FROM TURTLE POPULATIONS TO PROPERTY VALUES: THE EFFECTS OF LAKESHORE RESIDENTIAL DEVELOPMENT AND THE INVASIVE ZEBRA MUSSEL

By

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ABSTRACT

FROM TURTLE POPULATIONS TO PROPERTY VALUES: THE EFFECTS OF LAKESHORE RESIDENTIAL DEVELOPMENT AND THE INVASIVE ZEBRA MUSSEL

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Lakes offer a multitude of ecosystem services, including numerous recreational opportunities and aesthetically pleasing views. As a result, lakes have long been the site of residential anthropogenic development. This development is associated with changes to riparian and littoral habitat, with documented negative effects on aquatic organisms. This development has also been associated with the invasion of exotic species such as the detrimental zebra mussel (*Dreissena polymorpha*). Zebra mussels are prolific reproducers, often attaining large population sizes and filtering much of the phytoplankton from the water column. These attributes can lead to increased water clarity and primary productivity in littoral zones. Thus, both lakeshore residential development and zebra mussels have the potential to greatly affect lake ecosystems.

My dissertation research investigated the effects of lakeshore development and zebra mussel invasion on lake ecosystems and lakefront property values. In the first chapter, I looked at the effects of lakeshore residential development on population parameters such as sex ratios, size/age distributions, and incidence of human-related injuries of a long-lived species, the painted turtle (*Chrysemys picta*). My results suggest that some in-lake habitat features (e.g., vegetation, coarse woody habitat) may be important sites of refuge while anthropogenic features, such as piers, may pose a threat to male painted turtles.

In my second chapter, I investigated how lakeshore development affects in-lake habitat use for female northern map turtles (*Graptemys geographica*). Turtles selected for shallow areas with submersed and floating vegetation. Turtle home ranges included a lower percentage of

developed shoreline as compared to the lake, yet turtles demonstrated a preference for piers, developed shores, and bulkhead seawalls within their home ranges. These patterns of habitat use can provide insight into critical turtle habitat including submersed and floating vegetation.

In chapter three, I studied the effects of lakeshore development and zebra mussel invasion on lake food webs. Using two species of fish (bluegill [*Lepomis macrochirus*] and largemouth bass [*Micropterus salmoides*]) and two food web metrics (proportion of the fish's diet coming from benthic sources and fish trophic position), I found that shoreline development had a negative effect on bluegill trophic positions. Contrary to expectations, I found no further relationships between food web metrics and these two anthropogenic stressors, nor any interactions between the two stressors. These results may be due to a lack of effect or to the opposing effects of these two benthic zone stressors cancelling out the effects of each other.

In chapter four, I studied the effect of zebra mussels on lakefront property values. Although zebra mussels have a number of negative ecological and economic effects, they are also associated with increased water clarity and with features that make lakes desirable for recreational boating (the source of most zebra mussel introductions). I found that lakefront property values were positively related to zebra mussel presence in the lake and the time since zebra mussels first invaded the lake. Including potential confounding variables in the models did not change these positive relationships, indicating that we may be missing additional covariates or that there is a positive relationship between this invasive species and property values.

The results of my dissertation show that anthropogenic changes to lakes can affect both the organisms within the lake and the ecosystem services these lakes provide to humans. Lake management plans that are designed to minimize the effects of lakeshore residential development and zebra mussel invasion could protect lake organisms and what humans enjoy about lakes.

To all the strong women in my life who always believed in me,
especially my mom, my Aunt Noel, and my grandmothers

and

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always making my life more interesting

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INTRODUCTION

Lakes offer a wealth of ecosystem services, including scenic views and a number of recreational opportunities, such as boating, fishing, and swimming (MA 2005). As a result, lakes have been the site of residential development for decades (Gonzalez-Abraham et al. 2007). This development at the lake shoreline is associated with many changes to littoral and riparian habitat (reviewed in Strayer and Findlay 2010) as well as with the invasion of non-native species (Elias and Meyer 2003). One particularly detrimental exotic invasive species in the Great Lakes region of the United States is the zebra mussel (reviewed in Higgins and Vander Zanden 2010).

Both lakeshore residential development and invasion by zebra mussels can greatly affect processes, habitat, and organismal interactions in nearshore areas. Due in large part to their complex physical habitat, nearshore areas provide a prey base for many fish (Vadeboncoeur and Vander Zanden 2002, Sass et al. 2006) and turtles (Lindeman 2006, Bulte et al. 2008), habitat for fish reproduction (Wagner et al. 2006), and a refuge from predators (Sass et al. 2006, Carriere and Blouin-Demers 2010). As a result, littoral and benthic areas are essential for whole-lake functioning. Because these areas are important to many lake organisms and to whole-lake productivity and functioning, I was especially interested in how changes to these nearshore areas that result from shoreline development and zebra mussel invasion may extend throughout the lake and riparian areas.

My dissertation is focused on the ecological and economic effects of lakeshore residential development and zebra mussel invasion in Michigan inland lakes, with the central question:

How do anthropogenic stressors affect lake ecosystems and the services that lakes provide?

Chapter 1: Long-lived species and human-mediated habitat changes: a case study of painted turtles (*Chrysemys picta*) in Michigan inland lakes

Co-Author: Kendra Spence Cheruvelil

Question: How does lakeshore residential development affect painted turtle populations, particularly age/size structure, sex ratios, and human-mediated injuries?

Painted turtles, a long-lived species, rely on both lake and riparian habitat for their life history and, as a result, may be especially vulnerable to changes at the lake-water interface that occur with lakeshore development. In this chapter, I discuss the threat of habitat loss for long-lived species like the painted turtle and then use an intensive field study to investigate the relationship between painted turtle population parameters and one source of habitat loss, measures of lakeshore development. Then, I discuss both the difficulties of studying long-lived species and conservation strategies specific to long-lived species.

Chapter 2: Northern map turtle (*Graptemys geographica*) in-lake habitat use and the effects of residential lakeshore development

Co-Author: Kendra Spence Cheruvelil

Questions: (1) What is the spatial ecology of female northern map turtles in natural inland lakes?

(2) How is female northern map turtle habitat selection related to natural and anthropogenic lake features, with an emphasis on features of lakeshore development?

Habitat loss is one of the major threats to reptile populations world-wide. In this chapter, I use an intensive field study to investigate female northern map turtle spatial ecology and habitat selection in relation to multiple measures of lakeshore residential development and other lake features. Previous studies of northern map turtle habitat use have focused on streams and/or reservoirs. This study is the first to quantify the spatial ecology of female northern map turtles in natural lakes. In addition, this is the first detailed study of the effects of lakeshore residential developed on habitat selection in this species.

Chapter 3: Effects of human lakeshore development and the exotic invasive zebra mussel (*Dreissena polymorpha*) on benthic-pelagic linkages in lakes

Co-Author: Mary Tate Bremigan

Question: What is the effect of each stressor (lakeshore development and zebra mussel invasion) on whole-lake food webs? And, what is the effect of the two stressors combined?

Lakes are subject to a number of anthropogenic stressors; yet, most studies focus on the effects of a single stressor. However, stressors should be evaluated simultaneously because stressors may interact with one another to produce unexpected effects on lake ecology. In this chapter, I use stable isotope analysis to explore the effect of two stressors, lakeshore development and invasion of zebra mussels, on the diets of two fish species. Specifically, I look at how these two stressors affect the proportion of benthic prey in fish diets and fish trophic position.

Chapter 4: The role of an aquatic invasive species, the zebra mussel, on lakefront property values

Co-Authors: Daniel B. Kramer, Kendra Spence Cheruvelil

Question: What is the association between zebra mussels and lakefront property values?

Zebra mussels are associated with a number of negative ecological and economic effects. However, they are also associated with improved lake water clarity and, potentially, desirable lake recreation features that make the lake both desirable for boating and vulnerable to invasion by exotic species. In this chapter, I explore the association between zebra mussel presence and time since zebra mussel invasion and lakefront property values. This is the first study of the association between zebra mussels and lakefront property values.

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CHAPTER 1

LONG-LIVED SPECIES AND HUMAN-MEDIATED HABITAT CHANGES: A CASE STUDY OF PAINTED TURTLES (*CHRYSEMYS PICTA*) IN MICHIGAN INLAND LAKES

Abstract

Long-lived species are associated with life history characteristics that make them especially vulnerable to permanent anthropogenic habitat changes. We studied one long-lived species, the painted turtle (*Chrysemys picta*), in four Michigan inland lakes that have experienced lakeshore residential development and associated changes in littoral and riparian habitat. Using two years of trap data, we related painted turtle population parameters (sex ratios, carapace length [a proxy for age], and human-related injuries) to multiple measures of shoreline development to determine how changes in littoral and shoreline habitat might affect this long-lived species. We found that a higher pier density favored females while a higher proportion of emergent vegetation cover favored males. Male painted turtle carapace length was positively related to both the proportion of floating vegetation, coarse woody habitat (CWH) density, and greater incidence of human-related injuries. This last result suggests that older/larger male turtles may be accruing human-related injuries over their long life spans. Our results provide insight into habitat features that could be important to painted turtle persistence (i.e., emergent and floating vegetation and CWH) and into at least one measure of shoreline development (i.e. pier density) could pose a threat to the persistence of this long-lived species. Future shoreline development that protects these important habitat features could promote painted turtle persistence in these lakes.

1.1 Introduction

The major threats to many species, regardless of life history characteristics, are anthropogenic in nature (Gibbons et al. 2000, Bohm et al. 2013). Habitat degradation in particular, is among the most detrimental human-mediated disturbance for many taxa (Andren 1994, Stuart et al. 2004, Hostetler et al. 2009, Bohm et al. 2013). Habitat loss can negatively affect populations through increased energetic demands (Homyack and Haas 2009), decreased or changed prey sources (Sass et al. 2006), or other negative effects on physiological processes (Dodd and Dreslik 2008). Roadway construction can result in loss of migratory or movement habitat (Forman and Alexander 1998, Trombulak and Frissell 2000) and be a major source of mortality during migratory events (Trombulak and Frissell 2000, Kuo and Janzen 2004, Hostetler et al. 2009, Langen et al. 2012). Other human-imposed barriers to movement include wind farms, that can negatively affect birds and bat migrations (e.g., Carrete et al. 2009), and dams, that can prevent fish from reaching spawning grounds (e.g. Lippe et al. 2006) and can lead to fragmentation of formerly contiguous turtle populations (Bennett et al. 2009, Bennett et al. 2010).

Long-lived species are especially vulnerable to such anthropogenic habitat changes because the life history characteristics that have co-evolved with their long life span (Rowe 2008, Carrete et al. 2009). Traits such as delayed sexual maturity, long generation times, and slow population growth rates (Congdon et al. 1993, Congdon et al. 1994) typically result in slow evolutionary responses as compared to relatively rapid environmental changes (Rowe 2008). Such life history characteristics are well-suited for relatively stable environments with sporadic, low-intensity disturbances (Dodd et al. 2006, Rowe 2008). As a result, long-lived species are typically at a greater risk of extinction in the face of repeated, high-intensity, or more permanent environmental changes than their shorter-lived counterparts (Webb et al. 2002).

In this chapter, we discuss the threats to persistence of long-lived organisms associated with habitat loss, difficulties of studying such species due in large part to the slow response rates to anthropogenic change, and conservation strategies designed particularly for long-lived species. As a case study, we present data on painted turtles (*Chrysemys picta*), a relatively tolerant long-lived species, from four Michigan inland lakes that have experienced permanent changes to lake shoreline and littoral habitat as a result of lakeshore residential development. We asked: how has painted turtle population parameters, particularly sex ratios, age/size structure, and human-related injuries, responded to lakeshore residential development? Our findings identify potential threats to these painted turtle populations and suggest avenues for future protection of this long-lived species.

1.1.1 Habitat loss and painted turtle persistence

Painted turtles occupy lakes, streams, and wetlands during summers in temperate zones in the northern hemisphere (Ernst and Lovich 2009), migrate to uplands to lay eggs (Baldwin et al. 2004, Rowe et al. 2005), and return to permanent waterbodies to overwinter (Ernst and Lovich 2009). Therefore, painted turtles are important integrators of terrestrial and aquatic habitats, using both in-lake and riparian habitats. Unfortunately, this also means that painted turtles may be vulnerable to anthropogenic changes, both on the land and in water, during the course of their lifetime.

Though they are subject to many of the same anthropogenic disturbances that threaten other long-lived species, painted turtles might be less vulnerable to anthropogenic changes than other North American turtles because of their generalist diet (Ernst and Lovich 2009), their tendency to occupy most types of waterbodies (i.e., wetlands, lakes, and rivers of all sizes; Lagler 1943, Tran et al. 2007, Ernst and Lovich 2009), and because they are one of the most common turtle species throughout their range (Ernst and Lovich 2009).

Painted turtles appear relatively resistant to some human disturbances. For example, this species has shown few changes in population parameters such as sex ratios and age/size distribution in developed habitats as compared to more pristine sites (e.g., Mitchell 1988, Browne and Hecnar 2007, Eskew et al. 2010). In addition, human presence near nest sites appears to have little effect on nest site selection (Bowen and Janzen 2008) or on nest success (Strickland and Janzen 2010).

However, other research has shown that some anthropogenic-induced environmental changes have negative effects on painted turtle populations. For example, roadways are a major source of mortality for painted turtles (Baldwin et al. 2004, Steen and Gibbs 2004, Langen et al. 2012). Roadway mortality is especially high when the roadways are positioned between two waterbodies (Langen et al. 2012) or between the home waterbody and suitable nesting habitat (Baldwin et al. 2004). Lakes surrounded by high roadway densities tend to have male-skewed populations (Marchand and Livaitis 2004, Steen and Gibbs 2004, DeCatanzaro and Chow-Fraser 2010, Patrick and Gibbs 2010), likely due to higher roadway mortality for nest-seeking females. Thus, roads appear to present a similar threat in painted turtles as has been observed in other turtle species (Gibbs and Steen 2005).

This vulnerability of painted turtles to roadways may be acerbated by the loss of suitable nesting habitat near waterbodies as a result of human development, including lakeshore residential development. Traveling a long distance to nesting sites can result in a high likelihood of encountering, and suffering mortality on, roadways (Baldwin et al, 2004). In addition, some females may select roadway shoulders as nesting sites when nesting habitat is scarce, again placing them at greater risk of roadway mortality (Browne and Hecnar 2007, Laporte et al. 2013). Roadway density near waterbodies is also associated with a greater proportion of males in the population, suggesting painted turtle recruitment is also negatively affected by roadways (Marchand and Litvaitis 2004). Painted turtles may also be more at risk to injury or death from boat propeller collisions in lakes with high lakeshore development and the associated increase in boat traffic (Smith et al. 2006). Therefore, although this species is common and seems relatively robust to some human disturbances, painted turtle populations may be susceptible to anthropogenic changes such as changes in littoral and riparian habitat as a result of lakeshore residential development.

1.1.2 Painted turtles and lakeshore residential development

In their aquatic environments, painted turtles utilize a number of lake habitat features that are negatively affected by lakeshore development. Painted turtles prefer shallower nearshore areas (Jaeger and Cobb 2012), feed on aquatic vegetation and macroinvertebrates (Rowe 2003, Padgett et al. 2010), and bask on fallen logs, also known as coarse woody habitat (CWH; Peterman and Ryan 2009). Lakeshore residential development is associated with the decline of many of these habitat features, including the loss of aquatic and terrestrial vegetation (Radomski and Goeman 2001, Jennings et al. 2003, Radomski 2006, Radomski et al. 2010), a reduction in CWH (Christensen et al. 1996, Roth et al. 2007), and a change in macroinvertebrate community diversity (Brauns et al. 2007, Brauns et al. 2011). In addition, lakeshore development is associated with the construction of piers (Radomski et al. 2010) and increased recreational activity (Strayer and Findlay 2010). Thus, we predicted that painted turtle populations would be affected by lakeshore residential development due to the associated habitat loss in littoral and riparian zones combined with the potential increase in human-related injuries from boat collisions (Smith et al. 2006).

To investigate the effects lakeshore development on painted turtles, we quantified the relationship between three measures of painted turtle populations (population sex ratios, incidence of human-related injuries, and age/size structure) and a variety of natural and anthropogenic littoral and riparian features, as well as characteristics of individual turtles. We expected that more developed lakes would have male-skewed sex ratios because females are more vulnerable to roadway mortality while making overland movements during nesting excursions (Marchand and Litvaitis 2004, Steen and Gibbs 2004). We also expected a greater incidence of human-related injury with high levels of shoreline development because high roadway density can cause crushing injuries, and high pier density may lead to an increase in boat propeller-related injuries (Smith et al. 2006, Bulte et al. 2010). Finally, for carapace length, we expected shoreline development to affect turtle populations in one of two ways: (1) the population would be skewed toward older and larger individuals if recruitment was negatively affected or (2) the population would be skewed toward younger and smaller individuals if adult turtles were more susceptible to human-related mortality.

1.2 Methods

1.2.1 Study lakes and lake sampling

We collected painted turtles from four inland lakes in southeastern Michigan (Table 1.1) from May through August of 2009 and 2010. We selected lakes that were hydrogeomorphically similar (i.e., relatively small and shallow), in close proximity to one another, and where we had observed painted turtles. We captured turtles using basking traps we constructed (following Browne and Hecnar 2005), baited hoop traps (2.5’ diameter hoops with 1.5” diameter mesh, Memphis Net and Twine Co., Inc.), and by hand using dip nets. Basking traps were placed both at known basking sites and at sites where basking had not been observed. Hoop traps were placed, at both developed and undeveloped sites, in shallow waters near the shoreline to allow for sufficient breathing space for captured turtles and to avoid trap-boat collisions. Each captured turtle was sexed, aged (juvenile or adult, with juveniles identified as having carapace lengths <7cm for males and <9.7cm for females; Steen and Gibbs 2004, Ernst and Lovich 2009), weighed, measured (carapace length and width), and marked with a unique identifying code by notching the marginal scutes with a hand file. We recorded incidences of injury and specified whether the injury was believed to be from a human source (i.e. boat propeller or crushing injury from a car or other motor vehicle; Figure 1.1) or not. For the analysis, we included only those injuries that could be confidently attributed to human sources (following Bulte et al. 2010, Figure 1.1).

We measured a number of lake habitat features that turtles potentially use. Once each summer we estimated emergent, floating, and submersed macrophyte cover using the point-intercept method (Madsen 1999). Following Madsen (1999), we calculated the necessary number of macrophyte sampling points based on the lake surface area, lake depth, shoreline length, and littoral area. We then divided the surface area of the lake by the number of points to determine the distance between points, which ranged between 35 and 55 m for a total of 314 to 488 sample points per lake. Finally, at each point, we estimated the percent cover for each vegetation class (i.e. emergent, floating, and submersed). We also recorded the location of coarse woody habitat

(CWH) ≥10cm in diameter that was sufficiently above the water's surface to allow for basking (Lindeman 1999).

For anthropogenic lake features, we measured features of human shoreline development that we expected to influence turtle populations, including pier locations and the proportion of the shoreline that was developed. Pier locations were marked with a hand-held GPS (Garmin GPSmap 76S). To calculate pier density, we then divided the total number of piers in each lake by the total length of each lake's shoreline (kilometers). Shorelines were classified as developed if there was any human modification to the land immediately adjacent to the lake; thus, shorelines with houses/structures, lawns, agricultural lands, retaining walls, boat ramps, and man-made beaches were classified as developed. For the shoreline development variable included in subsequent analysis, we calculated the total proportion of the shoreline that was classified as developed. We also calculated the road density in a 100 m buffer surrounding each of the four lakes as an indicator of the potential for road-related injury and mortality that may disproportionately affect female turtles (Marchand and Litvaitis 2004). We used publically available GIS roadway layers (MiGDL 2012) clipped to a 100 m buffer around each lake to determine roadway linear distance (in kilometers) which was then divided by the total buffer area (in square kilometers) to get roadway density (Marchand and Litvaitis 2004).

