05$). In contrast,

for muskellunge the number of prey shoals was significantly affected by prey species ($df = 1, 79$; $F = 13.79$; $P < 0.01$); but not by CWH or their interaction. Across all structural complexity treatments bluegills averaged a slightly greater number of independent shoals than golden shiners (Table 4.3).

The number of isolated individual prey with largemouth bass mirrored those for the numbers of independent shoals being significantly affected by the main effect of prey species ($df = 1, 79$; $F = 8.71$; $P < 0.01$) and the interaction between prey species and CWH complexity ($df = 3, 79$; $F = 4.07$; $P = 0.01$). There were significantly greater numbers of non-shoaling bluegills than golden shiners at zero and low CWH complexity (all $P < 0.04$) whereas the two prey species did not differ at moderate and high CWH complexity levels (all $P > 0.4$; Table 4.3). There were fewer non-shoaling bluegills at moderate and high CWH complexity than at in either zero or low CWH complexity (Tukey test; all $P < 0.01$). Golden shiners exhibited an increase in the number of isolated individuals at moderate and high CWH complexity relative to zero or low complexity treatments (Tukey test; all $P < 0.02$). The number of isolated individual prey with muskellunge was significantly affected by prey species ($df = 1, 79$; $F = 16.59$; $P < 0.01$). Across all CWH complexities the number of isolated individual bluegills was greater (7 times) than the number of golden shiners (Table 4.3). The difference between prey species was consistent across habitat context with significantly more isolated bluegills than golden shiners in each level (Linear contrasts; all $P < 0.03$).

With largemouth bass prey activity (square root transformed) was significantly affected by the main effect of CWH complexity ($df = 3, 79$; $F = 6.75$; $P = < 0.01$). No significant differences existed in activity rates between prey species in any of the levels of CWH complexity. Averaged across prey species activity rates decreased at high CWH complexity relative to the

zero, low and moderate complexity treatments (Tukey tests; all $P < 0.03$; Table 4.3). With muskellunge there were no significant effects on prey activity (square root transformed; all $P > 0.7$; Table 4.3).

The average distance between largemouth bass and the nearest prey fish was significantly affected by an interaction between prey species and CWH complexity ($df = 3, 79$; $F = 2.76$; $P < 0.05$). Bluegills increased their distance from the piscivore with increasing CWH complexity while the distance between piscivores and golden shiners decreased. Golden shiners maintained a greater distance from piscivores than bluegills in the zero complexity treatment (Linear contrast; $P < 0.03$) while the two species did not differ at low and moderate complexity treatments (Linear contrasts; all $P > 0.26$). Furthermore bluegills maintained a greater distance from piscivores than golden shiners in the high CWH complexity treatment (Linear contrast; $P < 0.04$; Table 4.4). The average distance between largemouth bass and the nearest bluegill prey was significantly greater in the high CWH complexity treatment than all other levels of habitat complexity (Tukey test; $P < 0.03$). In contrast the average distance between largemouth bass and the nearest golden shiner prey was significantly shorter at high CWH complexity than either zero or low complexity (Tukey test; $P < 0.05$) while moderate complexity was intermediate. When muskellunge were the piscivore there was a significant effect of prey species ($df = 1, 79$; $F = 9.86$; $P < 0.01$) on the mean distance between piscivores and the nearest prey fish. Golden shiners maintained a greater distance from piscivores (1.2 times larger) than bluegills in all habitat treatments (Linear contrasts; all $P < 0.04$) with the exception of moderate CWH complexity (Linear contrast; $P > 0.20$; Table 4.4).

DISCUSSION

My results did not support a role of coarse woody habitat in the form of single coniferous deadfalls as a predation refuge for any of the species examined, thus rejecting the hypothesis that largemouth bass combined with bluegill prey would yield a refuging effect with increasing habitat complexity. In contrast, I show that golden shiners and bluegills being preyed upon by largemouth bass experienced similar rates of daily survival in a structure free environment whereas golden shiner survival rates declined with increases in CWH complexity. Golden shiners and bluegills exhibited different shoaling behavior, and proximity to piscivores as CWH complexity increased. Shoaling behavior is a known anti-predatory strategy thought to reduce predation risk in several ways including predator confusion, increased diligence, lowered encounter probability with predators, and lower per capita mortality risk during an attack (Milinski and Heller 1978; Turner and Pitcher 1986; Lima 1995). Many studies with shoaling fish have shown that predator success is increased when feeding on smaller shoals or isolated individuals (Milinski 1984; Allan and Pitcher 1986; Landeau and Terborgh 1986). Furthermore predator and prey proximity can be expected to be related to predation risk in aquatic predator-prey interactions as most piscivores attack from short distances (0.25-0.5 m; Savino and Stein 1989) and rely on visual contact with prey. Anti-predator behaviors of prey fish often include moving quickly out of strike range (Lima and Dill 1990). Consistent with these findings previous studies have documented that attacked prey fish are often significantly closer to piscivores than those not attacked (Savino and Stein 1982; Savino and Stein 1989*a*). Based on these previous studies all of these changes in anti-predatory behavior would serve to increase vulnerability of golden shiners as CWH complexity increased but decrease vulnerability of bluegills. These behaviors may offer a mechanistic explanation for the observed differences

between golden shiner and bluegill daily survival when preyed upon by largemouth bass across the gradient of CWH complexity in my experimental arenas.

Previous studies have documented declines in shoal size with increasing habitat complexity for other obligate shoaling aquatic species and have speculated that complex structure may disrupt the ability of prey to maintain large shoals due to visual or physical barriers (Eklöv 1999, Flynn and Ritz 1999). For example, a study examining the mortality rates of mysids (*Paramesopodopsis rufa*) fed upon by a generalist predator (Australian salmon; *Arripis trutta*) and an ambush predator (big-bellied seahorse; *Hippocampus abdominalis*) found that increased seagrass complexity disrupted the coherence of mysid swarms resulting in an increase in the number of independent swarms (Flynn and Ritz 1999). Decreased coherence and shoal size lead to an increase in predation rates by Australian salmon. Combined with my study these results suggest that interactions with habitat complexity in obligate shoaling/swarming aquatic prey such as golden shiners and mysids may be a common emergent effect of local scale habitat complexity.

Differential behavioral responses of prey species in my experimental arenas to increasing habitat complexity may offer testable hypotheses to explain patterns of field abundances in lakes where bluegills and golden shiners coexist. Previous studies comparing competitive ability between bluegills and golden shiners have found similar competitive ability in unstructured environments whereas bluegills were favored in structured environments dominated by aquatic vegetation (Paszkowski 1986). Vulnerability to largemouth bass in my experimental arenas was equal in an open water habitat whereas golden shiners were significantly more vulnerable in the presence of habitat structure. Littoral zone habitat complexity may alter the direction of two major ecological forces (predation and competition) in the interaction between golden shiners

and bluegills in largemouth bass dominated lakes. In addition to competitive ability, differential effects of habitat on predation risk between these two species offers a testable hypothesis to explain why bluegills dominate in some lakes but coexist with large numbers of golden shiners in others (Hall et al. 1979).