1.2.2 Analytical methods

We first quantified the associations between measures of anthropogenic shoreline development and natural lake features. Then, we related these natural and anthropogenic features to three turtle population parameters: sex ratios, incidence of human injury (Figure 1.1), and total carapace length (to represent age/size structure of the population). We used univariate regressions to quantify relationships between the predictor and response variables. For binary response variables (sex ratio and human-related injuries), we used logistic univariate regressions. Sex ratios were represented by the probability of being female (i.e. 0 if male, 1 if female) and human-related injuries were represented by the probability of having a human injury (i.e. 0 if no evidence of human-related injury, 1 if the turtle has a human-related injury). For the continuous response variable (total carapace length), we used linear univariate regressions. For injury and carapace length analyses we analyzed females and males separately due to differences in body size (Ernst and Lovich 2009). All analyses were conducted in R version 2.13.2.

We collected a total of 172 painted turtles (48 females and 124 males) from the four study lakes. Because 100 of the 172 turtles sampled were from a single lake (Joslin Lake), we selected a random subset of turtles (n = 25 from 2009 and n=4 from 2010) from this lake (Table 1.2) to use to remove bias as a result of unequal sample sizes in analyses of across-lake variation in turtle populations parameters. Further, all recaptures and individuals that could not be sexed were removed from the data set. Thus, we analyzed data on 101 turtles, with 73 males (n = 73 adults, n = 0 juveniles) and 28 females (n = 24 adults, n = 4 juveniles). Sex ratios were male-skewed for three of the four lakes and 1:1 (female:male) in the remaining lake (Table 1.2). The incidence of human-related injuries was low for males (between 0 and 11% of turtles were injured) and females (between 0 and 25% of turtles were injured; Table 1.2). Male carapace lengths in this subset ranged from 8.0 to 13.2 cm (Figure 1.2), with an overall average of 11.01±0.14 cm and female carapace lengths ranged from 7.6 to 14.5 cm (Figure 1.3), with an overall average of 12.27±0.37 cm.

1.3 Results

Using 101 of the total 172 painted turtles trapped, we calculated basic population parameters for our study lakes (Table 1.2). Sex ratios were male-skewed for three of the four lakes and 1:1 (female:male) in the remaining lake (Table 1.2). The incidence of human-related injuries was low for males (between 0 and 11% of turtles were injured) and females (between 0 and 25% of turtles were injured; Table 1.2). Male carapace lengths in this subset ranged from 8.0 to 13.2 cm (Figure 1.2), with an overall average of 11.01±0.14 cm and female carapace lengths ranged from 7.6 to 14.5 cm (Figure 1.3), with an overall average of 12.27±0.37 cm.

Natural and anthropogenic lake features were frequently significantly correlated (Table 1.3).). All measures of development (i.e., the percentage of developed shoreline, pier density, and road density) were strongly negatively correlated with percent cover of emergent vegetation ($r = -0.72$, -0.98, and -0.68 respectively, and $p<0.01$ for all; Table 1.3). Percent of shoreline developed was also positively correlated with percent cover of submersed vegetation ($r = 0.75$, $p<0.01$). In addition, all measures of development were highly, positive correlated with one another (all $r>0.75$, all $p<0.01$; Table 1.3). For natural features, CWH density was negatively correlated with submersed vegetation cover ($r = -0.69$, $p<0.01$) and positively associated with floating vegetation cover ($r = 0.85$, $p<0.01$; Table 1.3).

We found relationships between painted turtle population parameters and both natural and anthropogenic lake features, as well as with characteristics of the individual turtle (Table 1.4). For sex ratios, we found that a higher pier density favored females (positive relationship, $p = 0.05$) and a higher proportion of emergent vegetation cover favored males (negative relationship with probability of being female, $p = 0.02$; Table 1.4).

For human injuries in female turtles, we found no significant relationships between injury rates and features of the lake or of the individual turtle (Table 1.4). For male painted turtles, we found a marginally significant positive relationship between the probability of having a human-related injury and carapace length ($p = 0.09$), although no lake features were significantly related to probability of injury (Table 1.4).

Finally, for carapace length, we found significant results for male painted turtles (Table 1.4). Both proportion floating vegetation cover ($R^2 = 0.07$, $p = 0.03$) and the density of CWH ($R^2 = 0.04$, $p = 0.07$) were positively related to male carapace length, although the latter was marginally significant (Table 1.4). There were no significant associations between lake features and female carapace lengths (Table 1.4).

1.4 Discussion

We found that measures of lakeshore residential development, including percent shoreline development, pier density, and roadway density in a 100 m buffer surrounding the lake, were associated with natural in-lake habitat features and with painted turtle population characteristics.

1.4.1 Lakeshore development and habitat features

Similar to previous studies (e.g., Jennings et al. 2003, Radomski 2006), we found a negative association between all measures of shoreline development (i.e., percent shoreline developed, pier density, and roadway density) and emergent vegetation cover (Table 1.3). We also found a positive association between the percent of shoreline developed and submersed vegetation cover (Table 1.3). This finding was not expected as previous studies have typically found negative associations (e.g., Dodson et al. 2005, Alexander et al. 2008) or no associations (e.g., Jennings et al. 2003, Cheruvelil and Soranno 2008) between development and submersed vegetation cover.

1.4.2 Lakeshore development and painted turtles

We found male-skewed sex ratios for three of the four study lakes (Table 1.2), which is typical for painted turtle populations (e.g., Frazer et al. 1993, Gamble and Simons 2004, Browne and Hecnar 2007). In more developed lakes and in lakes with a greater density of roadways surrounding the lake, we expected more extreme male-skewed ratios as a result of higher mortality for nest-seeking females (Marchand and Litvaitis 2004, Steen and Gibbs 2004). However, we found that only one significant measure of development, pier density, was associated with more females in the population (Table 1.4). The fact that both percentage of shoreline developed and road density varied little across lakes (Table 1.1) may explain the lack of relationship between these variables and sex ratios.

The unexpected positive association between pier density and proportion of females in the population may be due to differential mortality between the sexes. Males may be less likely to survive boat propeller collisions, as compared to females, due to their smaller size (Bulte et al. 2010), resulting in relatively more female-skewed sex ratios in lakes with a greater density of piers. On the other hand, this result may be an artifact of the strong negative correlation found between pier density and emergent vegetation (Table 1.3). Emergent vegetation was positively associated with more males in the population and has been noted as preferred habitat for males of other species aquatic turtles, likely due to the refuge it provides (Carriere and Blouin-Demers 2010).

Male painted turtle carapace length, which can act as a proxy for age (Browne and Hecnar 2007), was positively associated with both floating vegetation and CWH. These lake features, which were strongly positively correlated (Table 1.3), likely provide refuge and food resources for painted turtles. Painted turtles are known to feed on macrophyte seeds, particularly those of floating macrophytes (Rowe 2003, Padgett et al. 2010), and on the macroinvertebrates that live on vegetation and CWH (Lindeman 1996, Rowe 2003, Padgett et al. 2010).

Male body size was also positively related to the probability of sustaining a human-related injury (Figure 1.1). These injuries primarily consist of boat propeller injuries (9 out of 10 human related injuries, or 90%, were classified as boat propeller injuries). Because body size is roughly correlated with age, this result suggests that the risk of human-related injuries could accumulate throughout their long life spans.

These results suggest that male painted turtles could be vulnerable to pier density, one feature of lakeshore development (Radomski et al. 2010). Alternatively, males may benefit from a greater percent cover of emergent vegetation, which is both strongly negatively correlated with pier density (Table 1.3) and is potentially an important refuge. Older males were also more frequently injured, with injuries primarily from boat propellers, providing further evidence that males may be especially vulnerable to boat traffic.

1.4.3 Difficulties of studying long-lived species

The fact that painted turtles are so long-lived presents a substantial challenge to collecting even their most basic life history data. Long-term monitoring (often a minimum of 15 years) is the best way to collect life history data on such long-lived species (e.g., Congdon et al. 1993, Congdon et al. 1994, Congdon et al. 2003, Smith et al. 2006). However, these types of long-term monitoring studies are rare (Gibbons et al. 2000) and short-term studies may not always accurately reflect the state of the population (e.g., Eskew et al. 2010, McCoy et al. 2010).

Long-lived species are difficult to study for a number of reasons in addition to their long life span. Certain long-lived species, such as reptiles (Gibbons et al. 2000), may rarely congregate to breed and/or generally occur in low population densities. In addition, many common, non-game species such as the painted turtle have little detailed distribution information, which makes it difficult to even locate study populations.

Another difficulty inherent to studying the effects of human-mediated disturbance on long-lived animals is that it can be hard to detect their responses to stressors. With relatively short-term or temporary disturbances, in particular, populations may need many subsequent years of study in order to fully observe the resulting effects. For example, a study of painted turtles in the two years preceding and the two years after suburban development did not detect a significant effect on the populations undergoing development (Eskew et al. 2010); however, the authors acknowledged that sufficient time may not have passed to detect a shift in the populations at the developed sites. Further complicating our understanding of how long-lived species will respond to stressors is the reality that these species are often facing multiple stressors (e.g., habitat loss and sub-lethal effects of pollutants) at once.

These concerns are also present in our study of painted turtles in four southeastern Michigan inland lakes. Our study lakes have experienced myriad human-mediated littoral and lakeshore changes in the past few decades. Although we found significant associations between some natural and anthropogenic lake features (emergent and floating vegetation, CWH, pier density) and population parameters, our study was limited by our small number of lakes ($n = 4$), its short period of study ($n = 2$ years), its relatively narrow range of shoreline development (from about 3% to 61% developed), and high correlations between a number of lake features (Table 1.3). We also had no data on painted turtle populations prior to the development of these lake shorelines nor on other natural features important to painted turtles and stressors facing these populations (e.g., food distributions, nest predation rates). Thus, there may have been changes in the painted turtle populations in individual lakes that were not detected when comparing across all the study lakes. Future studies of painted turtles and the effects of lakeshore development should include a larger sample of lakes, with a wide range of shoreline development to get a better sense of the relationships between measures of shoreline development and painted turtle population parameters. Ideally, studies would also be long-term to measure changes in painted turtle populations through time.

1.4.4 Conservation strategies for long-lived species

Conservation planning is difficult for long-lived species, in part because of their associated life history characteristics. Population viability studies of relatively long-lived species have found that habitat disturbances can have devastating effects, including half century-long delays until recovery (Homyack and Haas 2009) and local extinctions (Garber and Burger 1995, Hostetler et al. 2009, Bulte et al 2010). Therefore, the ideal situation is to monitor populations and protect them prior to dramatic decline (Lippe et al. 2006). However, this strategy is not always possible and many times long-lived species must be managed after they have already been greatly reduced in numbers.

Critical habitat includes migratory pathways between habitats or between two populations of the same species. Migration passages allow species to leave disturbed habitats for those that are less affected in order to minimize negative effects of disturbance on reproduction or mortality (Dodd et al. 2006). This movement is important when a species is long-lived, because having refugia can provide time for these species to wait out any effects of temporary disturbances (Dodd et al. 2006, Roe et al. 2011). For painted turtles, important movement corridors include pathways between waterbodies (Langen et al. 2012) and pathways between the waterbody and suitable nesting habitat (Baldwin et al. 2004). Oftentimes, these important movement corridors are also the sites of the highest roadway mortality (Langen et al. 2012). Thus, identifying these ‘hotspots’ of road-related mortality can allow for the construction of safer corridors that reduce road-related mortality in painted turtles (Langen et al. 2012) or for more thoughtful planning to prevent high-risk developments in critical habitat (Carrete et al. 2009), both within and outside of the lake.

For painted turtles, our results suggest that ‘critical habitat’ may include emergent and floating vegetation in addition to CWH (Table 1.4). This result is likely due to the combination of refuge and food resources these habitats provide. Lakeshore residential development can create patchy habitat, with developed shorelines having less riparian and in-lake vegetation (e.g., Jennings et al. 2003), less CWH (e.g., Christensen et al. 1996), altered lake sediments (e.g., Brauns et al. 2007), and less diverse macroinvertebrate communities (Brauns et al. 2007, Brauns et al. 2011) when compared to undeveloped sites. Protecting this remaining habitat at undeveloped shorelines could encourage painted turtle persistence in these lakes. In addition, painted turtles could benefit from lakeshore development regulations that encouraged more natural shorelines, as opposed to seawalls made of hard substrates (e.g., concrete, wood, steel) that are associated with loss of nearshore vegetation (Jennings et al. 2003, Strayer and Findlay 2010), and for homeowners to leave some CWH in the lake. These habitat features are also important to a number of other lake species (e.g., macroinvertebrates in Brauns et al. 2007 and

Brauns et al. 2011, fish in Sass et al. 2006). Though turtles have been rarely considered in waterbody management plans (Bodie 2001), management designed to preserve painted turtle habitat could benefit a number of other organisms as well.

1.5 Conclusions

Anthropogenic changes negatively affect many species; however long-lived species can be particularly vulnerable to the negative consequences of such changes, and research studies and conservation approaches have to be designed with consideration for the life history characteristics associated with a long life. Long-lived species, such as painted turtles, are dependent on high adult survival (e.g. Congdon et al. 1993, Congdon et al. 1994), but are less vulnerable to fluctuations in yearly recruitment due to naturally low annual reproductive success (Morris et al. 2008). Thus, long-lived species may be able to ride out short-term disturbances in their environments (Dodd et al. 2006, Dodd et al. 2012). However, the long generation times of most long-lived species result in correspondingly slow adaptation to environmental changes that ultimately make long-lived species more vulnerable to permanent habitat changes and eventual extinction (Spencer and Janzen 2010).

The best strategy for long-lived organisms is to protect the populations and their critical habitat before they become dangerously depleted (Lippe et al. 2006). Life history characteristics of long-lived species can often result in very slow recovery times, which has been observed in a number of species, including the Emperor Penguin (*Aptenodytes forsteri*; > 40 years projected; Jenouvrier et al. 2009), the killer whale (> 50 years projected; Hickie et al. 2007), the green turtle (*Chelonia mydas*; approximately 40 years; Chaloupka and Balazs 2007), and the Nile crocodile (*Crocodylus niloticus*; >200 years projected; Bishop et al. 2009). However, due to their long generation times and naturally low reproductive rates, there is also often a lag in detection of negative consequences of human-mediated changes for these populations (e.g. Homyack and Haas 2009, McCoy et al 2010). Therefore, protection of species prior to their decline may not be an obvious conservation priority.

Overall, further study of these long-lived organisms is vital to their conservation (Gibbons et al. 2000). Reptiles, in particular, have been undergoing rapid decline, with 20% of reptile species listed as at risk of extinction and another 20% so understudied that their extinction risks cannot be assessed (Bohm et al. 2013).With more information on the basic biology of these long-lived species, which typically must be gathered as a part of a long-term study (Congdon et al. 1993, Congdon et al. 1994, Congdon et al. 2003, Smith et al. 2006), we could help minimize the effects of anthropogenic change. In our study of painted turtles, we found that emergent and floating vegetation, as well as CWH could be important habitat. With further knowledge on the ecology of this species, human development can be designed to have the least possible impact on habitat that is critical for the persistence of this long-lived species (Carrete et al. 2009).

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APPENDIX

APPENDIX 1

1.1 TABLES

Table 1.1. Study lake characteristics, listed from lowest to highest shoreline development. CWH=coarse woody habitat

	Latitude	Longitude	Area (km^2)	Proportion Shore Developed	Pier Density (#/km)	Road Density (km/km^2)	CWH Density (#/km)
South Lake	42° 23.56’ N	84° 4.06’ W	0.818	0.033	1.330	1.107	7.062
Crooked Lake	42° 19.29’ N	84° 6.45’ W	0.459	0.454	11.698	4.754	16.951
Grass Lake	42° 15.37’ N	84° 13.00’ W	1.428	0.515	5.902	4.674	8.572
Joslin Lake	42° 25.07’ N	84° 4.15’ W	0.786	0.612	19.713	4.106	1.556

Table 1.2. Summary of number of turtles (n), female:male sex ratio, and the proportion of turtles with a human-related injury for male and female painted turtles for each study lake. Note: because Joslin Lake had a much higher sample size than the other three lakes (n=100), we took a random subset of turtles and used those for the subsequent analyses. Only the sub-sample is shown here.

Lake	n	Sex Ratio (F:M)	Prop Male with Human Injury	Prop Female with Human Injury
South Lake	27	0.23:1	0.09	0
Crooked Lake	20	1:1	0	0
Grass Lake	25	0.19:1	0.05	0.25
Joslin Lake	29	0.45:1	0.11	0

Table 1.3. Correlation coefficients for all anthropogenic shoreline development metrics and natural in-lake features for painted turtles in the four study lakes. Note: CWH = coarse woody habitat, prop = proportion, and veg = vegetation.

	Prop Shore Dev	Pier Density	Road Density	Prop Submersed Veg	Prop Floating Veg	Prop Emergent Veg	CWH Density
Prop Shore Dev	1						
Pier Density	0.84**	1					
Road Density	0.92**	0.78**	1				
Prop Submersed Veg	0.75**	0.42**	0.48**	1			
Prop Floating Veg	0.25*	0.08	0.59**	-0.22*	1		
Prop Emergent Veg	-0.72**	-0.98**	-0.68**	-0.25*	-0.03	1	
CWH Density	-0.16	-0.07	0.23*	-0.69**	0.85**	0.00	1

** $p<0.01$, *$p<0.05$, $^{+}p<0.10$

Table 1.4. Results from linear (CL or carapace length) and logistic (sex ratios, injury) univariate regressions for male and female painted turtles, with predictor variables in columns and response variables in rows. Only significant associations are included along with the parameter estimate. Note: gray = no significant relationship, CWH = coarse woody habitat, CL=carapace length, prop = proportion, and veg = vegetation. na = relationship was not tested because it would not be ecologically meaningful

		Prop Shore Dev	Pier Density	Road Density	Prop Submersed Veg	Prop Floating Veg	Prop Emergent Veg	CWH Density	CL (cm)
	Sex Ratio		0.11^{+}				-0.29*		*na*
M	CL					0.23*		0.05^{+}	*na*
	Injury								0.89^{+}
F	CL								*na*
	Injury								

** $p<0.01$, *$p<0.05$, $^{+}p<0.10$

1.2 FIGURES

Figure 1.1. Examples of injuries classified as ‘human injuries.’ The left-most and center pictures are examples of suspected boat propeller injuries and the right-most picture is an example of a crushing injury, suspected to be from a vehicle. For interpretation of the references to color in this and all other figures, the reader is referred to the electronic version of this dissertation.

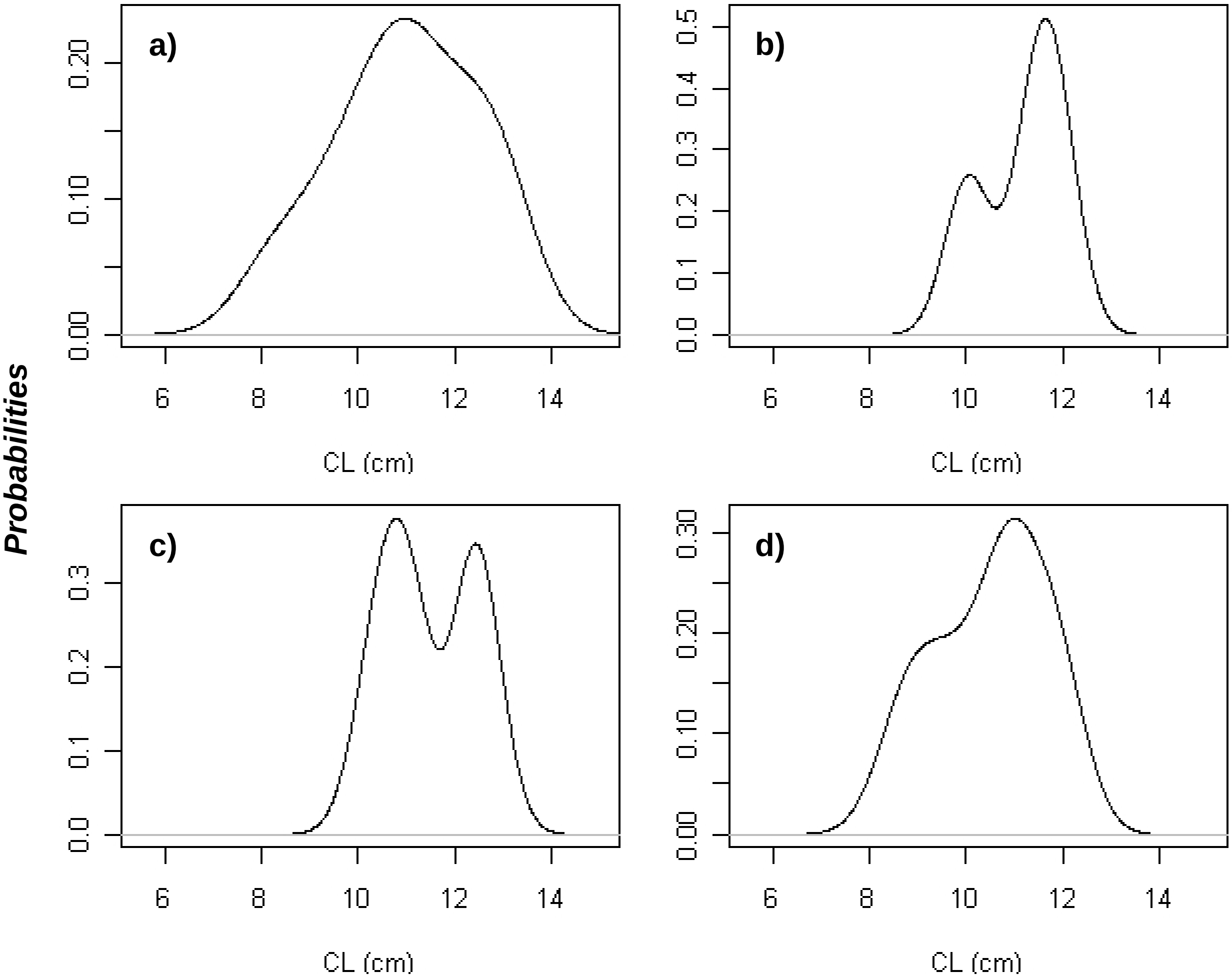

Figure 1.2. Distribution of male carapace lengths (CL; measured in cm) for each of the four study lakes: South Lake (a), Crooked Lake (b), Grass Lake (c), and Joslin Lake (d).

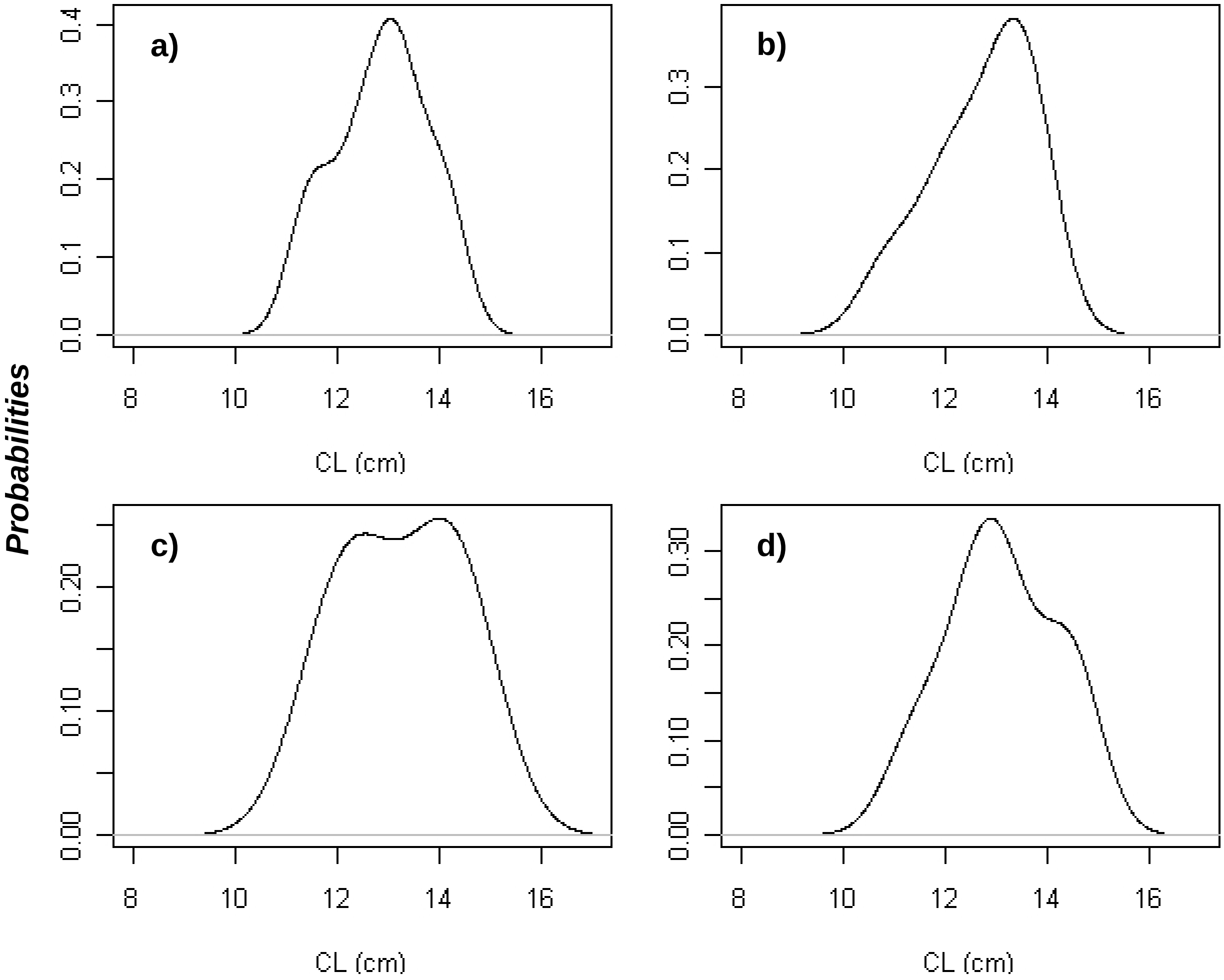

Figure 1.3. Distribution of female carapace lengths (CL; measured in cm) for each of the four study lakes: South Lake (a), Crooked Lake (b), Grass Lake (c), and Joslin Lake (d).

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CHAPTER 2

NORTHERN MAP TURTLE (*GRAPTEMYS GEOGRAPHICA*) IN-LAKE HABITAT USE AND THE EFFECTS OF RESIDENTIAL LAKESHORE DEVELOPMENT

Abstract

Lakes are popular sites for residential development and experience turtle habitat loss in both littoral and riparian areas as a result of this development. In this study of three Michigan inland natural lakes, we examined female northern map turtle (*Graptemys geographica*) spatial ecology (including home range and core area sizes) as well as how their habitat selection relates to lakeshore residential development. Using radio telemetry, we quantified in-lake habitat selection at two different spatial scales (macro- and microhabitat), using two different approaches (classification- based and distance-based), and multiple measures of lakeshore development. Turtles selected for submersed and floating vegetation and against deeper waters at the macrohabitat scale and selected for submersed vegetation and against deeper waters at the microhabitat scale. We also found that, although turtle home ranges contained a significantly lower percentage of developed shoreline as compared to the entire lake, turtles demonstrated within-home range preferences for developed shorelines, including shorelines with bulkhead walls, and piers. This relationship could not be explained by a general preference for nearshore areas. This preference for anthropogenic lake features could be a concern if it is increasing human-induced female turtle risk of injury or mortality, such as from boat propeller collisions. This study also provides evidence of habitat features (i.e., submersed and floating vegetation) and areas of the lake (i.e., shallower waters, nearshore areas) that should be a focus for northern map turtle management and conservation.

2.1 Introduction

Globally, reptile populations are in decline (Gibbons et al. 2000, Buhlmann et al. 2009, Todd et al. 2010), with up to one in five species threatened with extinction. Freshwater reptiles, including turtles, are among those most at risk (Buhlmann et al. 2009, Bohm et al. 2013). One suspected cause of this decline is the loss of critical habitat (Buhlmann et al. 2009, Todd et al. 2010, Bohm et al. 2013). Some reptiles, such as aquatic turtles, rely on lakes, streams, and wetlands for foraging and shelter, in addition to requiring the surrounding riparian areas for nesting habitat (Bodie 2001). As a result of their obligate use of both aquatic and riparian areas, aquatic turtles may be especially vulnerable to human activities, such as lakeshore residential development, that alter both nearshore terrestrial and aquatic habitat.

Lake shorelines, due in large part to the picturesque views and wealth of recreational opportunities that they offer, have long been popular sites for people to live (Gonzalez-Abraham et al. 2007). However, residential development can lead to changes in turtle habitat used for feeding, refuge, and basking. For example, when people build and maintain lakeshore homes, they often remove aquatic and terrestrial vegetation (Radomski and Goeman 2001, Jennings et al. 2003, Radomski 2006, Radomski et al. 2010). Aquatic vegetation is an important food source for some turtles (Padgett et al. 2010) and mats of vegetation floating at the water's surface can serve as basking sites (Peterman and Ryan 2009). In addition, the removal of riparian vegetation decreases the number of fallen trees, or amount of coarse woody habitat (CWH), entering the lake (Christensen et al. 1996, Francis and Schindler 2006, Roth et al. 2007). This CWH is used by aquatic turtles for refuge (Ernst and Lovich 2009) and basking (Lindeman 1999).

Homeowners may also stabilize the shoreline from further erosion by placing seawalls of concrete, riprap rocks, or other material at the land-water interface (Strayer and Findlay 2010).

This shoreline ‘hardening’ can affect littoral habitat. For example, concrete or other bulkhead-type walls are associated with high energy wave action (Strayer and Findlay 2010), which can uproot vegetation and alter sediments (Jennings et al. 1999). This loss of littoral habitat complexity associated with lakeshore residential development also negatively affects aquatic macroinvertebrate populations (Brauns et al. 2007, Brauns et al. 2011). Macroinvertebrates are often found by turtles at sites of CWH and aquatic vegetation (Lindeman 1999, Carriere and Blouin-Demers 2010) and can make up a large portion of aquatic turtle diets (Vogt 1981, Lindeman 2006, Bulte et al. 2008).

With increased lakeshore residential development we also see an increase in human recreational activities, such as swimming and boating (Strayer and Findlay 2010, Radomski et al. 2011). These activities can result in increased injury and mortality for turtles (Bulte et al. 2010, Heinrich et al. 2012). Therefore, shoreline development may discourage turtles from utilizing such high traffic areas.

Although we expect that all of these potential habitat changes associated with residential lakeshore development negatively affect turtle populations, only two studies have examined this idea. A study of northern map turtles (*Graptemys geographica*) found that turtles preferred shoreline habitat over open water habitat and were found at closer to undeveloped shorelines than to developed shorelines (Carriere and Blouin-Demers 2010). In addition, a long-term study of an Indiana lake turtle community found a decline in painted turtles (*Chrysemys picta*) over time that was attributed increased adult mortality due to a coincident combination of greater lakeshore residential development and increased boat traffic (Smith et al. 2006). This conclusion was supported, in part, by a concomitant increase in boat propeller injuries in this species (Smith et al. 2006). These studies suggest that turtle populations may be affected by, and changing their habitat use in response to, shoreline development.

In this study, we investigated female northern map turtle (*Graptemys geographica*) spatial ecology and habitat use in three Michigan inland natural lakes to determine how lakeshore residential development affects habitat selection in this species. Using radio telemetry, we quantified in-lake habitat use at two different spatial scales: the macrohabitat (defined as the home range) and the microhabitat (defined as the habitat selected within the home range). We used two different approaches to quantify habitat selection (classification- based and distance-based) and we calculated multiple measures of lakeshore development (location of developed and undeveloped shorelines, type of modification to shoreline [bulkhead seawall, rock seawall, man-made beach], and pier locations).

We explored the effects of lakeshore residential development on female northern map turtles for four main reasons. First, these native turtles' aquatic life history is closely tied to the shoreline. Northern map turtles have a relatively narrow diet, feeding primarily on mollusks and other nearshore invertebrates (Lindeman 2006, Bulte et al. 2008) that often live on the plants and CWH that are affected by lakeshore development (Jennings et al. 2003 and Christensen et al. 1996, respectively). In addition, CWH along the shoreline is an important basking site for this species (Pluto and Bellis 1986). Second, because females tend to nest close to their home waterbodies (Carriere et al. 2009, Steen et al. 2012), their nesting sites are also vulnerable to the negative effects of lakeshore development. Third, this species is listed as a species of concern in neighboring Ontario because relatively little is known about its ecology (COSEWIC 2011). Fourth, we focus solely on females because, as a sexually dimorphic species, females are much larger than males and, therefore, habitat selection is not as likely to be dictated by swimming ability (Carriere et al. 2009) but rather, preferences (Lindeman 2003).

Relatively little is known about the spatial ecology of female northern map turtles, generally, or site selection in response to shoreline development, more specifically. Although northern map turtles inhabit most waterbody types, including lakes (Ernst and Lovich 2009), previous studies of their spatial ecology and habitat selection have focused primarily on rivers (Pluto and Bellis 1986, Fuselier and Edds 1994, Carriere et al. 2009, Carriere and Blouin-Demers 2010) and/or reservoirs (Bulte et al. 2008, Carriere et al. 2009). The only study of northern map turtle spatial ecology in a lentic environment found that adult and juvenile females in a large reservoir had a mean home range size of approximately 1.5±0.25 km^2 (Carriere et al. 2009).

We know a little more about turtle habitat selection from studies in rivers and reservoirs than we do about lake habitat selection. Female northern map turtles in rivers and reservoirs have a documented preference for shallower, nearshore areas and an avoidance of the deepest waters (Bulte et al. 2008, Carriere and Blouin-Demers 2010). In rivers, female map turtles preferred areas with little submersed or emergent vegetation (Fuselier and Edds 1994) and open sandy shorelines (Fuselier and Edds 1994, DonnerWright et al. 1999). However, the habitat available for turtles in rivers and reservoirs differs substantially from natural lakes. Rivers have shallow flowing water and often have higher productivity than lakes (Randall et al. 1995). Reservoirs are typically much larger and deeper than natural lakes (e.g., the reservoir in Bulte et al. 2008 and Carriere et al. 2009 is five times larger in surface area and almost twice as deep as the largest, deepest lakes in our study) and often have reduced water clarity (Whittier et al. 2002). Therefore, we expected that northern map turtle habitat use in our natural lakes could be quite different from that found in these previous studies.

We came up with a set of expectations regarding female northern map turtle spatial ecology and habitat selection based on past research and the recognition that natural lakes provide turtles with different habitats than do rivers and reservoirs. For spatial ecology, we expected that the turtles in our study would have smaller home ranges because of easier foraging in lakes than found in the reservoir study (i.e. Carriere et al. 2009). As compared to larger, deeper reservoirs with reduced water clarity (Whittier et al. 2002), northern map turtles may have a relatively easier time finding prey in our small, shallow study lakes with potentially greater visibility and more shallow areas to support benthic macroinvertebrate prey. However, we could not make predictions for the size of core areas because no previous studies have calculated this feature of northern map turtle spatial ecology. For habitat selection, we expected that females would avoid lakeshore development due to its negative effects on habitat, food sources, and basking sites, in addition to its associated higher risk of injury or death from boat traffic (Table 2.1). Our study provides the first look into the spatial ecology of female northern map turtles in natural inland lakes (including home range and core area sizes) and is the first detailed study of female northern map turtle habitat selection in relation to shoreline development.

2.2 Methods

2.2.1 Study site

We collected turtles during their active season (June through August) during 2009 and 2010 from four natural inland lakes located in southeastern Michigan (Figure 2.1). We selected lakes that were located in close proximity to one another and were hydrogeomorphically similar, with all lakes being relatively small and shallow (Table 2.2; Figure 2.1). We also selected lakes with a public boat ramp that represented a range of shoreline development (Table 2.1). In addition to northern map turtles, these lakes supported populations of painted turtles (*Chrysemys picta*), common snapping turtles (*Chelydra serpentina*), common musk turtles (*Sternotherus odoratus*), spiny softshell turtles (*Apalone spinifera*), Blanding's turtles (*Emydoidea blandingii*), and had active sportfisheries.

2.2.2 Turtle data collection

We captured turtles using basking traps we constructed (following Browne and Hecnar 2005), baited hoop traps (2.5' diameter hoops with 1.5" diameter mesh, Memphis Net and Twine Co., Inc.), and by hand using dip nets. Traps were set in areas of the lake where turtles had previously been observed basking or where there was suitable habitat and depth for each trap type (i.e., shallow enough to allow air space in hoop traps and deep enough for the net on the basking trap to be fully submerged). Each captured turtle was sexed, aged (juvenile or adult, with juvenile females identified as having carapace lengths <17cm; Harding 1997), weighed, measured (carapace length and width), and marked with a unique identifying code by notching the marginal scutes with a hand file. We provided data for all northern map turtles captured in this study in Table 2.3.

Our unit of analysis was the individual female northern map turtle. We fitted 15 females (12 adults and 3 juveniles; Table 2.4) with radio transmitters purchased from Holohil Systems Ltd. (model RI-2B, 12 months of battery life). The transmitters, which did not exceed 5% of the body weight of the turtle (transmitters weighed 10g and the smallest turtle weighed 0.25 kg), were affixed to the left posterior carapace using a two-part epoxy. Transmitters were affixed to turtles while in the boat and turtles were released at the point of capture that same day. From the date of capture, turtles were tracked every 1-3 days by boat during their active season using a hand-held 3-element Yagi antenna (Telonics, Inc. model RA-17) and telemetry receiver (Telonics, Inc. model TR-4). The coordinates of each turtle relocation were recorded with a hand-held GPS (Garmin GPSmap 76S). We had 100% survival of radio tracked turtles and were able to detect transmitter signals even when turtles occupied deeper areas of the lake.

2.2.3 Lake habitat features

We measured a number of potential habitat features of the lake and its shoreline that might be preferentially selected or avoided by turtles, including macrophyte cover, water depth, and location of coarse woody habitat (CWH). Once each summer we estimated emergent, floating, and submersed macrophyte cover using the point-intercept method (Madsen 1999). Following Madsen (1999), we calculated the necessary number of macrophyte sampling points based on the lake surface area, lake depth, shoreline length, and littoral area. We then divided the surface area of the lake by the number of points to determine the distance between points, which ranged between 35 and 55 m for a total of 314 to 488 sample points per lake. Finally, at each point, we estimated the percent cover for each vegetation class (i.e. emergent, floating, and submersed). We obtained water depth throughout the lake from publically available, digitized bathymetric map layers (MiGDL 2012). We also recorded the location of coarse woody habitat (CWH) ≥10cm in diameter that was sufficiently above the water's surface to allow for basking (Lindeman 1999).

In addition to these natural lake features, we also measured features of human shoreline development that we expected turtles would preferentially use or avoid, including pier locations and residential shoreline development. Shorelines were classified as developed if there was any human modification to the land immediately adjacent to the lake; thus, shorelines with houses/structures, lawns, retaining walls, boat ramps, and man-made beaches were classified as developed. In addition to developed or undeveloped, we more finely classified the shoreline by the type of material at the water's edge: bulkhead retaining wall (i.e., wall composed of concrete, wood, or steel), rock retaining wall (i.e. wall composed of glacial stones or riprap), boat ramp, beach (man-made or natural), or natural shoreline. Natural shorelines had not been modified per one of the previous descriptions, although they were not necessarily completely undeveloped (i.e., there could be a structure or other non-shoreline modification sitting back from the shoreline at these sites).

For each of these natural and anthropogenic lake features, we predicted whether turtles would prefer or avoid the feature based on how each relates to northern map turtle life history (Table 2.1). Features that provide prey, refuge, and basking opportunities, including submersed vegetation, undeveloped and natural shorelines, and coarse woody habitat, were expected to be preferred (as cited in Table 2.1). We expected turtles to avoid locations that lacked prey, refuge or basking opportunities, such as developed shorelines and bulkhead walls, and locations with greater risk of injury and mortality, such as developed shorelines or piers (as cited in Table 2.1). For those features that are associated with both negative and positive attributes, we could not predict if they would be preferred or avoided (Table 2.1).