Although I did not find an effect of CWH complexity on the total rate of prey capture by piscivores there were significant effects of CWH and prey species on largemouth bass behavior including the number of prey follows, efficiency of prey capture as well as activity rates. Largemouth bass capture efficiency was greater at high levels of CWH complexity as compared to low and moderate complexity levels for both prey species. Capture efficiency was also high in my structureless control treatment however piscivore activity and the frequency with which piscivores followed prey was also significantly higher in these treatments than treatments containing more complex CWH in treatments with bluegill prey. These increased activity rates in low complexity environments were not offset by any changes in the rate of prey capture. These results suggest that prey species and CWH complexity may affect piscivore energy balance and growth rates through shifts in fish behavior as the rate of energy return would be maximized at high levels of CWH either through increases in capture rates of schooling prey or through reduced activity rates when preying on more behaviorally flexible prey such as bluegills. Consistent with my results a recent tracking study across lakes of varying CWH abundance found a reduction in home range size, overall activity levels and increases in largemouth bass consumption rates in lakes with abundant CWH relative to those with lower abundances also suggesting an effect of CWH on largemouth bass energetics (Ahrenstorff et al. 2009). These findings are also in agreement with several recent field scale studies that documented declines in largemouth bass growth with decreasing CWH abundance. A positive relationship has been

observed between CWH abundance and size specific growth rates of largemouth bass (Schindler 2000). Declines in largemouth bass growth rates in a northern Wisconsin lake have been documented in response to a reduction in CWH abundance (Sass et al. 2006a). Collectively these results suggest that largemouth bass growth may be reduced in systems with low CWH abundances due to the effects of CWH on piscivore behavior and foraging efficiency and that these effects are also influenced by prey species traits.

My results for muskellunge support the findings of previous studies that have shown a lack of an effect of habitat complexity on sit-and-wait predators (Tomcko et al 1984; James and Heck 1994; Eklöv and Diehl 1994; Flynn and Ritz 1999; Ostrand et al. 2004; Schultz and Kruschel 2010). Lack of sensitivity of muskellunge to habitat complexity is not surprising considering that the esocid body form is thought to have been largely selected for foraging in such complex habitats (Webb 1984). Furthermore muskellunge appeared to elicit fewer and weaker behavioral responses from prey compared to largemouth bass presumably due to differences in foraging mode. There was no effect of CWH on prey activity rates with muskellunge whereas prey decreased their activity rates across habitat complexity with largemouth bass. Muskellunge foraging efficiency was higher in the presence of CWH than in an open environment for golden shiner prey; except at moderate CWH complexities due to an increase in attack rate. Based on my findings I would predict that muskellunge may exhibit increased growth in the presence of CWH relative to open environments when soft rayed prey such as golden shiners are available as previous studies with esocids have found that laboratory patterns did scale up to affect growth in the field (Hart and Connellan 1984; Wahl and Stein 1988). Differences in vulnerability of bluegills and golden shiners to muskellunge have been noted between bluegills and golden shiners have been noted previously with higher vulnerability

of golden shiner prey as compared to bluegills (Weithman and Anderson 1977). Differences were mediated by lower capture efficiency for muskellunge when foraging on bluegill prey as compared to golden shiners. Collectively these results suggest a beneficial effect of CWH on muskellunge energetics however this effect may not be realized when soft rayed prey such as golden shiners are not available.

My finding of a lack of refuge effects of CWH for fish prey is in contrast to two previous studies that supported a role of CWH as a predation refuge. A simple log structure increased grass shrimp (*Palaemonetes pugio*) survivorship (Everett and Ruiz 1993). Overwinter survival of a smaller cohort (below 126mm) age-0 largemouth bass increased with surface area of brush coverage in small ponds suggesting refuge from predation (Miranda and Hubbard 1994). Discrepancies between these findings and ours are not readily explainable with the available data but may be due to several factors including differences in species specific behavior, water temperatures, refuge architecture (artificially assembled brush and simple logs vs deadfall trees). Other confounding factors could include interactions between habitat and fish size and prey availability. Predation in natural communities is often driven by many concurrent and interrelated factors. Future work will be required to identify the importance of species-specific behavior, refuge architecture, and interactions with biotic and abiotic variables in explaining discrepancies between studies.

Conclusions and Limitations

Past research of specific mechanisms by which habitat complexity interferes with piscivore foraging has identified the size of interstitial spaces (e.g. stem density, branching density), the coverage of habitat structure and the relative body sizes of predators (which may

amplify the effects of stem/branching density; Bartholomew et al. 2002) as important mechanisms affecting predator capture success. My results indicate that complex CWH in the form of single coniferous branches does not reduce foraging ability of piscivorous fishes across the species and size ranges examined in my experimental arenas. I cannot rule out the possibility that CWH may affect the foraging success of larger piscivores, or other species. In addition, larger CWH or more dense aggregations may affect piscivores foraging success by increasing visual barriers and or reducing sizes of interstitial spaces and require further research.

The woody structure I utilized was chosen to reflect reported dimensions (diameter, complexity, and areal density) found within the range of common structures in surveys of natural systems (Mallory et al. 2000; Newbrey et al. 2006). These studies suggest that highly complex CWH of larger dimensions and higher densities than those employed in my study are relatively rare in most natural systems. The majority of CWH in the littoral zone of an Ontario headwater lake was highly decayed with around 1% representing freshly deposited highly complex structure (Mallory et al. 2000). Furthermore the distribution of CWH in a northern Wisconsin lake was highly skewed toward single, short (2.5m), structurally simple pieces (Newbrey et al. 2006). I caution however that if such rare structures do indeed function as significant prey refuges then the loss of these larger pieces or denser aggregations of CWH may make many lakes exceptionally sensitive to the loss of these structures. Future research should focus on these potentially rare habitats to judge their ecological importance.

Another limitation of my study may be the unique histories of predator and prey source populations. Previous work has demonstrated that the ability of piscivorous predators to capture prey fish can be reduced in hatchery origin populations relative to wild fish (Savino et al. 1993). While the hatchery origin muskellunge used in our study had experience foraging on fish prey

(they were reared extensively in ponds with fathead minnows), they had less experience with spiny rayed prey fishes such as bluegills, which may complicate direct comparisons between predators and prey vulnerability in my study. Additionally, the wild bluegills collected for my experiment may have had greater experience with predators relative to the golden shiners acquired from a bait dealer. Prior studies suggest that exposing these naïve prey fish to predators prior to the experiment should have reduced these differences as it has been shown that prey fish rapidly acquire (less than 1 week or a single exposure) the ability to recognize predators through such chemical and visual conditioning (Brown et al. 1997; Mirza and Chivers 2000; Olson et al. 2012). For example a previous study examining responses of golden shiners to a single predator conditioning event (exposure to excretions from predators fed a diet of golden shiner) found that fish acquired from bait dealers displayed strong shelter seeking behavior when exposed to these cues (Godard et al. 1998). These arguments aside, I cannot be absolutely certain that differences in source populations are not responsible for some of the patterns reported in my study and future studies should attempt to control for this variable as much as possible. In addition, future studies should consider the relative importance of innate vs. learned behaviors in studies focused on species level trait variation.

Examining piscivore-prey interactions in a confined laboratory environment may limit the inferences from such experiments and is a topic of ongoing debate (Carpenter 1996; Drenner and Mazumder 1999; Spivak et al. 2010). For example, habitat complexity may interact with depth, substrate, light levels as well as numerous additional factors. Furthermore, because predators and prey in such a laboratory setting are spatially constrained there may be an increase in the intensity of predator prey interactions (Butler 1988) and this must be considered when making extrapolations from the laboratory to the field. Studies such as mine may misrepresent

the temporal and spatial interactions in natural populations by assuming a mass action or “reaction vat” form of predator-prey interactions where piscivores and prey are continuously interacting and all segments of the prey population are equally vulnerable. In contrast, interactions between piscivores and prey fish in natural ecosystems may be spatially and temporally restricted into distinct “foraging arenas” whereby individual prey fish and different segments of prey populations are not continuously available or vulnerable to predators (Walters and Juanez 1993; Ahrens et al. 2012). By focusing solely on the direct interactions between predators and prey in a confined laboratory space I may have left out important effects such as scale predator and prey movements which may alter the importance of CWH as a refuge. In addition my experiments did not incorporate effects of littoral structure on production of invertebrate prey, potential consequences for prey fish production, and effects on local prey density that can affect piscivore foraging success (Canion and Heck 2009). My results should be tested in future larger scale experiments to better incorporate such factors which may be important at the whole-lake level.

I found that littoral woody structure did not serve as a predation refuge from two piscivores with different foraging modes for two behaviorally different prey fish in a mesocosm environment. My results reinforce the findings of previous researchers working with vegetative cover that species-specific traits interact with habitat complexity. For behaviorally inflexible prey species that rely on shoaling as a predator defense increasing woody habitat complexity can increase vulnerability to predators. Furthermore my results support a role of CWH complexity on predator foraging behavior and energetics which combined with recent field studies implies an important link between littoral piscivore behavior and habitat. A growing body of literature has begun to demonstrate that the circumstances under which aquatic habitats serves as a refuge from

predation are more complex than previously assumed. Much future work remains to explore the habitat contexts and species traits that are important in determining the refuge value of specific littoral freshwater habitats. An especially pertinent question is whether the results of mesocosm studies as presented here are consistent at the whole-lake scale. In addition, there remains a series of gaps in my knowledge of the field scale effects of littoral habitat changes (and subsequent changes in the spatial distribution of predation risk) on total prey mortality rates. There also remains a notable lack of empirical tests of the many model based predictions of refuge habitats on population dynamics and these areas are fruitful ground for future research.

LITERATURE CITED

- Ahrenstorff, T. D., G. G. Sass, and M. R. Helmus. 2009. The influence of littoral zone coarse woody habitat on home range size, spatial distribution, and feeding ecology of largemouth bass (*Micropterus salmoides*). *Hydrobiologia* 623:223-233.
- Allan, J. R. and T. J. Pitcher. 1986. Species segregation during predator evasion in cyprinid fish shoals. *Freshwater Biology* 16:653-659.
- Canion, C. R. and K. L. Heck Jr. 2009. Effect of habitat complexity on predation success: re-evaluating the current paradigm in seagrass beds. *Marine Ecology Progress Series*. 393:37-46.
- Carpenter, S. R. 1996. Microcosm experiments have limited relevance to community and ecosystem ecology. *Ecology* 77:677-680.
- Christensen, B. and L. Persson. 1993. Species-specific antipredatory behaviors: effects on prey choice in different habitats. *Behavioral Ecology and Sociobiology* 32:1-9.
- Christensen, D. L., Herwig, B. R., Schindler, D. E., Carpenter, S. R. 1996. Impacts of lakeshore residential development on coarse woody debris in north temperate lakes. *Ecological Applications* 6:1143-1149.
- Cooke, S. J. and C. M. Bunt. 2004. Construction of a junction box for use with an inexpensive, commercially available underwater video camera suitable for aquatic research. *North American Journal of Fisheries Management* 24:253-257.

- Drenner, R. W. and A. Mazumder. 1999. Microcosm experiments have limited relevance to community and ecosystem ecology: comment. *Ecology* 80:1081-1085.
- Bartholomew, A. 2002. Total cover and cover quality: predicted and actual effects on a predators foraging success. *Marine Ecology Progress Series* 227:1-9.
- Bishop, T. D., and J. A. Brown. 1992. Threat-sensitive foraging by larval threespine sticklebacks (*Gasterosteus aculeatus*). *Behavioral Ecology and Sociobiology* 31:133-138.
- Butler, M. J. 1988. In situ observations of bluegill (*Lepomis macrochirus*-Raf) foraging behavior – the effects of habitat complexity, group size, and predators. *Copeia* 4:939-944.
- Ehlinger, T. J. and D. S. Wilson. 1988. Complex foraging polymorphism in bluegill sunfish. *Proceedings of the National Academy of Sciences of the United States of America*. 85(6):1878-1882.
- Eklöv, P. and S. Diehl. 1994. Piscivore efficiency and refuging prey: the importance of predator search mode. *Oecologia* 98:3440-353.
- Eklöv, P. and T. VanKooten. 2001. Facilitation among piscivorous predators: Effects of prey habitat use. *Ecology* 82:2486-2494.
- Everett, R. A., and G. M. Ruiz. 1993. Coarse woody debris as a refuge from predation in aquatic communities. An experimental test. *Oecologia* 93:475-486.
- Faber, D. 1980. Observations of the life of the golden shiner, *Notemigonus crysoleucas* (Mitchell), in Lac Heney, Quebec. *Proceedings of the 4th Annual Larval Fish Conference, FWS/OBS-80*, 43:69-78.
- Flynn, A. J. and D. A. Ritz. 1999. Effect of habitat complexity and predatory style on the capture success of fish feeding on aggregated prey. *Journal of the Marine Biological Association of the United Kingdom*. 79:487-494.
- Gillen, A. L. 1981. Predation by pellet reared tiger muskellunge on minnows and bluegills in experimental systems. *Transactions of the American Fisheries Society* 110: 197-209.
- Greenberg, L. A., Pazkowski, C. A., and W. Tonn. 1995. Effects of prey species composition and habitat structure on foraging by two functionally distinct piscivores. *Oikos* 74:522-532.
- Gotceitas, V. and P. Colgan. 1989. Predator foraging success and habitat complexity – quantitative test of the threshold hypothesis. *Oecologia* 80:158-166.