2.2.4 Spatial ecology of female northern map turtles

We calculated home ranges for all turtles for which we had at least 20 location points that fell within the lake where the turtle was originally captured (Edge et al. 2010); relocations outside of the lake were omitted from the analysis. We estimated active season home ranges defined as areas with a specific probability of occurrence of the animal during a specific time period (Kernohan et al. 2001). These were calculated using a 95% fixed kernel estimate, following another study of turtle movement within a small inland lake (Rowe et al. 2009). We estimated core areas, or areas within turtle home ranges that were used disproportionately more often than the remainder of the home range (Kernohan et al. 2001), using a 25% fixed kernel estimate. For both home ranges and core areas, we used the plug-in bandwidth estimation method that works well with most types of point distributions (Gitzen et al. 2006). Home ranges and core areas were clipped in ArcGIS to lie within the perimeter of each individual turtle's home lake. All home ranges and core areas were calculated using Geospatial Modeling Environment version 0.7.2.0 (Beyer 2012), ArcGIS version 10, and R version 2.13.2.

2.2.5 Habitat selection

We quantified habitat selection at two spatial scales: (1) the macrohabitat or home range-scale (second order selection, Johnson 1980) and (2) the microhabitat or within home range-scale (third order selection, Johnson 1980). In addition, we measured habitat selection using both a classification-based and distance-based approach (see below for details). Using these two methods in conjunction can lend further insight into habitat selection that may not be apparent using each method in isolation (Conner et al. 2003, DeGregorio et al. 2011).

2.2.6 Classification-based approach for habitat selection

For the classification-based approach, we associated each home range and core area with natural and anthropogenic lake features within the lake and along the lake shoreline. However, we could only associate shoreline features (i.e., shoreline development, pier density, CWH density) with home ranges because most core areas did not come into direct contact with the lake shorelines (see Figure 2). Lake features were classified as percentages (i.e. percent vegetation cover, percent modified shoreline), densities (i.e. pier and CWH density), or as a summary value (i.e. mean or maximum depth). To quantify macrohabitat selection, we compared natural and anthropogenic lake features within home ranges to available features at the scale of the entire lake. For microhabitat selection, we compared features within the core areas to the same features within the corresponding home range. We compared habitat selection to habitat availability at both scales using Wilcoxon signed-rank tests because our variables of interest failed to meet normality assumptions even after transformation. All analyses were conducted in R version 2.13.2.

2.2.7 Distance-based approach for habitat selection

Distance-based habitat selection was based on Euclidean distances between turtle point locations and lake features (Conner and Plowman 2001). For this method, we first generated 1000 random points throughout each lake and 200 random points within each turtle's home range to compare with actual turtle telemetry relocations (n=352). For each habitat type (e.g., vegetation point, CWH location, pier location), we then calculated the distance from each random point and each turtle telemetry relocation point to the nearest point with a habitat feature (e.g., CWH, submersed vegetation).

To determine macrophyte habitat preferences, we calculated the distance from each random and actual turtle location point to the nearest vegetation point with any percent cover. The exception was submersed vegetation, for which we measured the distance to points with ≥50% submersed vegetation cover because ≥60% of the vegetation points throughout the lake had submersed vegetation cover. For water depth, we measured the distance from each point to a depth that exceeds the mean depth of all lakes (≥3 m) in order to quantify preferences for or against deep waters.

Habitat availability at the macrohabitat scale (l_{ij}) was defined as the mean distance from the 1000 random lake points to each habitat feature (*j*) for each individual (*i*). Therefore, macrohabitat use was quantified as the distance from random points in each turtle's home range to each habitat feature (r_{ij}). The ratio of macrohabitat use to availability ($d_{ij} = r_{ij} / l_{ij}$) was calculated for each turtle. If turtles were selecting habitat randomly, than $d_{ij} = 1$; values of $d_{ij} < 1$ indicate preference for a habitat and values of >1 indicate avoidance. We made a similar calculation for microhabitat use, with available habitat defined as the distance from random points in each home range to the nearest habitat feature of each type (r_{ij}) and microhabitat use defined as the distance from telemetry relocations in each home range to habitat features (u_{ij}). Again, ratios of use to availability ($d_{ij} = u_{ij} / r_{ij}$) were calculated for each habitat and each turtle. To quantify macro- and microhabitat selection, we used multivariate analysis of variance (MANOVA) to determine if ratios of habitat use to habitat availability (d_{ij}) differed from random (i.e., $d_{ij} = 1$) using a separate MANOVA for each scale of analysis. When there was evidence of habitat selection, we used two-tailed t-tests to determine which habitats were being used disproportionately to their availability. In addition, paired t-tests were used to rank habitat preferences when appropriate. All analyses were conducted in R version 2.13.2.

2.3 Results

2.3.1 Spatial ecology of female northern map turtles

Although we had 100% survival of our tracked turtles, four turtles were not included in analyses because they were captured too late in the season or were tracked to a location outside of the lake for an extended period resulting in an insufficient number of relocations (i.e. <20). Thus, we calculated home ranges for 11 turtles, (n=9 turtles from Joslin Lake and n=1 each for Crooked and Grass Lakes; Table 2.4). Turtle home ranges during the active season ranged in size from 0.23 to 0.79 km^2, with an average size of 0.51±0.6 km^2 (mean ± 1 SE ; Figure 2.2 and Table 2.4). These home range areas represent between 34.44 to 99.95% of the lake area, or an average 63.66±6.29% of the lake. Juvenile females, although smaller in size (mean carapace length of ~14 cm compared to adults at ~21 cm), had home ranges that fell within the range of adult home range sizes (Table 2.4). Thus, we included both juveniles and adults in our analysis. We did not find significant associations between home range area and carapace length (r = 0.38, p=0.25) or home range area and body weight (r = 0.40, p = 0.22) across all lakes. However, when home range size is represented as a proportion of the total lake area, we found a marginally significant association between home range area and both turtle carapace length (r = 0.59, p=0.06; Figure 2.4a) and turtle body weight (r = 0.59, p=0.05; Figure 2.4b) across all lakes. This suggests that home range size, on a lake by lake basis, may be affected by turtle body size.

In addition to the home ranges, we determined each turtle's core area(s) during the active season (Figures 2.2 and 2.3). Each turtle had either one or two core areas within their home range. These core areas ranged from 0.02 to 0.14 km^2 (mean = 0.06 ± 0.01 km^2) in size, or between 7.33% and 17.99% of the corresponding home range area (mean = 10.91 ± 1.19%). Joslin Lake's core areas had a great deal of spatial overlap for its multiple turtles (Figure 2.3). There was no correlation between core area size and carapace length or body weight (r<0.40,

$p > 0.20$ for both), nor was there a relationship between core area size as a percent of the home range and carapace length or body weight ($r < 0.40$, $p > 0.25$ for both).

2.3.2 Turtle habitat selection

We found evidence for non-random habitat selection at the macrohabitat and microhabitat scales using both classification-based and distance-based approaches. At the macrohabitat scale, female northern map turtles preferentially selected areas of the lake with more submersed and floating vegetation and avoided deeper areas of the lake. Home ranges also contained a significantly lower percentage of developed shoreline as compared to the entire lake. At the microhabitat scale, we found turtles selecting for submersed vegetation and against deeper waters. In addition, we found microhabitat selection for developed shorelines, especially bulkhead seawalls, and piers.

2.3.3 Classification-based approach for habitat selection

Although there was no difference in mean water depth between home ranges and the entire lake mean water depth, we found a significant difference between the maximum depth of home ranges and the entire lake. Home range maximum depths were 1.11m shallower ($p=0.05$) on average than the maximum lake depths (Table 2.5). The remaining natural lake features, including density of CWH and percent submersed, floating, and emergent vegetation, occurred at a frequency within the home range that was indistinguishable from what was measured in the corresponding lake (Table 2.5). For anthropogenic features, home ranges contained 10% less developed shoreline (48.81±3.54% developed) as compared to the entire lake (58.87±1.61%

developed), but there was no difference in density of piers or percentage of hardened (i.e., bulkhead) shoreline in home ranges as compared to the entire lake (Table 2.5).

When we compared the habitat in core areas to the habitat in corresponding home ranges, we found evidence of microhabitat selection. Core areas had a significantly shallower maximum depth (2.49±0.23m) and a greater percentage of submersed vegetation cover (78.94±3.34%) as compared to home ranges (4.71±0.52 m and 73.79±2.15%, respectively; Table 2.5). No other natural or anthropogenic habitat features in core areas differed significantly from the habitat available at the scale of the entire home range (Table 2.5).

2.3.4 Distance-based approach for habitat selection

We found evidence supporting non-random macrohabitat selection ($F_{[10,11]}$=215.7, p<0.0001; Figure 2.5) using the distance-based approach. Points within turtle home ranges were significantly closer to submersed vegetation locations (i.e., sites with at least 50% submersed macrophyte cover) than random points throughout the entire corresponding lake (d_{ij} = 0.82±0.03; p<0.005; Figure 2.5). In addition, turtle relocations within home ranges were significantly closer to floating vegetation than random lake points (d_{ij} = 0.72±0.03; p<0.005; Figure 2.5). Comparing these two habitats, we found that floating vegetation was significantly preferred over submersed vegetation (t=3.33, p<0.005). No other habitat features were selected non-randomly at the macrohabitat scale.

At the microhabitat scale, we also found evidence for non-random habitat selection ($F_{[10,11]}$=112.98, p<0.0001; Figure 2.6). Of the natural lake features, only deep water habitats were selected non-randomly. Turtle telemetry relocations were at a greater distance from deep waters than points throughout the home range (d_{ij} = 1.15±0.07, $p<0.05$) indicating that turtles are avoiding the deeper water areas within their home ranges. Turtle telemetry locations were located at a shorter distance from the three anthropogenic features (i.e., developed shorelines, piers, bulkhead retaining walls) as compared to the random points throughout the home range (Figure 2.6), indicating a preference for these features within the home range. Turtles were closest to developed shorelines (d_{ij} = 0.87±0.05; Figure 2.6) out of the three anthropogenic features, followed by piers (d_{ij} = 0.89±0.05) and bulkhead walls (d_{ij} = 0.92±0.04). However, the only difference in preference among these three features was between developed shorelines and shorelines with bulkhead walls, with developed shorelines marginally preferred over shorelines with bulkhead walls ($t=1.88$, $p=0.09$).

2.4 Discussion

With habitat loss cited as one of the greatest threats to reptiles (Bohm et al. 2013), it is important to identify and protect critical reptile habitat. There have been few studies of northern map turtle spatial ecology or habitat use, and existing studies have been conducted mainly in rivers and relatively large reservoirs. In this study, we quantified female northern map turtle in-lake habitat use in lakes at two different spatial scales using two different approaches and in relation to multiple measures of lakeshore development. Our results provide the first insight into the spatial ecology of female northern map turtles in natural lakes and their selection in relation to lakeshore development.

2.4.1 Spatial ecology of female northern map turtles

Female northern map turtle home ranges in this study were smaller in size but far exceeded the percentage of the waterbody used than home ranges calculated in the only previous study of this species in a lentic environment (0.51±0.6 km^2as compared to 1.5±0.25 km^2 in the large reservoir in Carriere et al. 2009). The fact that the majority of the lake was used by our turtles (63.66±6.29%) suggests that home range sizes in our study were not dictated solely by swimming ability. We might expect larger home ranges in more turbid reservoirs, and our smaller home ranges may imply easier turtle foraging in our relatively shallower systems. Alternatively, home range sizes may be affected by nesting locations, as suggested in Carriere et al. (2009), with fewer riparian nesting sites resulting in larger home ranges. Therefore, future research should quantify in-lake prey density and distribution and riparian nesting locations to determine whether food availability, nesting sites, or another important habitat feature (e.g, habitat used for basking or refuge) dictates home range sizes.

Ours was the first study to calculate core activity areas for this species; thus we had no predictions about core area size nor can we make comparisons with previous studies. However, we did see a large amount of spatial overlap among home ranges in the lake where comparison among turtles was possible (Figure 2.3). This suggests that core area locations may be dictated by a commonly used resource, as we explore below.

2.4.2 Habitat selection in female northern map turtles

Using two approaches, we found an avoidance of deeper waters at both macro- and micro-habitat scales (Table 2.5 and Figure 2.6). These results are similar to previous studies of northern map turtle habitat use (e.g., Bulte et al. 2008, Carriere and Blouin-Demers 2010) and make sense because deeper water will be colder, darker, and have fewer macroinvertebrate prey

(Weatherhead and James 2001) making deeper waters less desirable foraging locations. As we expected (Table 2.1), we also found that home ranges contained more submersed vegetation than was available at the scale of the entire lake using the distance-based approach (Figure 2.5). This result makes sense because submersed vegetation provides habitat for northern map turtles' invertebrate prey (Bulte et al. 2008, Butler and deMaynadier 2008, Carriere and Blouin-Demers 2010), refuge for younger, smaller turtles (Pluto and Bellis 1986), and large mats of submersed vegetation that can serve as basking sites (Peterman and Ryan 2009).

We found a strong preference for floating vegetation at the macrohabitat scale when using the distance-based method (Figure 2.5). Although we did not detect a similar preference using the classification approach (Table 2.5), the greater proximity to floating vegetation (than was observed with random points in the entire lake) might be indicative of its potential as a refuge. For instance, high speed boating is unlikely to occur in shallow areas with abundant floating vegetation. Turtle home ranges may not need to have disproportionately high floating vegetation cover if turtles stay relatively close to floating vegetation refuge sites. Previous studies have demonstrated male northern map turtle preference for vegetative cover (Carriere and Blouin-Demers 2010), but we believe our study provides the first evidence for female northern map turtle floating vegetation preference.

2.4.3 Habitat selection in relation to lakeshore development

We predicted that turtles would avoid most anthropogenic features at both the within-lake and within-home range scales (Table 2.1). Although turtle home ranges contained significantly less developed shoreline as compared to the total percentage of developed shoreline at the scale of the entire lake (Table 2.5), distance-based analyses demonstrated a preference for developed shorelines at the microhabitat, or within home range, scale (Figure 2.6). Furthermore, piers and bulkhead-reinforced shorelines were preferred at the microhabitat level (Figure 2.6), which was contrary to our expectations (Table 2.1). Piers may provide structure for invertebrate prey to live upon, making piers a site for foraging. Conversely, bulkhead walls are associated with lower abundance of mollusk prey (Brauns et al. 2007). Another explanation for these unexpected results is that female northern map turtles may have a preference for any nearshore habitat, regardless of whether or how it is developed. Such a preference has been documented in previous studies (Bulte et al. 2008, Carriere and Blouin-Demers 2010) and our results support the notion that turtles prefer shoreline within home ranges, regardless of development type (d_{ij} = 0.86±0.06, t = 2.15, p=0.06). We also expected to find a preference for undeveloped and natural shorelines that was not found at the microhabitat scale (d_{ij} = 0.89±0.07, t = 1.61, p=0.14 and d_{ij} = 0.89±0.07, t = 1.51, p=0.16, respectively). This result suggests that turtles prefer *any* shoreline habitat, independent of development, and that they counter intuitively prefer developed shorelines.

Although we cannot explain female map turtles preferring anthropogenic shoreline features over natural ones, this finding raises the concern that female northern map turtles may prefer areas of the lake that have high human traffic. This could increase their risk for injury or mortality from boat propellers. In fact, a study in the St Lawrence River and its reservoirs documented high boat injuries in female northern map turtles in high traffic areas (Bulte et al. 2010).

Habitat selection studies that include multiple spatial scales of habitat selection (i.e., macro- and microhabitat) and employ multiple approaches to quantify habitat selection (i.e., distance-based and classification-based) are necessary for identifying important turtle habitat preferences and potential risks associated with such preferences. Although we know that aquatic turtles are an important component of lake ecosystems, exceeding fish biomass in some freshwater systems (Aresco 2009), they are rarely considered when developing management plans for waterbodies and riparian zones (Bodie 2001). Our study provides evidence of important turtle habitat in small inland lakes, which can be used to inform lake management plans and ensure protection of critical northern map turtle habitat. For instance, management plans could encourage the installation of riprap or other natural shoreline stabilization methods. These methods would better protect the submersed and floating vegetated habitat (Jennings et al. 2003) and macroinvertebrate prey (Brauns et al. 2007, Brauns et al. 2011) that are important resources for turtles and other lake organisms (e.g., fish feeding on benthic macroinvertebrates in Schindler and Scheuerell 2002, green frogs [*Rana clamitans*] utilizing shorelines with floating vegetation in Woodford and Meyer 2003). Because habitat loss is one of the biggest threats to reptile populations world-wide (Bohm et al. 2013), quantifying habitat selection is necessary to identify and protect important habitat features, particularly for understudied species such as the northern map turtle.

2.5 Acknowledgements

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APPENDIX

APPENDIX 2

2.1 TABLES

Table 2.1. Habitat features, their relation to northern map turtles (NMT), and our predictions about turtles' relative preference for each habitat type.

Predicted Preference	***Habitat Feature***	***Relation to Northern Map Turtle***
Preferred	Submersed Vegetation	Source of prey (invertebrates living on plants[1,2,3]), refuge for smaller, younger turtles[3,4], basking site[5]
	Coarse Woody Habitat	Basking site[4,6,7], source of prey (invertebrates living on CWH[6])
	Undeveloped Shorelines	Habitat intact (e.g., vegetation[8], CWH[9]), source of prey[10,11], refuge[4]; preferred in previous studies[3]
Unknown	Floating and Emergent Vegetation	Potential refuge and forage[3] but may also impede movement with thick, rigid stems; both preferred[2,3] and avoided[4] in previous NMT studies
	Deep Water	Deeper water may be darker and colder and sites of high human activity[12]; fewer littoral macroinvertebrates[14] but other prey (mussels) is abundant[3]; both preferred[4] and avoided[3] in previous NMT studies
	Natural Shorelines	Habitat intact (e.g., vegetation[8], CWH[9]), source of prey[10,11], but still potential site of high human activity (i.e., shoreline intact but may still have human presence)

Table 2.1. (cont'd)

Predicted Preference	***Habitat Feature***	***Relation to Northern Map Turtle***
Not Preferred	Piers	Sites of high human activity[13], boat noise, potential injury or death[12]
	Developed Shorelines	Sites of high human activity, changes in habitat (e.g., decrease in vegetation[8] and CWH[9]); avoided in previous studies[3]
	Bulkhead Retaining Walls	Changes in vegetation[8] and macroinvertebrate communities[10,11]

[1] Vogt (1981), [2] Bulte et al. (2008), [3] Carriere and Blouin-Demers (2010), [4] Pluto and Bellis (1986), [5] Peterman and Ryan (2009), [6] Lindeman (1999), [7] Ernst and Lovich (2009), [8] Jennings et al. (1999), [9] Christensen et al. (1996), [10] Brauns et al. (2007), [11] Brauns et al. (2011), [12] Bulte et al. (2010), [13] Radomski et al (2010), [14] Weatherhead and James 2001

Table 2.2. Study lake characteristics, listed from lowest to highest shoreline development. No=number, CWH=coarse woody habitat

	Latitude	Longitude	Area (km^2)	Mean Depth (m)	Max Depth (m)	Proportion Shore Developed	Pier Density (#/km)	CWH Density (#/km)
Crooked Lake	42° 19.29’ N	84° 6.45’ W	0.459	2.900	6.096	0.454	11.698	16.951
Grass Lake	42° 15.37’ N	84° 13.00’ W	1.428	1.559	3.048	0.515	5.902	8.572
Joslin Lake	42° 25.07’ N	84° 4.15’ W	0.786	2.300	6.096	0.612	19.713	1.556

Table 2.3. Summary of all captured northern map turtles, including total number captured (n), female:male sex ratio, the proportion of turtles with a human-related injury for males and females, and the mean (± standard error) carapace length for males and females in each study lake. CL = carapace length, na = not available

Lake	n	Sex Ratio (F:M)	Prop Male with Human Injury	Prop Female with Human Injury	Mean Male CL ± SE (cm)	Mean Female CL ± SE (cm)
Crooked Lake	17	0.55:1	0	0	10.29 ± 0.50	16.78 ± 1.45
Grass Lake	3	3:0	*na*	0	*na*	14.90 ± 3.21
Joslin Lake	27	1:1	0.07	0.07	11.09 ± 0.51	19.97 ± 1.19