- Guyette, R. P. and W. G. Cole. 1999. Age characteristics of coarse woody debris (*Pinus strobus*) in a lake littoral zone. *Canadian Journal of Fisheries and Aquatic Sciences* 56:496-505
- Hall, D. J., Werner, E. E., Gilliam, J. F., Mittelbach, G. G., Howard, D., Doner, C. G., Dickerman, J. A. and A. J. Stewart. 1979. Diel foraging and prey selection in the golden shiner (*Notemigonis crysoleucas*). *Journal of the Fisheries Research Board of Canada* 36: 1029-1039.
- Hart, P. J. B., and B. Connellan. 1984. Cost of prey capture, growth rate, and ration size in pike, *Esox lucius* L., as functions of prey weight. *Journal of Fish Biology* 25:279-292.
- Hayse, J. W. and T. E. Wissing. 1996. Effects of stem density of artificial vegetation on abundance and growth of age-0 bluegills and predation by largemouth bass. *Transactions of the American Fisheries Society* 125:422-433.
- Helmus, M. R., and G. G. Sass. 2008. The rapid effects of a whole-lake reduction of coarse woody debris on fish and benthic macroinvertebrates. *Freshwater Biology* 53(7):1423-1433.
- Houde, E. D. 1997. Patterns and consequences of selective processes in teleost early life histories. Pages 169–193 in R. C. Chambers and E. A. Trippel, editors. *Early life history and recruitment in fish populations*. Chapman and Hall, New York.
- Hoyle, J. A., and A. Keast. 1987. The effect of prey morphology and size on handling time in a piscivore, the largemouth bass (*Micropterus salmoides*). *Canadian Journal of Zoology* 65: 1972-1977.
- James, P. L. and K. L. Heck Jr. 1994. The effects of habitat complexity and light intensity on ambush predation within a simulated seagrass habitat. *Journal of Experimental Marine Biology and Ecology* 176:187-200.
- Křivan, V. 1998. Effects of optimal antipredator behavior of prey on predator-prey dynamics: the role of refuges. *Theoretical Population Biology* 53:131-142.
- Landeau, L. and J. Terborgh. 1986. Oddity and the confusion effect in predation. *Animal Behavior* 34:1372-1380.
- Laurel, B. J., Laurel C. J., Brown, J. A. and R. S. Gregory. 2005. A new technique to gather 3-D spatial information using a single camera. *Journal of Fish Biology* 66: 429-441.
- Laurel, B. J., and J. A. Brown. 2006. Influence of cruising and ambush predators on 3 dimensional habitat use in age 0 juvenile atlantic cod *Gadus morhua*. *Journal of Experimental Marine Biology and Ecology* 329: 34-46.

- Lima, S. L. 1995. Back to the basics of anti-predatory vigilance – the group size effect. *Animal Behavior* 49:11-20.
- Pitcher, T. J. 1983. Heuristic definitions of shoaling behaviour. *Animal Behaviour* 31: 611–613.
- Mallory, E. C., Ridgway M. S., Gordon A. M., and N. K. Kaushik. 2000. Distribution of woody debris in a small headwater lake, central Ontario, Canada. *Archiv Für Hydrobiologie* 148: 587-606.
- Mattila, J., K.L. Heck Jr., E. Millstein, E. Miller, C. Gustafsson, S. Williams and D. Byron. 2008. Increased habitat structure does not always provide increased refuge from predation. *Marine Ecology Progress Series* 361:15-20.
- Michel, M. J. and M. M. Adams. 2009. Differential effects of structural complexity on predator foraging behavior. *Behavioral Ecology* 313-317.
- Millinski, M. and R. Heller. 1978. Influence of a predator on optimal foraging behavior of sticklebacks (*Gasterosteus-aculeatus* L). *Nature* 275:642-644.
- Millinski, M. 1984. A predators costs of overcoming the confusion effect of swarming prey. *Animal Behavior* 32:1157-1162.
- Miranda, L. E. and W. D. Hubbard. 1994. Winter survival of age-0 largemouth bass relative to size, predators, and shelter. *North American Journal of Fisheries Management* 14:790-796.
- Newbrey, M. G., M. A. Bozek, M. J. Jennings, and J. E. Cook. 2005. Branching complexity and morphological characteristics of coarse woody structure as lacustrine fish habitat. *Canadian Journal of Fisheries and Aquatic Sciences* 62:2110-2123.
- Ostrand, K. G., and D. H. Wahl. 2004. Consequences of vegetation density and prey species on spotted gar foraging. *Transactions of the American Fisheries Society* 133:794-800.
- Pazkowski, C. A. 1986. Foraging site use and interspecific competition between bluegills and golden shiners. *Environmental Biology of Fishes* 17:227-233.
- Rasband, W.S., Image J, U. S. National Institutes of Health, Bethesda, Maryland, USA, <http://imagej.nih.gov/ij/>, 1997-2011.
- Reid, S. M., Fox, M. G. and T. H. Whillans. 1999. Influence of turbidity on piscivory in largemouth bass (*Micropterus salmoides*). *Canadian Journal of Fisheries and Aquatic Sciences* 56:1362-1369.

- Sass, G. G., C. M. Gillie, J. T. Hinke, and J. F. Kitchell. 2006*b*. Whole lake influences of littoral structural complexity and prey body morphology on fish predator-prey interactions. *Ecology of Freshwater Fish* 15(3):301-308.
- Sass, G. G., J. F. Kitchell, S. R. Carpenter, T. R. Hrabik, A. E. Marburg, and M. G. Turner. 2006*a*. Fish community and food web responses to a whole-lake removal of coarse woody habitat. *Fisheries* 31(7):321-330.
- Sass, G. G., S. R. Carpenter, J. W. Gaeta, J. F. Kitchell and T. D. Ahrenstorff. 2011. Whole-lake addition of coarse woody habitat: response of fish populations. *Aquatic Science in press*.
- Savino, J. F. and R. A. Stein. 1989*a*. Behavioral interactions between fish predators and their prey: effects of plant density. *Animal Behavior* 37:311-321.
- Savino, J. F. and R. A. Stein 1989*b*. Behavior of fish predators and their prey: habitat choice between open water and dense vegetation. *Environmental Biology of Fishes* 24(4):287-293.
- Savino, J. F., and R. A. Stein. 1982. Predator-prey interaction between largemouth bass and bluegills as influenced by simulated, submersed vegetation. *Transactions of the American Fisheries Society*. 111:255-266.
- Scheuerell, M. D. and D. E. Schindler. 2004. Changes in the spatial distribution of fishes in lakes along a residential development gradient. *Ecosystems* 7:98–106.
- Schindler, D. E., Geib, S. I., and M. R. Williams. 2000. Patterns of fish growth along a residential development gradient in north temperate lakes. *Ecosystems* 3:229-237.
- Schultz, S.T., and C. Kruschel. 2010. Frequency and success of ambush and chase predation in fish assemblages associated with seagrass and bare sediment in an Adriatic lagoon. *Hydrobiologia* 649:25-37.
- Sih, Andrew. 1987. Prey refuges and predator-prey stability. *Theoretical Population Biology*. 31:1-12.
- Smokorowski, K. E., and T. C. Pratt. 2007. Effect of a change in physical structure and cover on fish and fish habitat in freshwater ecosystems – a review and meta-analysis. *Environmental Reviews* 15:15-41.
- Spivak, A. C., M. J. Vanni, and E. M. Mette. 2010. Moving on up: can results from simple aquatic mesocosm experiments be applied across broad spatial scales? *Freshwater Biology* 56:279-291.
- Swisher, B. J. 1998. Non-additive predation in littoral habitats: influences of habitat complexity. *Oikos* 81: 30-37.

- Tomcko, C. M., R. A. Stein and R. F. Carline. 1984. Predation by tiger muskellunge on bluegill: effects of predator experience, vegetation, and prey density. Transactions of the American Fisheries Society 113:588-594.
- Turner, G. F. and T. J. Pitcher. 1986. Attack abatement- A model for group protection by combined avoidance and dilution. American Naturalist 128:228-240.
- Wahl, D. H. and R. A. Stein. 1988. Selective predation by three esocids: The role of prey behavior and morphology. Transactions of the American Fisheries Society 117:142-151.
- Wagner, C. P. and D. H. Wahl. 2007. Evaluation of survival, growth and behavior differences among genetic stocks of muskellunge. Master's Thesis, University of Illinois at Urbana-Champaign. 115 pp.
- Webb, P. W. 1984. Body form, locomotion, and foraging in aquatic vertebrates. American Zoologist 24:107-120
- Webb, P. W. 1986. Effect of body form and response threshold on the vulnerability of four species of teleost prey attacked by largemouth bass (*Micropterus salmoides*). Canadian Journal of Fisheries and Aquatic Sciences 43:763-771.
- Weithman, A. S. and R. O. Anderson. 1977. Survival growth and prey of esocidae in experimental systems. Transactions of the American Fisheries Society 106:424-430.
- Winemiller, K. O., and D. H. Taylor. 1987. Predatory behavior and competition among laboratory housed largemouth and smallmouth bass. American Midland Naturalist 117: 148-166.

Table 4.1. Qualitative rankings for coarse woody habitat complexity used to select individual deadfall red pine boughs of low, moderate, and high complexity. Qualitative rankings and criteria were adapted from Mallory et al. 2000 and Wagner and Wahl 2007.

Classification	Complexity Score	Description
1	Low	Bark absent, no primary and no secondary branches, few or no stubs of primary branches present.
2	Moderately Low	Bark absent, only stubs of primary branches present, no secondary branches present.
3	Moderate	Bark broken, most primary branches present, most secondary branches absent, no fine branching present.
4	Moderately High	Bark entirely intact, all primary branches present, many secondary branches present with some fine branching.
5	High	Bark intact, all primary and secondary branching present large amounts of fine branching present, foliage may remain.

Table 4.2. Physical characteristics of coarse wood used to examine effects of habitat complexity on piscivore-prey interactions of four freshwater fish species. Complexity and complexity score are as defined in table 1. Volume was determined by displacement whereas mass, diameter and total length were measured directly.

CWH Complexity	Complexity Score	Dry Mass (g)	Volume (cubic cm)	Bole Diameter (cm)	Length (m)
Low	0	420	957.45	12.8	1.31
Moderate	3	880	1436.17	15.4	1.15
High	5	2120	3829.80	16.8	1.48

Table 4.3. Average numbers of shoals, isolated individuals and prey activity rates across three levels of coarse woody habitat complexity and a no habitat control for either bluegills (*Lepomis machrochirus*) or golden shiners (*Notemigonus crysoleucas*) being preyed upon by either largemouth (*Micropterus salmoides*) or muskellunge (*Esox masquinongy*). Means represent averages taken over 1-hour observations while standard errors are in parentheses. Asterisks indicate significant differences between prey species within each CWH level based on pre-planned linear contrasts while non-significant (ns) contrasts are also noted. Letters indicate significant differences within prey species across CWH levels based on Tukey tests.

Predator	Prey	CWH Complexity			
		Zero	Low	Moderate	High
Number of Shoals					
Largemouth Bass	Bluegill	1.65(0.10) ^a *	1.72(0.09) ^a *	1.43(0.10) ^b *	1.16(0.10) ^b ns
	Golden Shiner	1.09(0.10) ^a	1.09(0.11) ^a	0.98(0.11) ^a	1.44(0.11) ^b
Muskellunge	Bluegill	1.30(0.12) ^a *	1.26(0.09) ^a *	1.27(0.09) ^a *	1.13(0.09) ^a ns
	Golden Shiner	1.04(0.08) ^a	1.05(0.09) ^a	1.05(0.08) ^a	1.05(0.10) ^a

Number Not Shoaled					
Largemouth Bass	Bluegill	2.11(0.40) ^a *	2.70(0.36) ^a *	1.42(0.40) ^b ns	0.93(0.40) ^b ns
	Golden Shiner	0.74(0.40) ^a	0.47(0.42) ^a	1.79(0.42) ^b	1.35(0.34) ^b
Muskellunge	Bluegill	2.69(0.60) ^a *	0.95(0.42) ^a *	1.49(0.40) ^a *	1.26(0.40) ^a *
	Golden Shiner	0.09(0.40) ^a	0.11(0.42) ^a	0.17(0.40) ^a	0.39(0.49) ^a

Prey Activity (Sec/Min)					
Largemouth Bass	Bluegill	0.51(0.05) ^a ns	0.45(0.04) ^a ns	0.38(0.06) ^a ns	0.31(0.05) ^b ns
	Golden Shiner	0.54(0.05) ^a	0.45(0.05) ^a	0.44(0.04) ^a	0.35(0.04) ^b
Muskellunge	Bluegill	0.46(0.08) ^a ns	0.50(0.06) ^a ns	0.40(0.06) ^a ns	0.44(0.05) ^a ns
	Golden Shiner	0.54(0.05) ^a	0.41(0.06) ^a	0.39(0.05) ^a	0.35(0.07) ^a

Table 4.4. Average strike distance and proximity to nearest prey across three levels of coarse woody habitat complexity and a no habitat control for either largemouth bass (*Micropterus salmoides*) or muskellunge (*Esox masquinongy*) preying upon either bluegills (*Lepomis machrochirus*) or golden shiners (*Notemigonus crysoleucas*). Means represent averages taken over 1-hour observations while standard errors are in parentheses. Asterisks indicate significant differences between prey species within each CWH level based on pre-planned linear contrasts while non-significant (ns) contrasts are also noted. Letters indicate significant differences within prey species across CWH levels based on Tukey tests.