Table 2.4. Characteristics of individual female northern map turtles that were fitted with transmitters, including the lake where the turtle was captured, adult (Y for yes, N for juvenile), carapace length (CL), weight, and total number of relocations. For turtles with $\geq$ 20 relocations, we also include home range (HR) area, and core area (CA) area.*na* = not available

Turtle	Lake	Adult?	CL (cm)	Weight (kg)	No. Relocations	HR Area (km^2)	CA Area (km^2)
BCE	Crooked Lake	Y	19.5	0.90	41	0.23	0.02
CDE	Crooked Lake	Y	18.8	0.74	15	*na*	*na*
BCX	Grass Lake	N	16.2	0.51	21	0.71	0.06
CDF	Grass Lake	Y	19.7	0.89	10	*na*	*na*
ABS	Joslin Lake	Y	23.3	1.60	40	0.79	0.14
ABT	Joslin Lake	Y	24.5	1.75	30	0.63	0.06
ABU	Joslin Lake	Y	25.8	2.50	39	0.65	0.07
BCH	Joslin Lake	Y	18.4	0.70	37	0.64	0.11
BCI	Joslin Lake	Y	23.9	2.00	12	*na*	*na*
BCJ	Joslin Lake	Y	23.1	1.80	8	*na*	*na*
BCM	Joslin Lake	Y	20.3	1.10	34	0.27	0.02
BCO	Joslin Lake	Y	21.5	1.10	31	0.57	0.09
BCP	Joslin Lake	N	12.9	0.25	30	0.37	0.04
BCU	Joslin Lake	Y	17.7	0.63	25	0.32	0.03
BCV	Joslin Lake	N	13.0	0.25	24	0.48	0.04

Table 2.5. Macrohabitat and microhabitat results comparing habitat use in the entire lake to that in the home range or comparing habitat in the home range to that within core areas. Comparisons were done using a classification-based approach and the Wilcoxon signed-rank test. Numbers represent the mean difference in habitat use at each scale and the signs (+/-) show the direction of change when each available habitat feature is subtracted from the habitat selected. Habitat features that lie along the lake shoreline (i.e., shoreline development, pier density, CWH density), were not calculated for core areas because most core areas did not contain immediate shoreline habitat. *na*=not applicable

	Macrohabitat	*Microhabitat*
Submersed Vegetation Cover	+2.71%	**+5.17%**$^{+}$
Floating Vegetation Cover	-0.03%	-0.54%
Emergent Vegetation Cover	+0.86%	-1.79%
Mean Depth	-0.14 m	-0.08 m
Maximum Depth	**-1.11 m**$^{+}$	**-2.22 m***
Developed Shoreline	**-10.06%***	*na*
Bulkhead Wall	+3.92%	*na*
Natural Shoreline	-2.93%	*na*
Pier Density	+0.00/km	*na*
CWH Density	-0.00/km	*na*

** $p<0.01$, *$p<0.05$, $^{+}p<0.10$

2.2 FIGURES

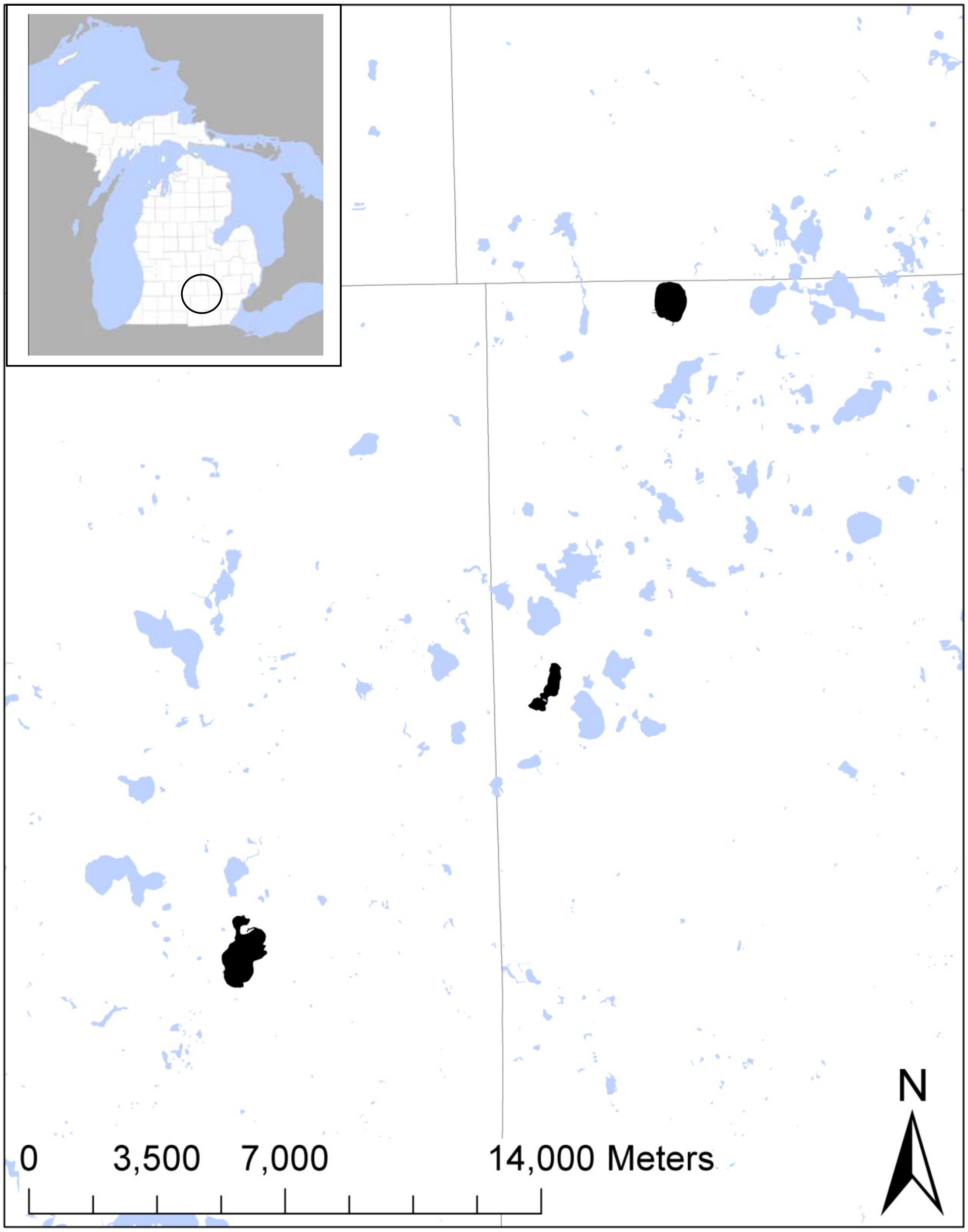

Figure 2.1. Map of our three study lakes (Joslin Lake, Crooked Lake, and Grass Lake from north to south) in southeastern Michigan, USA.

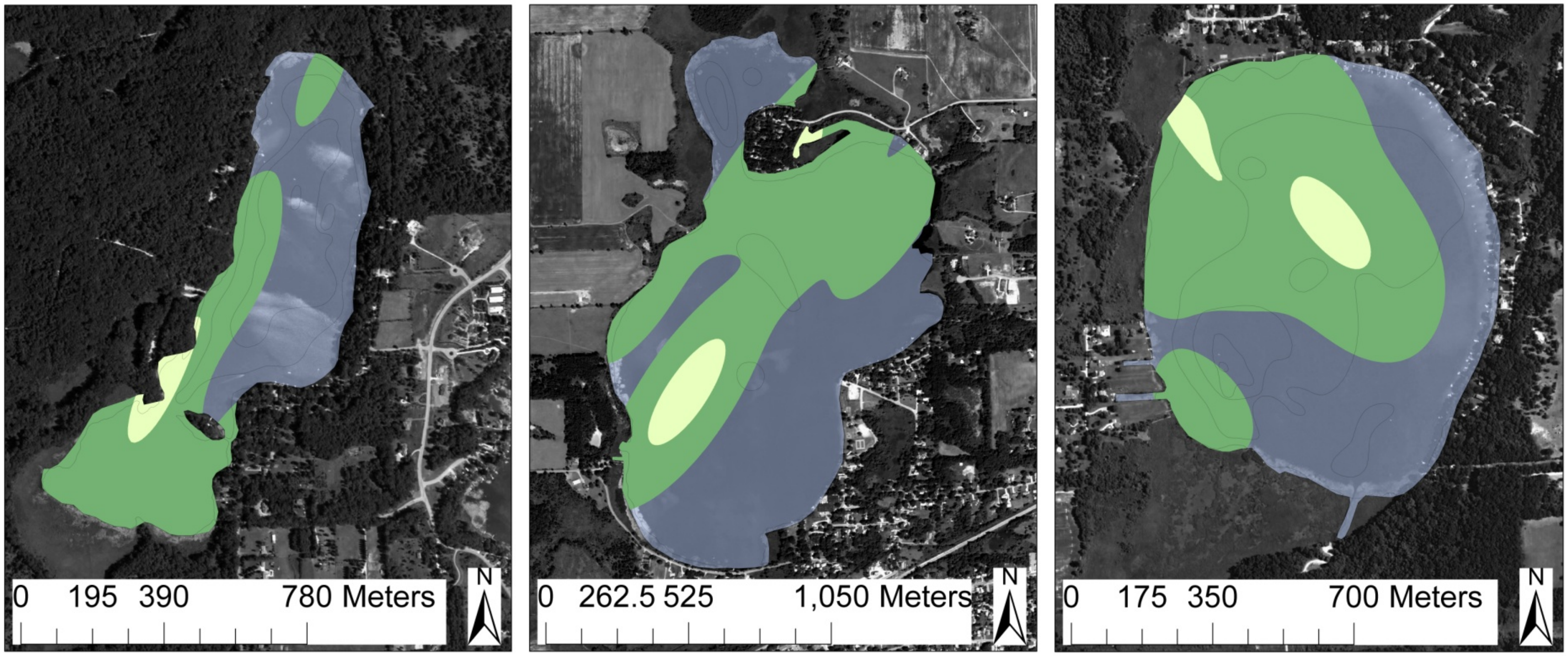

Figure 2.2. Our study lakes (Crooked Lake, Grass Lake, and Joslin Lake from left to right, lowest to highest development), including 1.5 m depth contours. An example home range for a single turtle in each lake is depicted in dark green and the corresponding core area is depicted in light green.

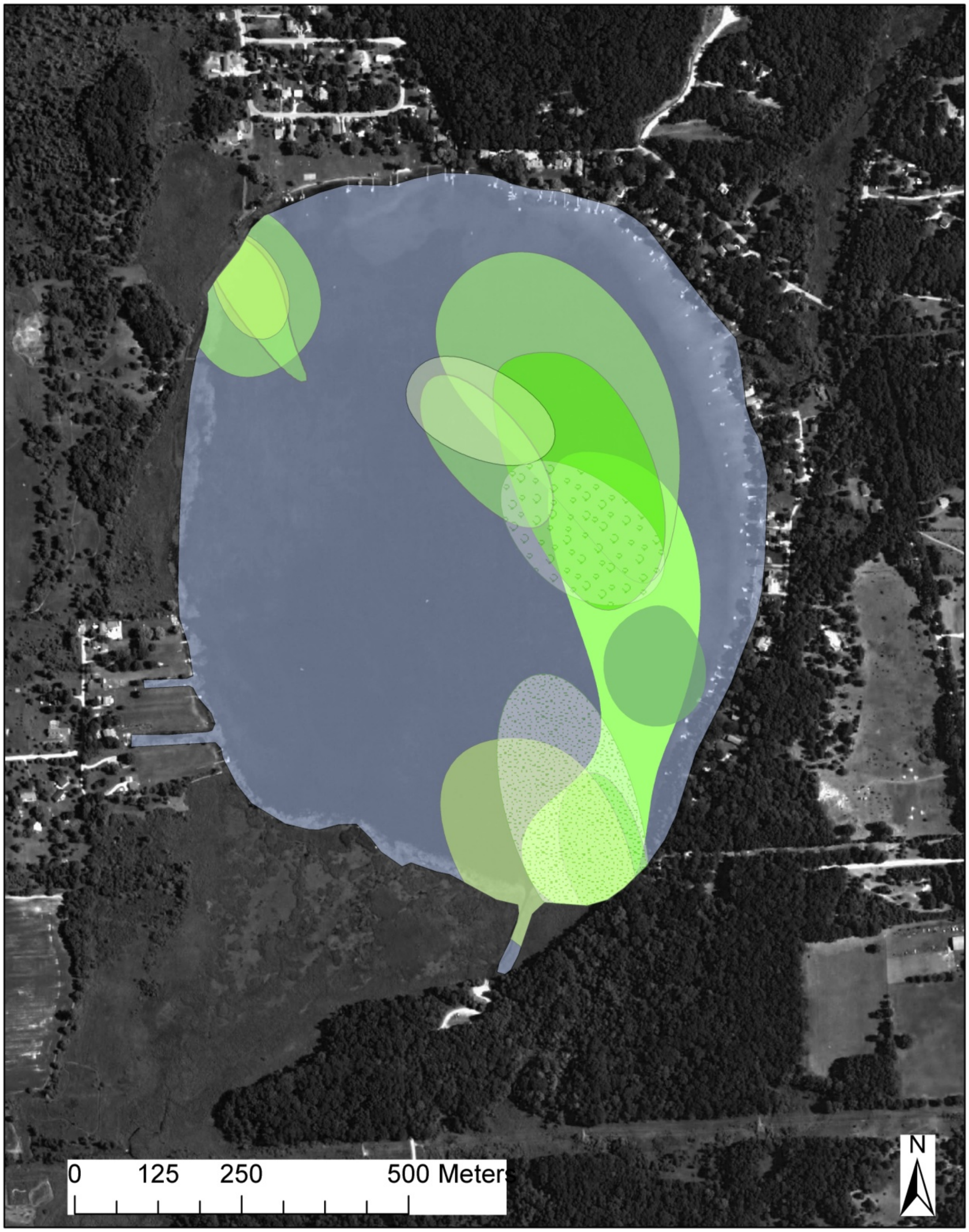

Figure 2.3. A map of Joslin Lake's core areas showing overlap in habitat used among turtles (n = 9).

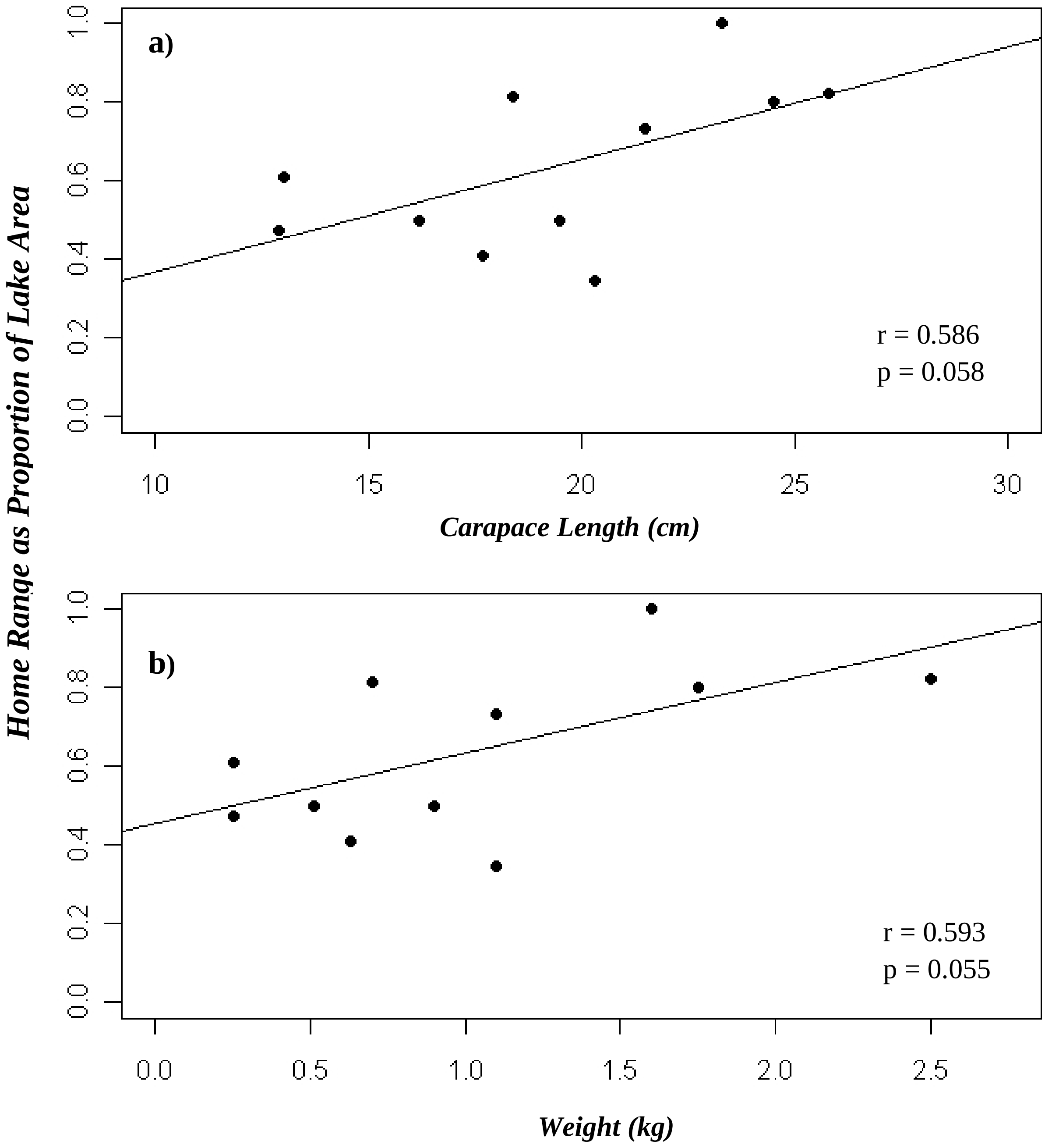

Figure 2.4. Correlation between turtle carapace length and home range area measured as proportion of total lake area (a) and between turtle weight and home range area as measured as proportion of total lake area (b).

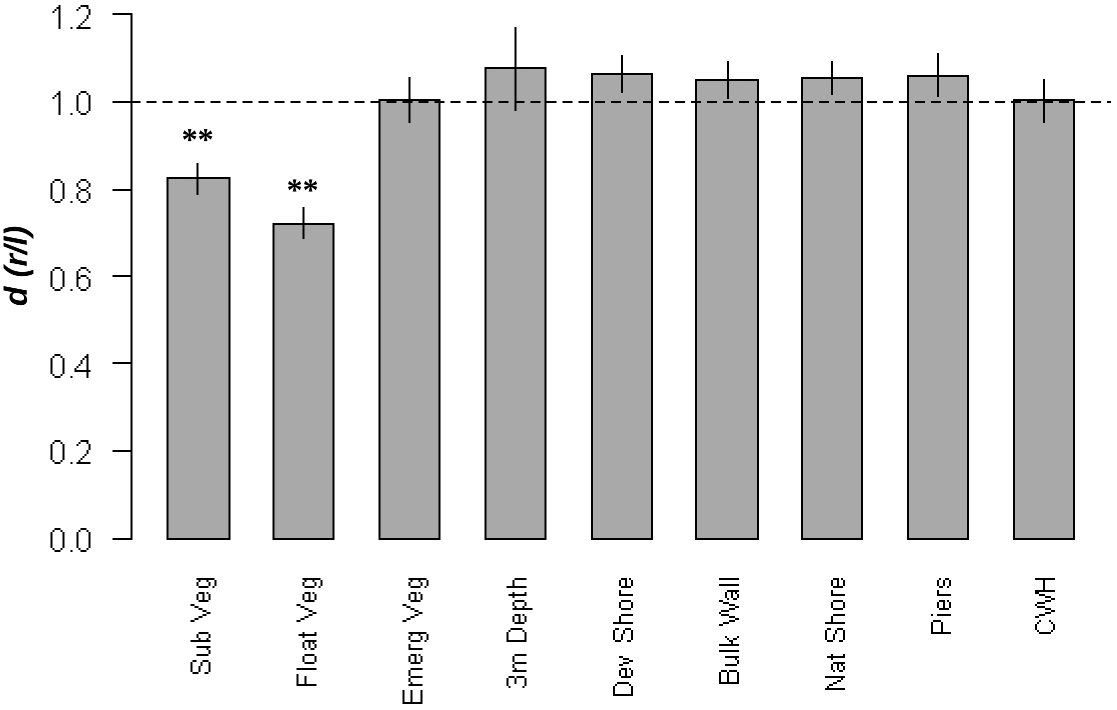

Figure 2.5. Results from the distance-based approach using MANOVA to identify non-random macrohabitat selection. Because the MANOVA was significant ($F_{[10,11]}$=215.7, $p<0.0001$), t-tests were used to identify significant differences in macrohabitat selection (**$p<0.01$, *$p<0.05$, $^{+}p<0.10$) from random (*d*=1), with a *d* value of <1 indicating preference for the habitat features and *d* value of >1 indicating avoidance of the habitat feature.