Predator	Prey	CWH Complexity			
		Zero	Low	Moderate	High
Predator Strike Distance (cm)					
Largemouth Bass	Bluegill	8.62(0.23) ^a ns	18.08(0.27) ^a ns	17.89(0.27) ^a ns	10.41(0.23) ^a ns
	Golden Shiner	13.36(0.18) ^a	15.25(0.18) ^a	15.00(0.21) ^a	13.96(0.21) ^a
Muskellunge	Bluegill	27.92(5.71) ^a ns	17.78(3.74) ^a ns	32.96(4.94) ^a ns	40.06(4.94) ^a ns
	Golden Shiner	27.72(3.50) ^a	17.93(3.74) ^a	25.29(4.04) ^a	28.22(5.71) ^a

Distance to Nearest Prey (cm)					
Largemouth Bass	Bluegill	40.83(7.85) ^a *	38.17(5.85) ^a ns	45.46(5.45) ^{ab} ns	52.91(5.45) ^b *
	Golden Shiner	60.51(5.45) ^a	47.98(5.78) ^a	36.70(5.78) ^{ab}	40.33(4.54) ^b
Muskellunge	Bluegill	64.16(7.85) ^a *	58.94(5.85) ^a *	60.03(5.55) ^a ns	62.11(5.85) ^a *
	Golden Shiner	79.86(5.85) ^a	74.07(6.20) ^a	71.54(5.85) ^a	73.12(7.16) ^a

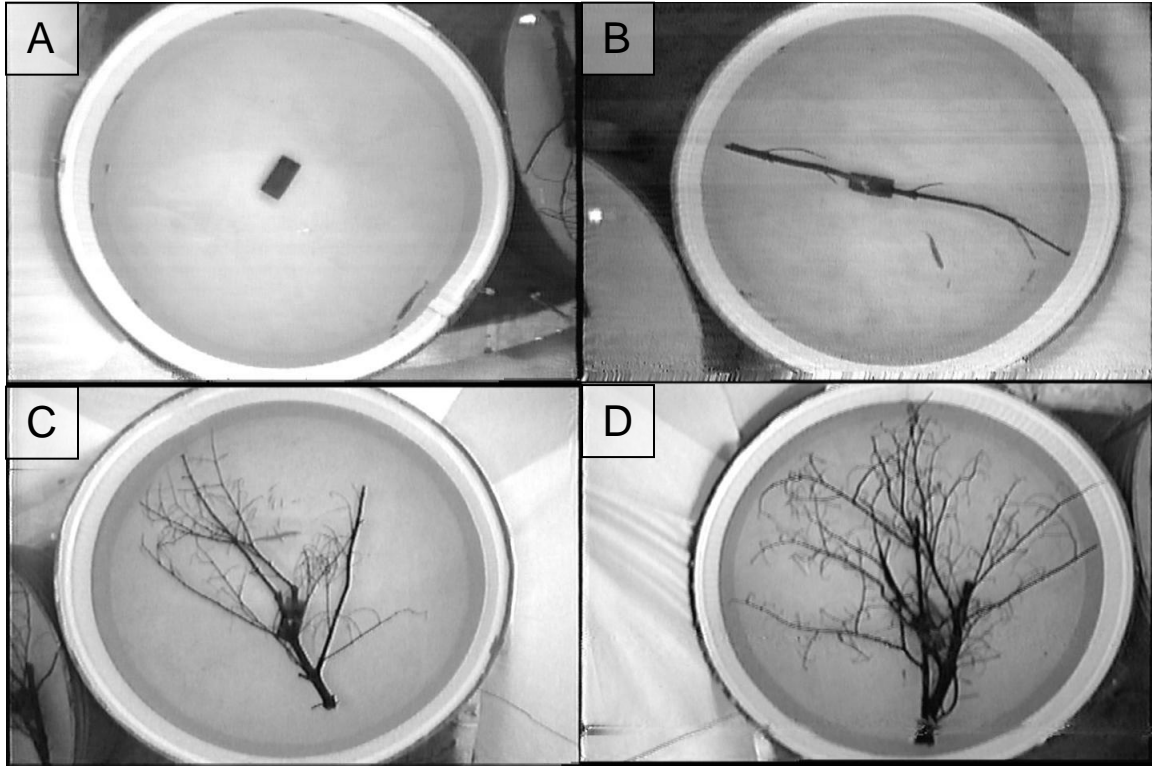


Figure 4.1. Physical layout of experimental arenas used to assess the effects of woody habitat complexity on piscivore-prey interactions of four freshwater fish species as depicted by overhead cameras. Treatments depicted include zero (A), low (B), moderate (C), and high (D) coarse woody habitat complexity. See methods section for dimensions of tanks. Physical dimensions of woody habitat can be found in Table 2.

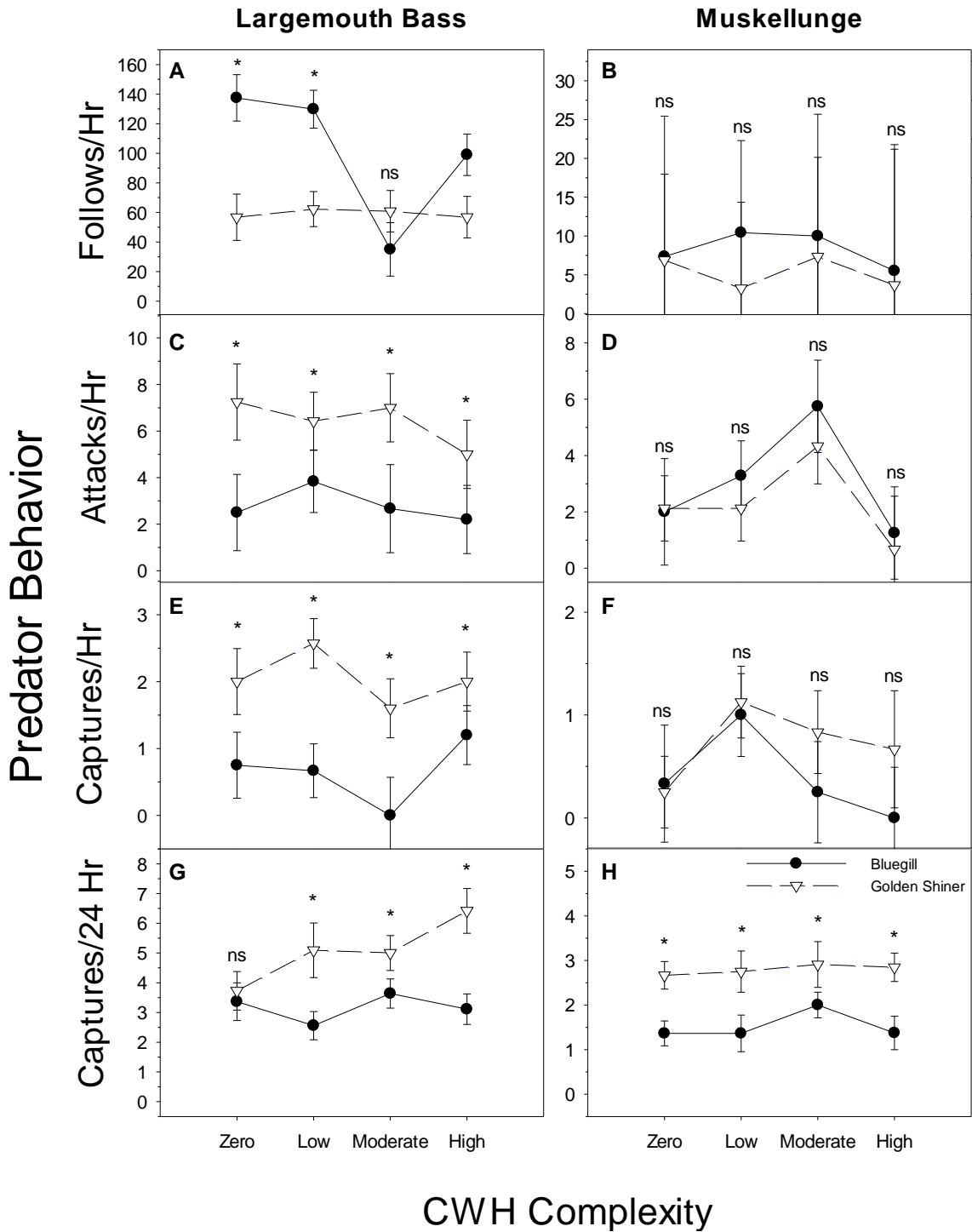


Figure 4.2. Average number of occurrences of piscivore behaviors across three levels of coarse woody habitat complexity and a no habitat control. Results are for largemouth bass (*Micropterus salmoides*) (left panels) and muskellunge (*Esox masquinongy*) (right panels) feeding on golden shiner (*Notemigonus crysoleucas*) (open triangles) and bluegill (*Lepomis machrochirus*) (closed circles). Means represent averages taken over either 1-hour observations or 24-hours as indicated and are for 11 total trials per treatment. Asterisks indicate significant differences between prey species within each CWH level based on pre-planned linear contrasts while non-significant (ns) contrasts are also noted. Error bars represent ± 1 standard error. See results text for main effects comparisons.

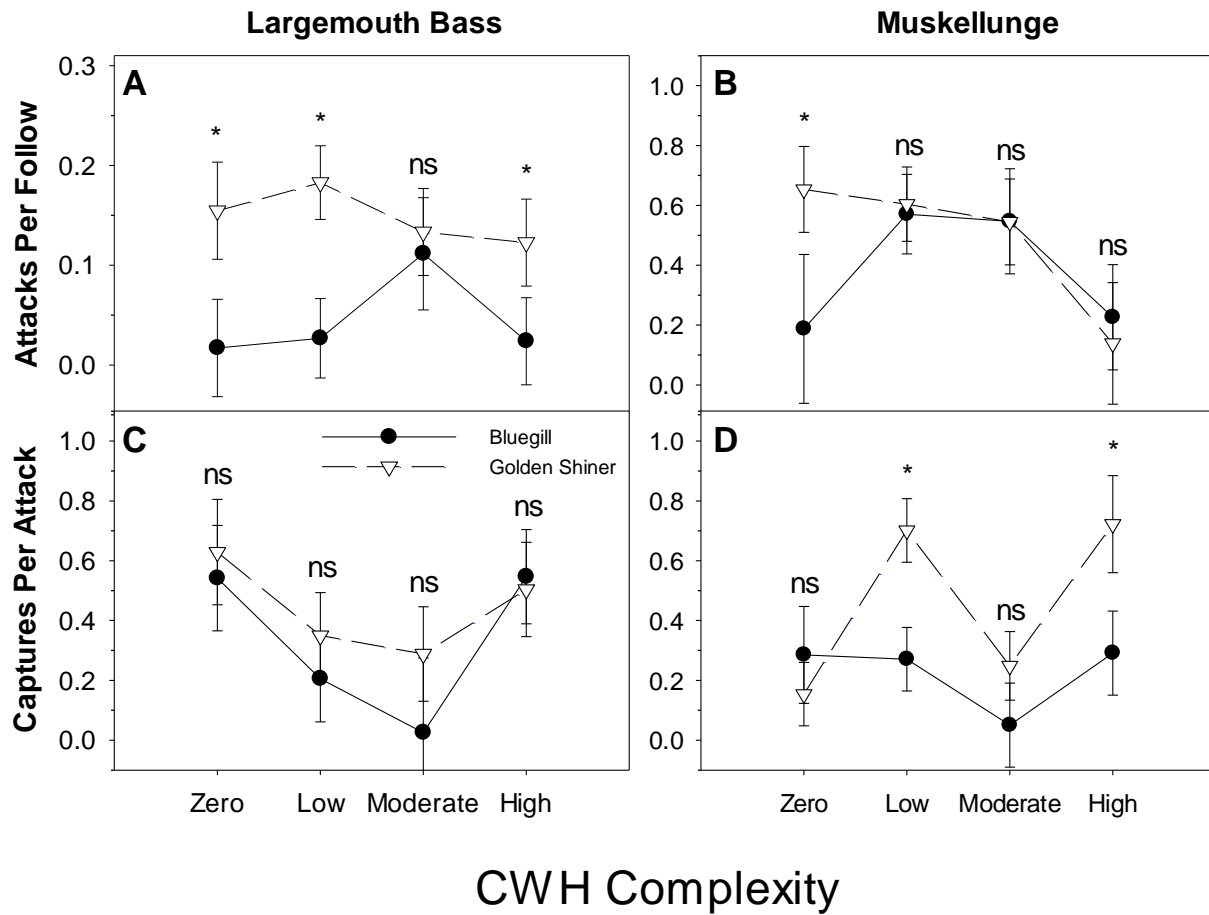


Figure 4.3. Average ratios of attacks per follow and captures per attack for largemouth bass (*Micropterus salmoides*) (A-C) and muskellunge (*Esox masquinongy*) (B-D) foraging on either golden shiners (*Notemigonus crysoleucas*) (open triangles) or bluegills (*Lepomis macrochirus*) (solid circles) across a gradient of coarse woody habitat complexity and a no habitat control. Asterisks indicate significant differences between prey species within each CWH level based on pre-planned linear contrasts with non-significant (ns) contrasts also noted. Error bars represent ± 1 standard error. See results text for main effects comparisons.