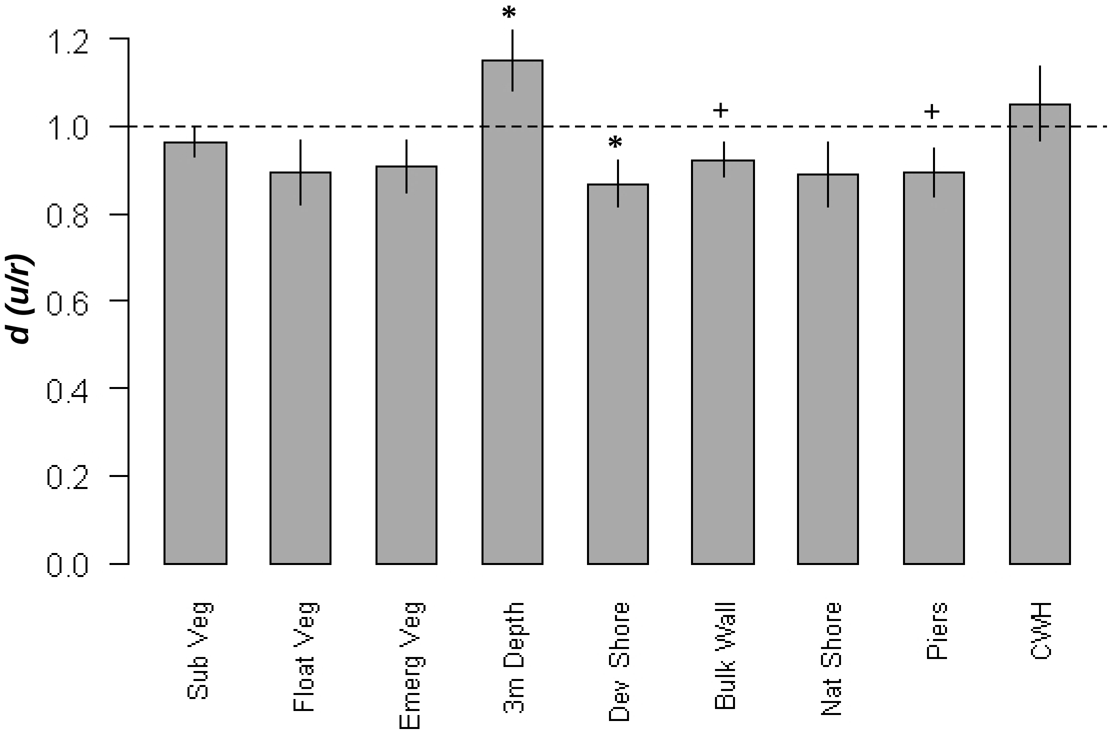

Figure 2.6. Results from the distance-based approach using MANOVA to identify non-random microhabitat selection. Because the MANOVA was significant ($F_{[10,11]}=112.98$, $p<0.0001$), t-tests were used to identify significant differences in microhabitat selection (**$p<0.01$, *$p<0.05$, $^{+}p<0.10$) from random (*d*=1), with a *d* value of <1 indicating preference for the habitat features and *d* value of >1 indicating avoidance of the habitat feature.

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CHAPTER 3

EFFECTS OF HUMAN LAKESHORE DEVELOPMENT AND THE EXOTIC INVASIVE ZEBRA MUSSEL (*DREISSENA POLYMORPHA*) ON BENTHIC-PELAGIC LINKAGES IN LAKES

Abstract

Aquatic systems are impacted by multiple stressors; however, most studies focus on the effects of a single stressor. In this study, we explored the food web effects of two potential anthropogenic stressors, lakeshore residential development and invasion by the exotic zebra mussel, on lake food webs. These two potential stressors are known to have profound effects on benthic areas that could result in lake-wide effects. Using stable isotopes, we quantified the effects of these two potential whole-lake stressors on the proportion of benthos in the diet and trophic position of two fish species (bluegill [*Lepomis macrochirus*] and largemouth bass [*Micropterus salmoides*]) across eight Michigan inland lakes with a range of shoreline development and zebra mussel presence/absence. We found a significant negative relationship between bluegill trophic position and lakeshore development; however, contrary to expectations, there were no other significant findings. These results could be due to the relatively low effect of these potential stressors on fish food web metrics; on the other hand, these findings could be indicative of the opposing effects of these two stressors, with zebra mussels increasing benthic macroinvertebrate, macrophyte, and algal productivity in opposition to the negative impacts of shoreline development on these same benthic organisms. Although difficult to undertake, studies of multiple stressors in lakes can provide a more thorough understanding of lake responses to anthropogenic changes.

3.1 Introduction

Aquatic ecosystems are increasingly exposed to and potentially impacted by multiple anthropogenic stressors simultaneously (Christensen et al. 2006, Crain et al. 2008, Darling and Cote 2008, Altshuler et al. 2011, O'Gorman et al. 2012). Yet, most studies consider a single stressor, limiting our understanding of how they function in combination (Crain et al. 2008). Lakes, in particular, have long been the site of intense residential development (Walsh et al. 2003, Gonzalez-Abraham et al. 2007) and recreation (Wilson and Carpenter 1999, Reed-Andersen et al. 2000, MA 2005), and this human activity is associated with a suite of anthropogenic stressors. Because they are at the human development-water interface, lake benthic areas may be particularly vulnerable to a number of such stressors, including lake shoreline modification (e.g., Brauns et al. 2011), aquatic vegetation manipulation (Jennings et al. 2003), and invasion by non-native species that can disproportionately affect the physical benthic habitat and ecological interactions in shallow nearshore areas (e.g., rusty crayfish [*Orconectes rusticus*] in Nilsson et al. 2011, zebra mussel [*Dreissena polymorpha*] in Higgins and Vander Zanden 2010).

Research during the past decade has demonstrated the many linkages that exist between lake benthic and pelagic zones and the importance of benthic zones to the functioning of the whole-lake ecosystem (Schindler and Sheuerell 2002, Vander Zanden and Vadeboncoeur 2002, Sass[b] et al. 2006, Reynolds 2008, Vander Zanden et al. 2011). These studies suggest that any stressors affecting benthic areas could potentially have lake-wide effects. Thus, there is a need for researchers to study the effects of *multiple* benthic stressors at the scale of the entire lake. In this study, we used stable isotopes to quantify the whole-lake food web effects of two anthropogenic stressors with potentially large effects on benthic areas: human lakeshore residential development and invasion by the non-native zebra mussel.

In addition to the construction that accompanies lakeshore residential development, there are a number of other alterations at residential development sites that directly affect the physical benthic habitat, including the stabilization and alteration of the shoreline with man-made materials, installation of piers, loss of riparian and aquatic vegetation and coarse woody habitat (CWH), and alteration of nearshore sediments (as cited in Table 3.1). Such modifications of nearshore habitat are associated with a number of indirect ecological effects including decreased diversity and density of submerged, floating, and emergent macrophytes, decreased diversity of benthic macroinvertebrates, altered nearshore fish assemblages and benthic algal communities, decreased benthic fish abundance, fewer observed instances of fish reproduction, and fewer linkages in benthic food webs (as cited in Table 3.1). Overall, lakeshore residential development can result in patchy littoral habitat, with developed sites being of poorer habitat quality due to less physical structure, lower organismal diversity, and overall greater homogeneity as compared to undeveloped shorelines.

Lakeshore residential development is also associated with the introduction of non-native species (Capelli and Magnuson 1983, Elias and Meyer 2003). One particularly detrimental invader, the zebra mussel, has wide-spread effects on lake productivity. Zebra mussels contribute to the ‘benthification’ of lakes by filtering copious amounts of phytoplankton (Strayer 2009, Higgins and Vander Zanden 2010). This decrease in phytoplankton often leads to improved water clarity and, in turn, increased rates of benthic primary productivity (as cited in Table 3.1). In addition, because they typically maintain large population sizes and inhabit benthic areas, zebra mussels have a direct effect on the benthic invertebrate community biomass. Invaded lakes have a much higher macroinvertebrate biomass, composed largely of zebra mussels, as compared to non-invaded lakes and a more homogenized benthic macroinvertebrate community that is dominated by isopods and zebra mussels (as cited in Table 3.1).

We generated predictions of the individual and combined effects of residential shoreline development and zebra mussel invasion on two relevant food web metrics: (1) the proportion of fish diets comprised of organisms dependent on benthic primary production and (2) fish trophic position. Because lakeshore residential development is associated with loss of benthic habitat and organismal diversity (Brauns et al. 2011), we expected higher levels of development to be associated with a lower contribution of benthos in fish diets and lower fish trophic position for species at least partially dependent on benthic resources. In contrast, because zebra mussel-invaded lakes have higher benthic primary productivity and greater benthic invertebrate biomass than un-invaded lakes (Higgins and Vander Zanden 2010), we expected fish to have more benthic-dependent diets in lakes containing zebra mussels. However, we have little evidence on which to base predictions for how zebra mussel invasion might affect fish trophic position because the relative effects of increasing benthic primary production but decreasing pelagic production on fish consumption are not clearly established.

Predicting the combined effects of these two potential stressors on food webs is very complex because stressors acting simultaneously do not always respond as predicted from the studies of each stressor in isolation (Paine et al. 1998, Folt et al. 1999, Darling and Cote 2008). However, we know of no published studies investigating the combined effects of any two benthic stressors on the whole-lake food web. Therefore, we base our predictions for the combined effects of these two potential stressors on previous studies of each stressor in isolation. We expected counteracting effects of lakeshore residential development and zebra mussel presence on percent benthos in fish diets, with the ultimate outcome depending on the relative strength of each stressor's effect. Given the negative effects of lakeshore residential development on the diversity of benthic food webs (Brauns et al. 2007, Brauns et al. 2011) and the propensity for benthic macroinvertebrate assemblages to be dominated by zebra mussels (which are not preferred by benthic-feeding fish) post-invasion (McNickle et al. 2006, Higgins and Vander Zanden 2010), we expected the combined effects of these two stressors on trophic position of fish at least partially dependent on benthic resources to be negative. In our study, we use stable isotope analysis to quantify the effects of residential shoreline development and zebra mussel invasion on the proportion of benthos in the diets and trophic positions of two fish species with diverse diets that typically include benthically-derived items, bluegill (*Lepomis macrochirus)* and largemouth bass (*Micropterus salmoides*), in eight Michigan lakes.

3.2 Methods

3.2.1 Study sites

We conducted this study on eight lakes in the southeastern lower peninsula of Michigan (Figure 3.1). We selected the study lakes to be hydrogeomorphically similar; all lakes were deep enough to stratify and, with the exception of one lake (Bruin Lake), lacked surface connections to other waterbodies to ensure closed fish populations. Although it was difficult to find lakes with high human activity that were not invaded by zebra mussels, we strove to select lakes across which zebra mussel presence and shoreline development were not confounded (Table 3.2). Five of the eight lakes had established zebra mussel populations and the remaining three lakes were free of zebra mussels (Table 3.2). We estimated dwelling density by counting the number of houses immediately visible from, and with property extending to, the lake shoreline. We also estimated proportion littoral area as the proportion of the lake's surface area that fell within a depth contour of 3 m on digitized bathymetric maps (MiGDL 2013), which gave us a measure of the available habitat for benthic primary producers and allowed us to account for bathymetric differences among lakes that could affect response variables.

3.2.2 Sample collection and processing

During July through October 2006, we collected mollusks (snails and mussels) and fish samples for isotopic analysis. We collected mollusks by snorkeling in both developed and undeveloped areas along the shoreline. We used snails and mussels as the littoral and pelagic end-members, respectively, in the calculation of proportion benthos in fish diets and used all mollusks as the end-members for calculating trophic position. We seined and electrofished for bluegill and largemouth bass in order to include individuals from various size classes. We selected these two species for isotopic analysis in order to examine the effect of shoreline development and zebra mussel invasion on a species that feeds largely on pelagic and benthic invertebrates (bluegill) and on a species that is piscivorous top predator (largemouth bass). We transported whole mollusks and smaller fish (<100mm) to the lab on ice for subsequent processing. For larger fish (>100mm), we took a tissue sample from the white dorsal muscle and a caudal fin clipping in the field, released the fish, and transported the samples to the lab on ice.

Upon returning to the lab, we immediately placed samples in the freezer. Later sample preparation for stable isotope analysis included removing all mollusks from their shells. For snails and native mussels, we used muscle tissue for isotope analyses; however, for the much smaller zebra mussels, we used all soft body tissue for analysis. For adult fish, we used the dorsal muscle tissue, with the exception of a single bluegill, where a caudal fin clipping was used for analysis because dorsal muscle tissue was not available (isotopic signatures of caudal fin clips and dorsal muscle tissue have a strong, positive relationship: $R^2 = 0.89$ for $\delta^{13}C$ for and $R^2 = 0.72$ for $\delta^{15}N$; J. Hessenauer, *unpublished data*). All samples were dried in a drying oven, homogenized, and stored dry in aluminum capsules until isotopic analysis. Samples were analyzed by the University of California, Davis, using a PDZ Europa 20-20 isotope ratio mass spectrometer, and by Michigan State University, using a Eurovector elemental analyzer interfaced to an Elementar Instruments Isoprime mass spectrometer.

3.2.3 Stable isotope and statistical analysis

We estimated the proportion benthos in the diet (α) of each fish species ($\delta^{13}C_{con)}$ with a two end-member mixing model, using mussels as the pelagic end-member ($\delta^{13}C_{pel}$) and snails as the benthic end-member ($\delta^{13}C_{ben}$), following Post (2002):

$$\text{Proportion benthic } (\alpha) = (\delta^{13}C_{con} - \delta^{13}C_{pel})/(\delta^{13}C_{ben} - \delta^{13}C_{pel})$$

To estimate the trophic position (TP) for each secondary consumer, or fish, species ($\delta^{15}N_{con}$), we used the following equation (Post 2002) that accounts for the trophic position (i.e., 2) of the end-members (snails [$\delta^{15}N_{ben}$] and mussels [$\delta^{15}N_{pel}$]) and that includes the proportion benthic (α) calculations obtained for each species using the aforementioned equation:

$$\text{Trophic position (TP)} = 2 + (\delta^{15}N_{con} – [\delta^{15}N_{ben} * \alpha + \delta^{15}N_{pel} * (1-\alpha)/3.4])$$

We used primary consumers, rather than primary producers, for end-members because they are more spatially and temporally integrative (Cabana and Rasmussen 1996, Vander Zanden et al.

2005). Bruin Lake (the lowest development lake) was the only lake to have both native and zebra mussels, which were averaged to calculate the pelagic end-member values used in these equations.

We adopted an analytical approach that 1) determined if there existed significant differences among the eight lakes in the proportion of benthos in fish diets and fish trophic position, and 2) explored what proportion of any existing variation in each response variable could be attributed to the density of residential shoreline development and/or the presence/absence of zebra mussels. To generate our response variables, we first controlled for the effect of fish size because these fish species often experience ontogenetic niche shifts, including shifts in diet. Bluegill typically experience a strong ontogenetic shift from feeding mostly on littoral invertebrates as juveniles to feeding primarily on zooplankton as adults (Mittelbach 1981, Osenberg et al. 1992) and largemouth bass switch from feeding heavily on zooplankton to feeding primarily on fish and other vertebrates with increasing body size (Yasuno et al. 2012). To account for this, we used the residuals from species-specific univariate regressions between total fish body length and proportion benthos in diet as the first response variable and between total body length and trophic position for the second response variable. Using these residuals to represent the proportion of benthos in a fish's diet and a fish's trophic position, we then conducted a one-way analysis of variance (ANOVA) to determine if response variables differed significantly among lakes. Then, to explore the relative ability of our two potential stressors to explain variation in the response variables we conducted a series of multiple linear regression models, for each fish species and response variable combination, that included three predictor variables: lakeshore residential development, zebra mussel presence/absence, and proportion of the lake that is littoral. We selected a best-fit model using Akaike information criteria (AIC) and calculated partial regression coefficients for each predictor in those final models. We conducted all statistical analyses in SAS (version 9.2).

3.3 Results

We collected a total of 52 snails, 19 native mussels, and 35 zebra mussels from our eight study lakes. As expected, $\delta^{13}C$ of our pelagic end-members (mussels) were consistently more depleted than $\delta^{13}C$ of the benthic end-member (snails) (Figure 3.2; paired t-test, t = -8.467, p<0.0001). Native mussels and zebra mussels had indistinguishable $\delta^{13}C$ signatures in the only lake where we found both native and zebra mussels (-30.4‰ and -30.9‰, respectively; Figure 3.2). Nitrogen signatures for all invertebrates were similar to one another (paired t-test, t = 0.340, p>0.70) and were always more depleted than $\delta^{15}N$ signatures for both fish species (Figure 3.3).

We had small sample sizes for our two fish species, collecting between 3 and 8 bluegill and between 1 and 8 largemouth bass per lake. In total, we collected 24 bluegill and 28 largemouth bass from our eight study lakes, with a total body length range of 67-181 mm and 40-418 mm, respectively. Fish $\delta^{13}C$ values, on average, generally fell between the benthic and pelagic end-member $\delta^{13}C$ values (Figure 3.2). Proportion of benthic prey in the diets of individual bluegill and largemouth bass ranged from 0 to 1, with overall mean values of 0.46 and 0.72 across all lakes for bluegill and largemouth bass (Figure 3.4). We also calculated size-class specific response metric values for bluegill; smaller bluegill (<100 mm in length) had a mean proportion benthos of 0.72 (range = 0.54-1) and larger bluegill (> 100 mm in length) had a mean of 0.38 (range = 0-1; Figure 3.4).

As expected, fish were always more enriched in $\delta^{15}N$ than the mollusk end-members (Figure 3.3). In addition, largemouth bass were more enriched in $\delta^{15}N$ than bluegill in all lakes, indicating that largemouth bass, as would be expected, were the higher-level consumer of the two species (Figure 3.3). The trophic position of individual bluegill ranged from 2.13 to 3.84 with an overall mean value of 3.09 (Figure 3.4). When separated by size, smaller bluegill (<100 mm in length) had a mean trophic position of 3.56 (range = 3.15-3.76) and larger bluegill (> 100 mm in length) had a mean trophic position of 2.96 (range = 2.10-3.56; Figure 3.4). For largemouth bass, trophic positions ranged between 2.84 and 4.35, with a mean value of 3.88 (Figure 3.4).

Our regression analysis, designed to account for effects of fish body length (and associated ontogenetic niche shifts in diet), revealed significant relationships for most species-response variable combinations. For bluegill, we found significant negative relationships between total body length and both proportion of the diet that was benthic ($R^2 = 0.28$, $p<0.01$; Figure 3.5) and trophic position ($R^2 = 0.29$, $p<0.01$; Figure 3.5). For largemouth bass, we found no relationship between total length and proportion benthos in the diet ($R^2 = 0.04$, $p=0.33$; Figure 3.5); however, as expected, we found a positive relationship between total length and trophic position ($R^2 = 0.19$, $p<0.05$; Figure 3.5). We used the residuals from these four regressions (two for each species) as the response variables in the remainder of our analyses.