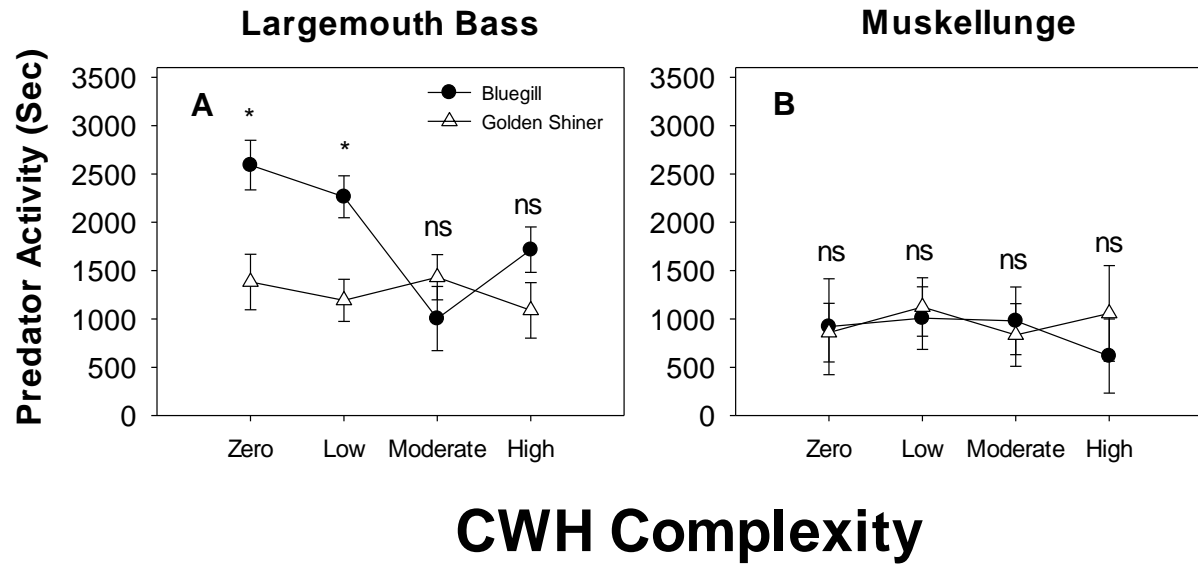


Figure 4.4. Average piscivore activity across three levels of coarse woody habitat complexity and a no habitat control for largemouth bass (*Micropterus salmoides*) (left panels) and muskellunge (*Esox masquinongy*) (right panels) predators feeding on golden shiner (*Notemigonus crysoleucas*) (open triangles) or bluegill prey (*Lepomis macrochirus*) (closed circles). Means represent averages taken over 1-hour observations and are for 11 total trials per treatment. Asterisks indicate significant differences between prey species within each CWH level based on pre-planned linear contrasts while non-significant (ns) contrasts are also noted. Error bars represent ± 1 standard error. See results text for main effects comparisons.

CHAPTER 5: CONCLUSION

Collectively the above studies have several implications for understanding the role of predation in lower latitude lake ecosystems in the central and southern U.S. In a series of controlled whole lake piscivore manipulations I found that piscivore enhancement caused a partial trophic cascade reducing the abundance of juvenile and small-bodied littoral fishes and subsequently increasing the total abundance of benthic macroinvertebrates. These results suggest that unlike previous studies in northern temperate lakes (where enhanced predation cascaded through the pelagic food web) increased predation in these systems may be expected to primarily affect the littoral and benthic food web. These differences between systems are likely due to differences in foraging traits between secondary consumers in lower latitude lakes versus northern systems that have been studied previously. Furthermore there is a consistent trend of studies which have found that gape limited piscivores foraging on species able to reach large body sizes may not strongly suppress populations of these prey. These findings suggest that further refinement and conceptualization of my understanding of food web structure in lower latitude lake ecosystems as well as patterns by which predation pressure is propagated through these structurally more complex food webs is needed. Such an understanding can only be developed through further study that embraces the unique ecological aspects of these ecosystems.

The introduction of new piscivore types into lake ecosystems is an ongoing trend that is likely to continue as the demand for recreational fishing remains high. In addition increasing urban development is often correlated with unregulated species introductions and will likely continue to drive species introductions in the near future. The current trend of muskellunge introduction into lower Midwestern lake and reservoir ecosystems does not appear to have any

immediate negative consequences for existing fish populations based on the limited timeframe and range of species examined in my study. Furthermore my results build upon recent manipulative studies supporting a potentially important interaction between resident largemouth bass and introduced muskellunge populations. Combined with previous work these results suggest that strong interactions between top predators may be a common outcome of introducing new piscivore species into lakes. Much research remains to fully understand the behavioral and mechanistic causes for these interactions and predicting these outcomes prior to a planned introduction remains elusive. Therefore while my results do not implicate a significant threat to the resident species examined by the introduction of muskellunge much work remains before definitive conclusions about the risk of introducing this species can be made. Due to the unpredictable nature of such introductions managers should be cautious before recommending any new species be introduced.

While previous studies have suggested a role of coarse woody habitat as a refuge from predation my results from a mesocosm setting suggest that the effects of this habitat on piscivore populations may be more directly linked to behavioral mechanisms and their effects on organism energy balance however further research at the whole-lake scale is needed to test the generality of these findings. Furthermore the importance of this habitat in predator-prey interactions is linked to species traits and therefore precludes any across species generalization concerning the influence of this habitat as a prey refuge. Future studies will be required to explore the potential for larger sizes of coarse woody habitat or more dense aggregations as potential prey refuges as my study was focused on single deadfalls and should not be considered to provide inference to other habitat types. More research is needed to understand how the diversity of behavioral traits among various freshwater predator and prey species interact with potential habitat refuges before

general predictions can be made in real world settings. Furthermore it remains to be seen whether the natural range of behavioral types can be classified into functional groups which may make such predictions tractable and this should be considered an important research area.