Prior to looking for relationships between our two potential whole-lake stressors and fish food web metrics, we looked for relationships among these two response variables and differences in each response variable across the study lakes. For the former, we regressed the proportion benthic residuals against trophic position residuals. We found that, after accounting for length, the proportion of benthos in the diet and the trophic position were positively related in both fish species ($r = 0.64$, $p<0.005$ in bluegill and $r = 0.52$, $p<0.005$ in largemouth bass, Figure 3.6). For the latter, we found no significant differences among lakes for the proportion benthos in the diet of either fish species after accounting for total body length (ANOVA for each species, $p>0.10$). Bluegill trophic position residuals differed significantly among lakes (ANOVA, $F=8.08$, $p<0.001$), but largemouth bass trophic position residuals did not differ across lakes (ANOVA, $F=1.60$, $p=0.19$).

3.3.1 Benthic Lake Stressors

In accordance with the lack of significant difference in proportion benthic residuals among lakes, there was not a significant final model predicting the proportion of either fish's diet that was benthic (Table 3.3). The final regression model for bluegill ($R^2=0.11$, $p=0.12$; Table 3.3) included only zebra mussel presence as a predictor of proportion benthos in the fish diet. Although the final model for largemouth bass included both zebra mussel presence and lakeshore development, neither had a significant relationship ($p = 0.23$ for each variable) with proportion benthos in their diet (Table 3.3). Thus, neither shoreline development nor zebra mussel presence was a significant predictor of proportion benthos in either fish species' diet.

In contrast, shoreline development was a significant predictor of bluegill trophic position. As predicted, trophic position residuals of bluegill were significantly negatively related to lakeshore residential development ($R^2=0.17$, $p<0.05$; Table 3.3 and Figure 3.7). The best model predicting largemouth bass trophic position (R^2=0.08, p=0.15; Table 3.4) included only zebra mussels, but this model was not significant.

3.4 Discussion

There have been few previous studies on the indirect effects of anthropogenic stressors in lake benthic areas and the resulting cumulative effects on whole-lake food webs. Two notable exceptions include documented changes in predator-prey dynamics following the removal of CWH (Sass[b] et al. 2006) and a documented decline in benthic fish abundance and changes in pelagic fish diets following the invasion of a non-native benthic piscivore (Vander Zanden et al. 1999). However, studies of multiple anthropogenic benthic stressors are essentially absent from the scientific literature. To our knowledge, this is the first study of multiple benthic anthropogenic stressors and their effects on the whole-lake food web.

3.4.1 Single benthic stressors

We found no significant effects of lakeshore development or zebra mussel invasion, at the lake-wide scale, on the amount of benthos in the diets of bluegill or largemouth bass. There are several possible explanations for this lack of observed effect. One concern is the small sample size of our study, especially for bluegill. We were not able to collect any bluegill in three lakes, including the one with the lowest and the one with the highest level of shoreline development (Figure 3.2). Both of these lakes were also invaded with zebra mussels (Figure 3.2), thus constraining the likelihood of detecting relationships between these individual potential stressors and our food web response metrics. However, we do know from a number of previous studies that lakeshore residential development negatively affects riparian and in-lake vegetation (e.g., Jennings et al. 2003), CWH (e.g., Christensen et al. 1996), and lake sediments (e.g., Brauns et al. 2007). Therefore, although the littoral habitat may be patchy, there may be enough habitat at undeveloped sites to support sufficient benthic productivity so that we do not see lower benthic contributions to fish diets in high development lakes. This idea is supported by a study that found a decrease in macroinvertebrate diversity at developed shorelines but no change in overall invertebrate biomass (Brauns et al. 2011).

For bluegill, we found a significant negative relationship between trophic position and shoreline development and no relationship between trophic position and zebra mussel presence (Figure 3.5; after controlling for fish size). Although it was difficult to predict the relationship between lakeshore development and trophic position, we expected a negative relationship because shoreline development is known to negatively affect benthic zones. Shoreline development is associated with simplified benthic food webs, decreasing the number of benthic food web linkages by an order of magnitude as compared to undeveloped sites, while still maintaining high invertebrate biomass (Brauns et al. 2011). Because almost 50% of the bluegill diets in our study lakes came from benthic food sources (Figure 3.4) and the proportion of benthos in the diet is positively associated with trophic position (Figure 3.6), we expected to see a decrease in trophic position of this fish species with increasing shoreline development and the associated effects on benthic invertebrate food webs.

Although largemouth bass diets had an even greater average benthic contribution (>70%) in these lakes than bluegill, there was no relationship between shoreline development and largemouth bass trophic position. There could be several explanations for this result that are related to largemouth bass' high trophic position in these systems. For instance, largemouth bass may actually be more efficient predators with higher shoreline development; in a study of lake predation rates, the incidence of predation was highest in nearshore areas that lacked macrophytes or CWH for refuge (Sass[a] et al. 2006). Furthermore, we know that macrophyte coverage is diminished with lakeshore residential development (Jennings et al. 2003), which may also allow these visual predators to forage more effectively. A second explanation is that largemouth bass, as a top predator in these systems, may have a more flexible diet. In one study, after the experimental removal of most of the CWH from a lake, simulating the CWH lost as a result of lakeshore residential development, largemouth bass adopted a diet comprised of more than 50% terrestrial vertebrates and invertebrates (Sass[b] et al. 2006). However, bluegill can also shift to more terrestrial invertebrates in their diet with the loss of nearshore habitat (Sass et al. 2012). Such reliance on terrestrially-based prey would be very difficult to detect with our stable isotope analysis because terrestrial δC^{13} signatures are difficult to distinguish from aquatic δC^{13} signatures (Cole et al. 2002, Carpenter et al. 2005, Larson et al. 2011), especially without collecting data on aquatic primary producers (e.g., Larson et al. 2011) or experimentally manipulating the system (e.g., Cole et al. 2002). Therefore, we are not able to discern if there was a shift in diet in either fish species that could be affecting our findings.

3.4.2 Multiple benthic stressors

Alternatively, we may not have detected significant effects of these two individual potential stressors in most cases due to the opposing effects of shoreline development and zebra mussel invasion and the positive correlation between lakeshore development and zebra mussel invasion in our study lakes (i.e., our highest development lakes were also invaded; Table 3.2). Previous studies provide us with sufficient evidence to suggest that the negative effects from one stressor could be counteracted by the other stressor. For instance, we know that both benthic algal and macrophyte productivity increase with zebra mussel invasion, as does benthic invertebrate biomass (summarized in Higgins and Vander Zanden 2010). Such increases may offset the loss of macrophytes (Jennings et al. 2003) and the changes in benthic food webs (Brauns et al. 2011) that are associated with higher levels of lakeshore development. Conversely, lakeshore residential development, and associated increases in nutrient loads and fishing pressure, has been associated with increased zooplankton biomass (Gelinas and Pinel-Alloul 2008). This result may partially counteract the losses in zooplankton biomass that occur with zebra mussel invasion (Higgins and Vander Zanden 2010).

3.4.3 Difficulty of Studying Multiple Stressors

Although lakes are subject to multiple anthropogenic stressors, most studies focus on the effects of a single stressor (Crain et al. 2008), likely due to the complexity of studying multiple stressors together (Altshuler et al. 2011). Many studies of multiple stressors are conducted in laboratory settings in which each stressor can be carefully controlled (Crain et al. 2008). However, for stressors such as zebra mussel invasion and lakeshore development, with myriad effects that occur at the scale of the entire lake, measuring the full extent of these effects in the laboratory is impossible. In designing our study of the whole-lake effects of two benthic stressors, we selected lakes that represented the diversity of lakeshore development and zebra mussel presence/absence in southern Michigan. We also selected two fish species that typically occupy different trophic positions, with one feeding primarily on invertebrates (bluegill) and one feeding primarily on other fish (largemouth), yet both feed on benthic and pelagic prey (Vander Zanden and Vadeboncoeur 2002, Sass et al. 2012).

Quantifying the combined effects of these two benthic stressors on the whole-lake food web did not come without significant challenges, including sample size, both in terms of the number of lakes and the number of organisms collected in each lake, and a study design encompassing a sufficient range for each potential stressor, while also ensuring that the two stressors were not confounded. One consequence of quantifying these stressors at the whole-lake scale is having few lakes, or a small sample size. In addition, there is the added difficulty of collecting a sufficient number of each fish species, as well as benthic and pelagic invertebrate baselines, in each lake. For this particular study, the design was further complicated by finding highly developed lakes that were not invaded by zebra mussels *and* lakes with little development that were invaded (Table 3.2). These complications led to relatively low sample sizes that make it more difficult to detect significant trends.

Further, one of our chosen fish species (largemouth bass) showed variation in trophic position and benthic diet *within* lakes but very little variation in these variables *across* lakes (Figure 3.4). These results may be due to the high trophic position of this species, which may allow for more diet flexibility or foraging behavioral flexibility (i.e. different ways to locate prey in response to these potential stressors). Overall, largemouth bass appear to be more tolerant to these stressors and/or have a more flexible diet, making them not ideal as a focal organism for this type of multiple stressor food web study.

Finally, we must consider the potential role of additional stressors. Lakes in this area are subject to a number of other potential anthropogenic stressors, including invasion by other non-native species (such as the non-native macrophyte Eurasian watermilfoil [*Myriophyllum spicatum*]) and to management actions including plant removal, dredging of lake sediments, and stocking of sport fish. These relationships likely increase the complexity of fish responses to our two focal stressors, making it more difficult to identify relationships between our stressors and fish diets.

3.5 Conclusions

We expected to see a decline in the proportion of benthos in fish diets with increasing development along the shoreline and to see an increase in the proportion of benthos in fish diets with zebra mussel invasion. However, we found no evidence of either relationship. Although we observed the expected negative effect of lakeshore development on bluegill trophic position, we did not observe the same relationship with largemouth bass, nor did we observe any effect of zebra mussel invasion. This could indicate that the proposed relationships, based on the results of previous studies of each potential stressor focusing only on benthic or pelagic zones, do not hold up at the whole-lake scale. Alternatively, these results could be due to the opposing effects of these two stressors and the difficulty we experienced in finding high development lakes that were not invaded with zebra mussels.

It is relatively rare to find studies that set out to concurrently quantify the effects of more than one stressor in lakes. Studies of multiple stressors are more complicated to design and to implement, especially in the case of stressors that impact the system in complex ways, and many of the most complex stressors cannot not be recreated in the laboratory. Although our study did not provide conclusive evidence of cumulative effects of multiple stressors, we believe that scientists must continue to consider multiple stressors at the whole-lake scale in order to quantify and understand the many likely drivers of observed relationships.

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APPENDIX

APPENDIX 3

3.1 TABLES

Table 3.1. Summary of previous studies on each stressor in isolation.

	Direct Effects to Benthic Areas	**Indirect Effects**	**Consumer Diets**	**Trophic Position**
Lakeshore Residential Development	Loss of benthic habitat (CWH[1,2], macrophytes[3,4,5]) Alter nearshore sediments[3] Alter shoreline[6], install piers[5]	Decrease diversity of macrophytes[3,4,7], benthic macroinvertebrates[6,8,9] Changes to littoral fish[10,11, 12, 13] and benthic algal[14] assemblages Negative association with fish reproduction[15]	Less benthic consumer biomass from terrestrial-derived CPOM[9]	Fewer linkages in benthic macroinvertebrate food webs[9]
Zebra Mussels	Dominate[16] and homogenize[17] benthic macroinvertebrate community	Increase water clarity, benthic productivity by 200 to 2000%[16]	Increase benthos in diet of profundal fish[18]	Decrease trophic position of profundal fish[18]

Table 3.1. (cont'd)

[1]Francis and Schindler 2006, [2]Christensen et al. 1996, [3]Jennings et al. 2003, [4]Cheruvelil and Soranno 2008, [5]Radomski et al. 2010, [6]Brauns et al. 2007, [7]Elias and Meyer 2003, [8]De Sousa et al. 2008, [9]Brauns et al. 2011,[10]Jennings et al. 1999, [11]Scheuerell and Schindler 2004, [12]Sass[b] et al. 2006, [13]Roth et al. 2007, [14]Rosenberger et al. 2008, [15]Wagner et al. 2006, [16]Higgins and Vander Zanden 2010, [17]McNickle et al. 2006, [18]Rennie et al. 2009

Table 3.2. Lake physical habitat features from the eight inland lakes. Lakes are listed from lowest to highest level of shoreline development. Shoreline development measured as number of structures per kilometer of lake shoreline. ZM=zebra mussels.

	Latitude	Longitude	Shoreline Development	Lake Area (acres)	% Littoral	ZM Present?
Bruin Lake	42°25.10’N	84°2.21’W	7.76	128.98	51.89	Yes
Cedar Lake	42°18.52’N	84°4.46’W	8.84	67.58	55.48	No
Orchard Lake	42°35.10’N	83°22.14’W	11.61	847.85	55.19	Yes
Tipsico Lake	42°42.54’N	83°40.34’W	20.76	297.91	65.82	No
North Lake	42°23.36’N	84°0.27’W	21.47	225.44	52.03	No
White Lake	42°40.05’N	83°33.49’W	22.45	650.73	64.87	Yes
Whitmore Lake	42°25.38’N	83°45.15’W	30.94	559.34	59.58	Yes
Union Lake	42°36.25’N	83°25.56’W	44.99	468.25	42.46	Yes

Table 3.3. Results from the proportion benthic and trophic position regression models. The first column lists the response variable (after accounting for total body length), the second column lists the species, and the third column gives the R^2 for the final model. The remaining columns give the partial R^2 or the proportion of variation explained by each variable (± indicates the sign followed by the regression coefficient).

		Model R^2	Shoreline Development	Proportion Littoral	ZM Presence
Proportion Benthic	Bluegill	0.11	-	-	0.11(+0.18)
	Largemouth bass	0.08	0.05(+0.07)	-	0.03(-0.14)
Trophic Position	Bluegill	0.17*	0.17(-0.03)*	-	-
	Largemouth bass	0.08	-	-	0.08(-0.17)

* = significant at <0.05

3.2 FIGURES

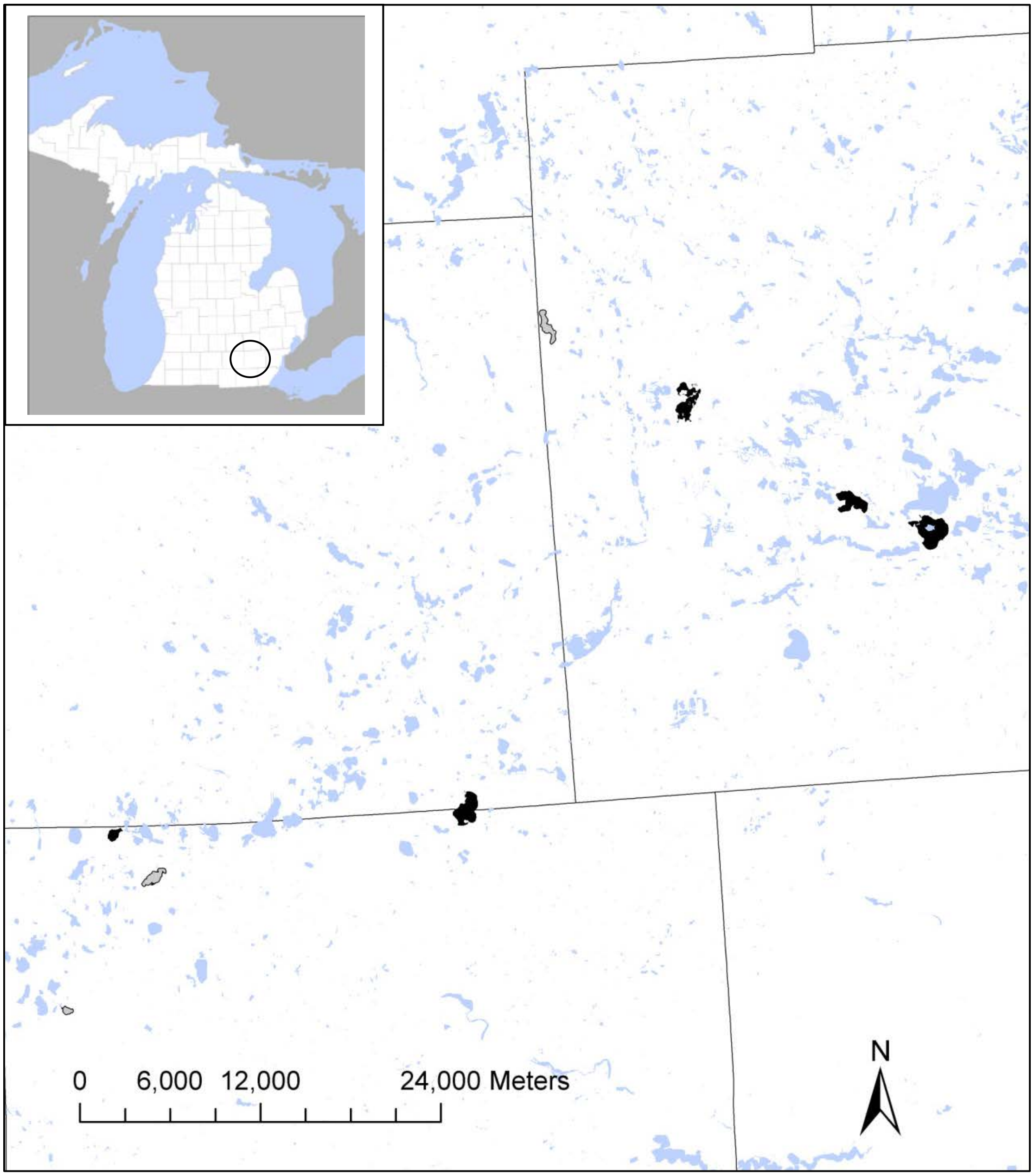

Figure 3.1. Map of the eight study lakes, including the five zebra mussel invaded lakes (black lakes, from east to west, Orchard Lake, Union Lake, White Lake, Whitmore Lake, and Bruin Lake) and the three uninvaded lakes (gray lakes, from east to west, Tipsico Lake, North Lake, and Cedar Lake), in Michigan, USA.

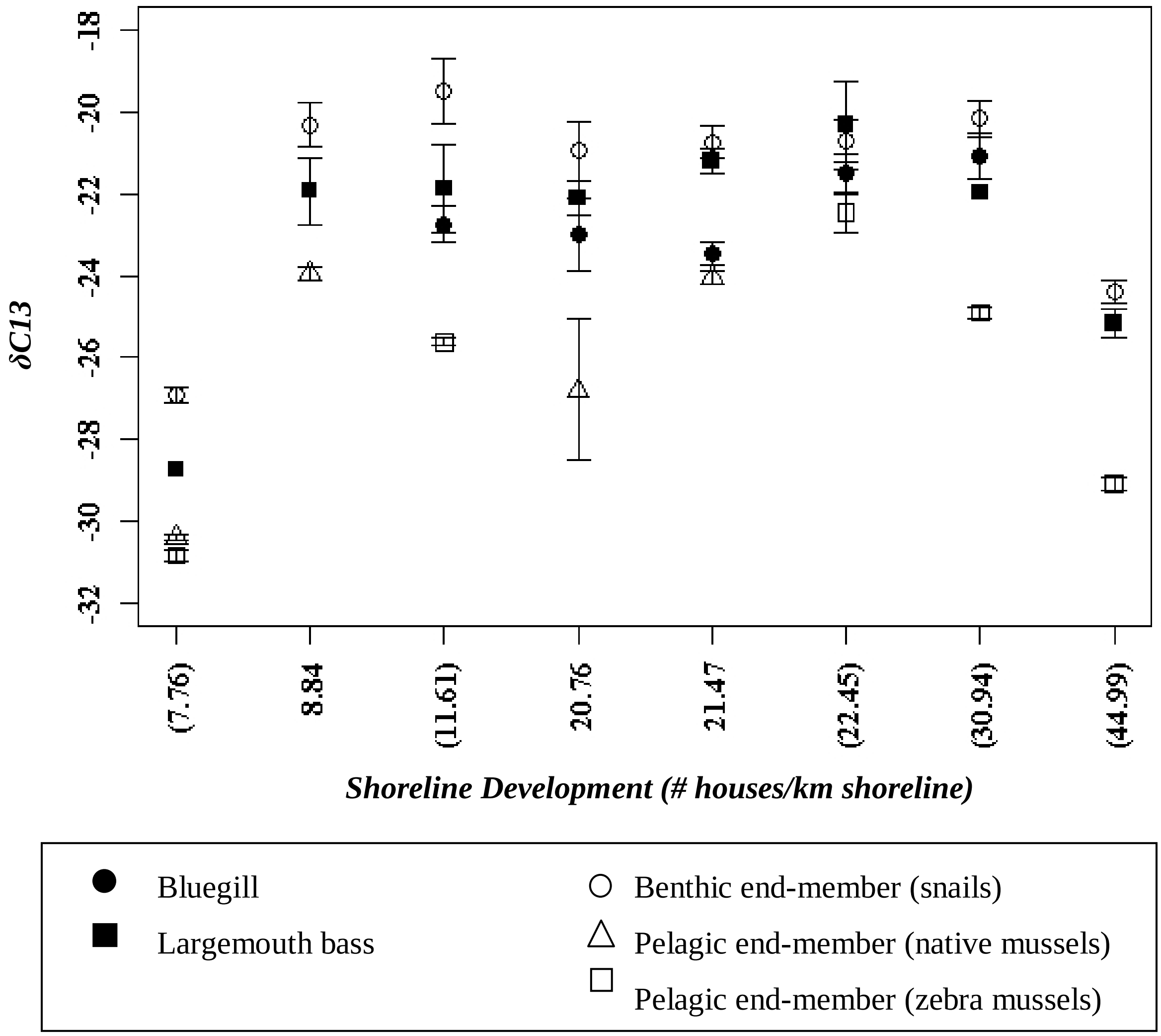

Figure 3.2. Average carbon isotope values for the eight study lakes with standard error bars. Lakes are listed from lowest to highest level of shoreline development (see Table 2) and those lakes in parentheses have been invaded by zebra mussels.

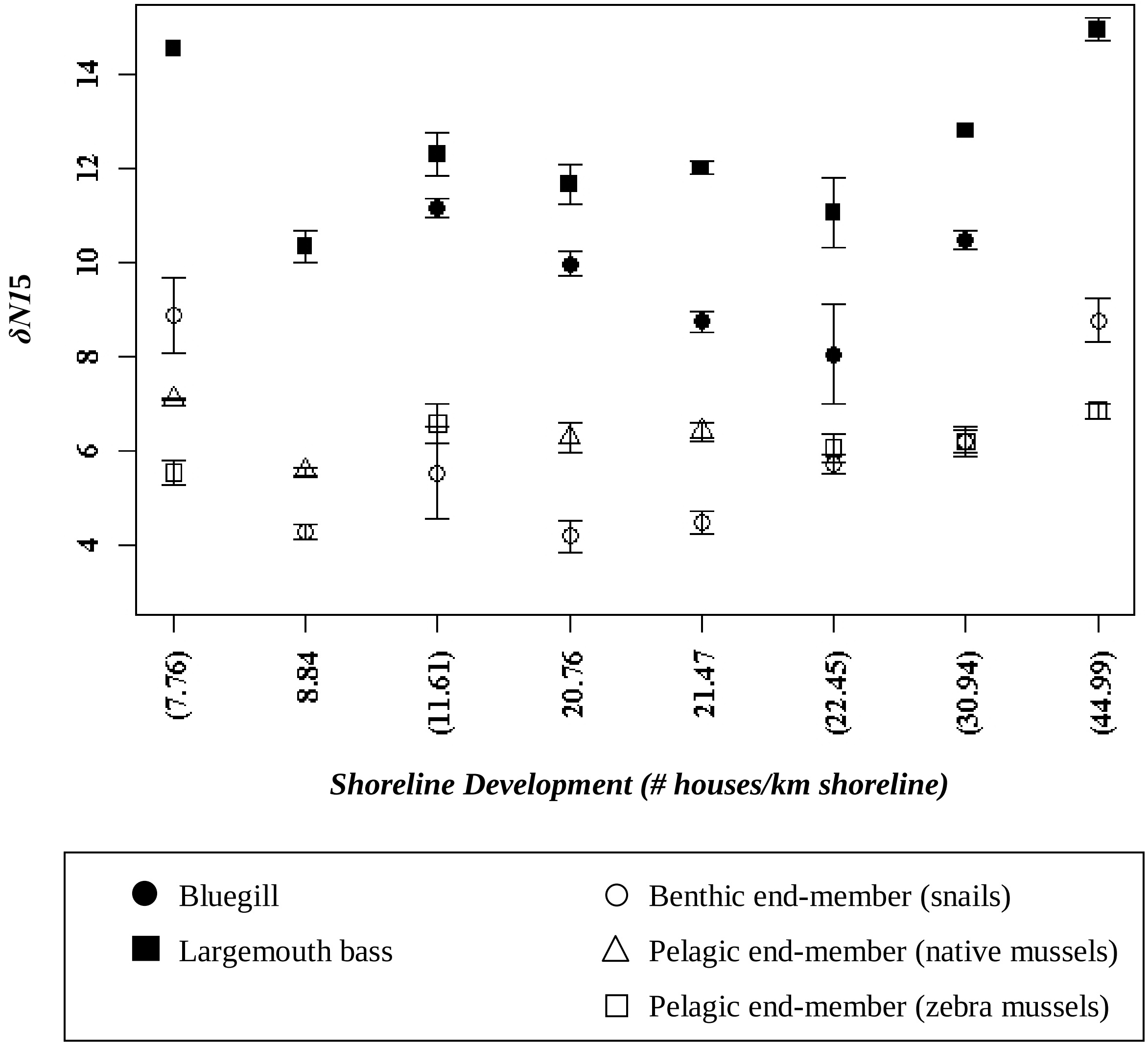

Figure 3.3. Average nitrogen isotope values for the eight study lakes with standard error bars. Lakes are listed from lowest to highest level of shoreline development (see Table 2) and those lakes in parentheses have been invaded by zebra mussels.

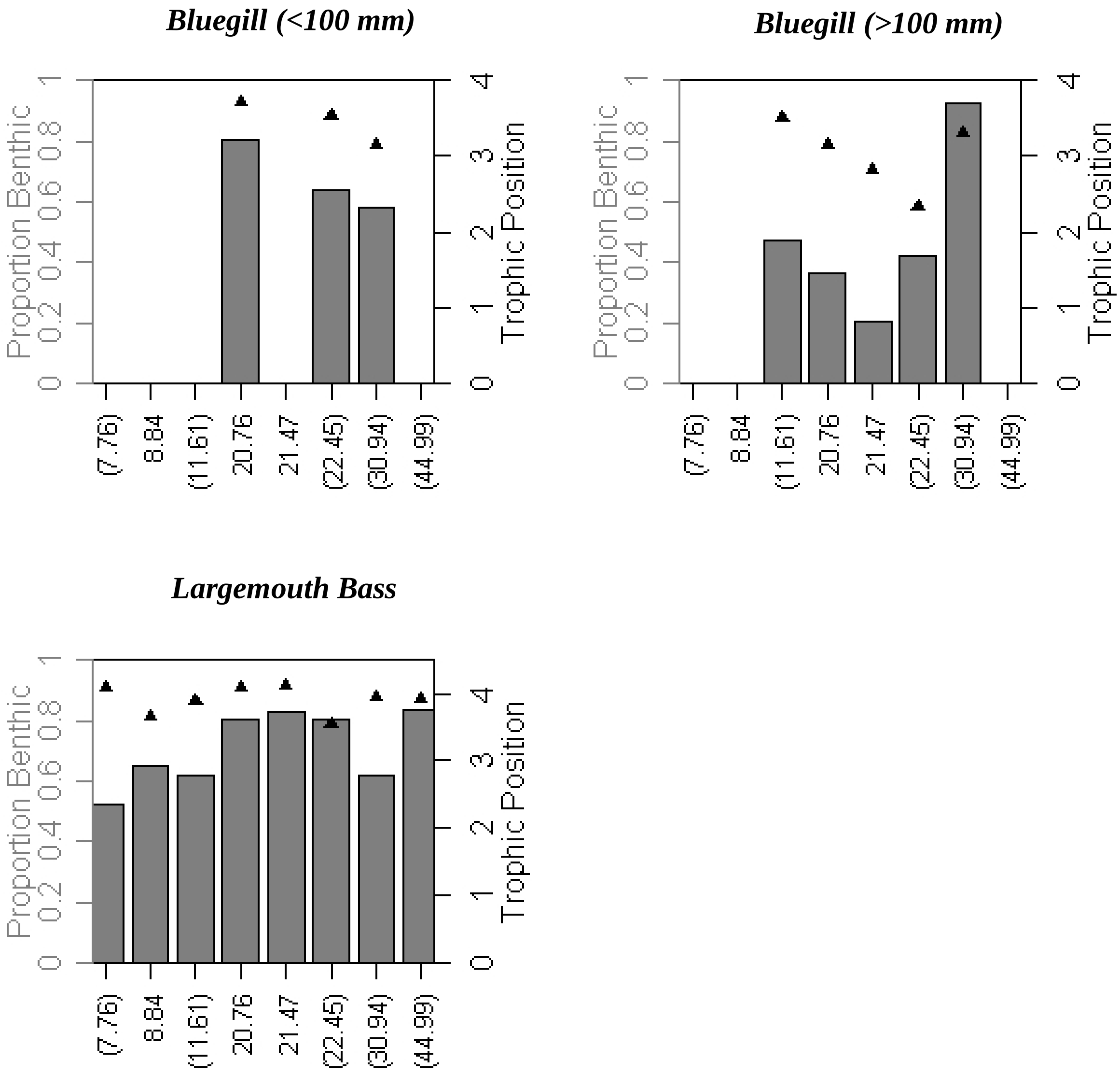

Figure 3.4. The mean proportion of benthos in the diet (in gray bars) and the mean trophic position (in black triangles) for each species and each lake in order of shoreline development, with those in parentheses have been invaded by zebra mussels. Bluegill were separated into two size classes (<100 mm in length and >100 mm in length) to represent ontogenic niche shift in diet and habitat use.

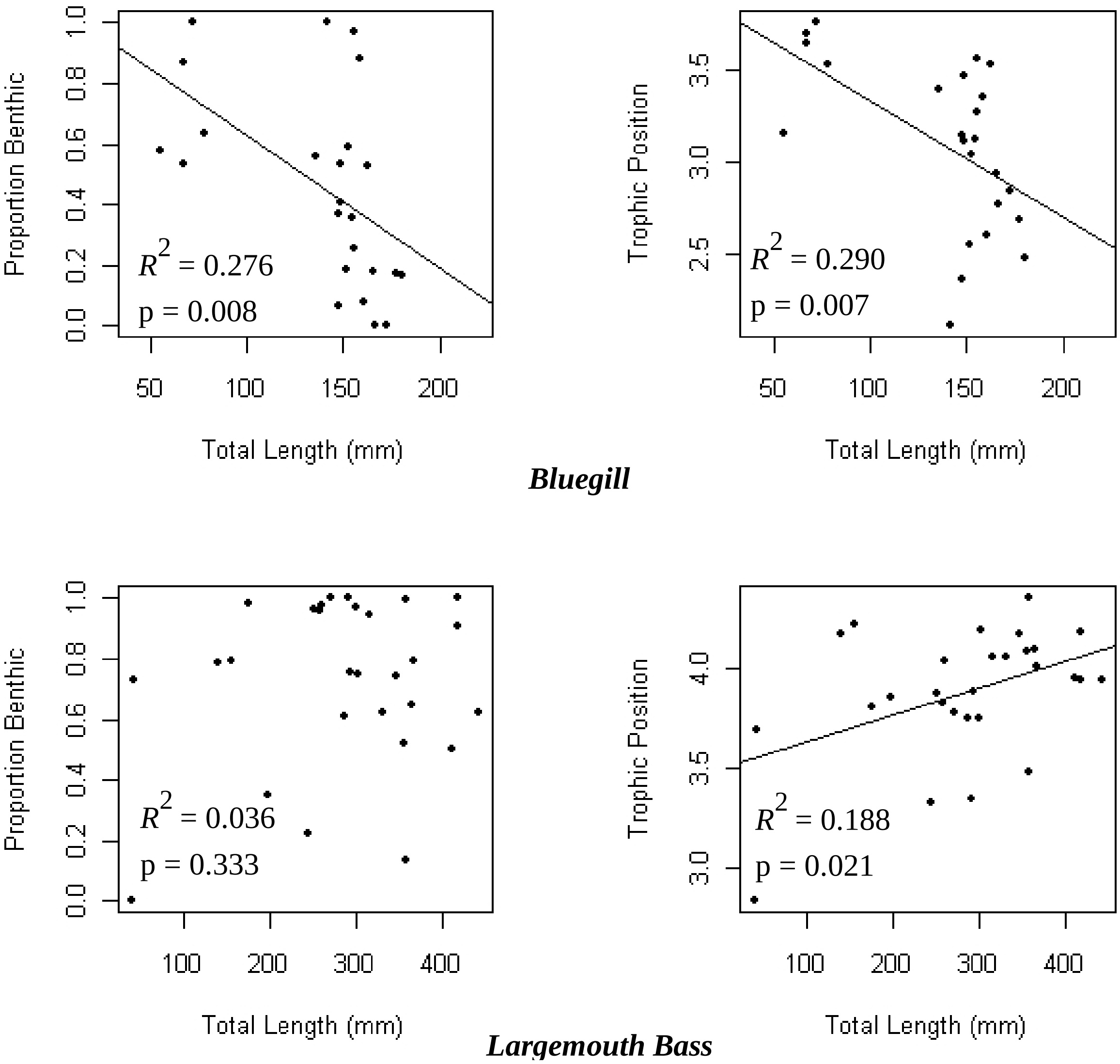

Figure 3.5. Plots of total fish body length versus proportion benthic and trophic position for bluegill (top) and largemouth bass (bottom). Residuals from these relationships were used as the response variables in our models.

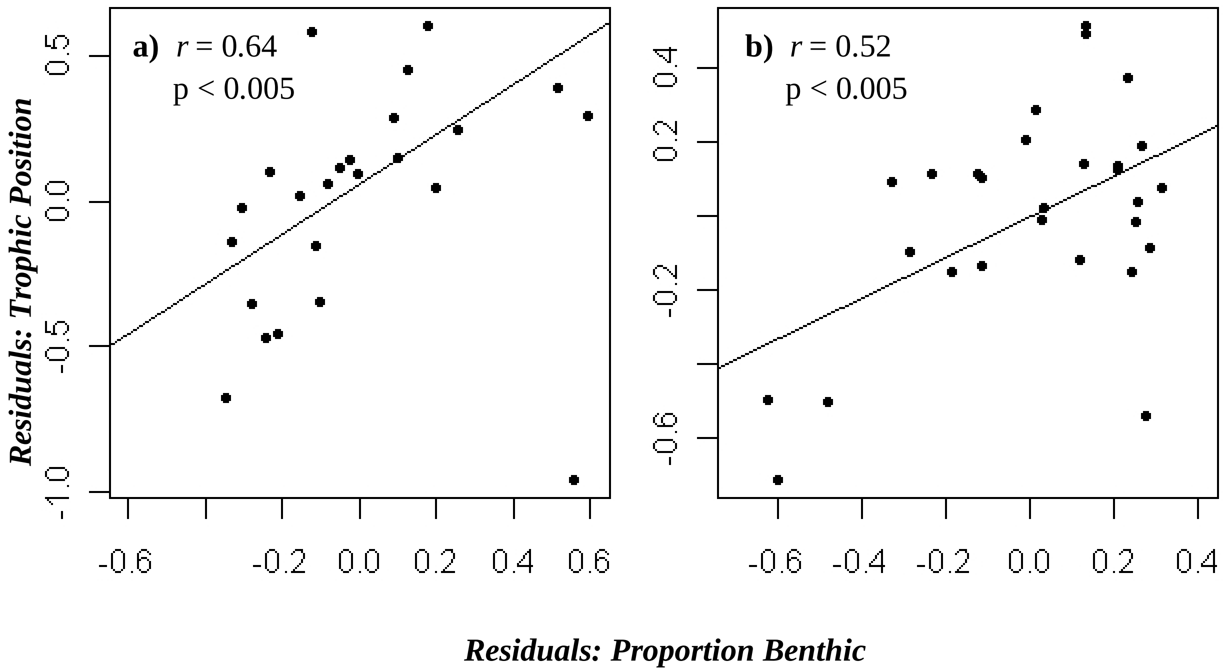

Figure 3.6. Plots of proportion benthic residuals and trophic position residuals (see Figure 4) for bluegill (a) and largemouth bass (b). We conducted the regression of bluegill trophic position residuals versus proportion benthic residuals with the omission of the outlier in the bottom right quadrant of the figure; however all data were included in all other analyses.

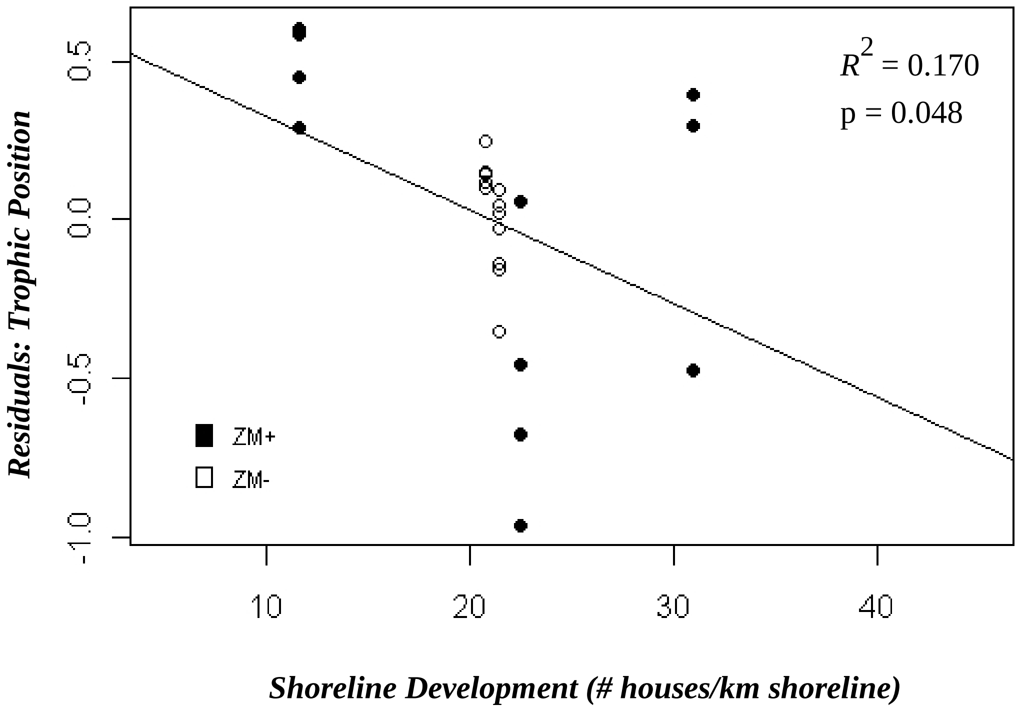

Figure 3.7. Plot of bluegill trophic position residuals versus shoreline development (R^2=0.17, p<0.05). Zebra mussel-invaded lakes are represented by black points and uninvaded lakes are represented by white points.

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LITERATURE CITED

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CHAPTER 4

THE ROLE OF AN AQUATIC INVASIVE SPECIES, THE ZEBRA MUSSEL (*DREISSENA POLYMORPHA*), ON LAKEFRONT PROPERTY VALUES

Abstract

Many negative economic and ecological consequences of exotic invasive species have been documented, yet we know little about the public's perceptions of or preferences for these species. Because some exotic invasive species can be associated with both ecosystem services and disservices, we cannot simply assume a public preference against all such species. We used multilevel hedonic models to estimate the association between zebra mussel (*Dreissena polymorpha*), an aquatic exotic invasive species , and lakefront property values in Michigan. Zebra mussels are linked to a number of negative ecological and economic consequences, similar to other nuisance aquatic invasive species. However, dissimilar to other aquatic invaders, the expected association between zebra mussels and property values is not straightforward; in addition to myriad negative effects, zebra mussels are also associated with the valuable ecosystem service of improved lake water clarity and with desirable lake features for recreational boating (the major vector for zebra mussel introduction). Contrary to previous studies, we did not find a negative association between zebra mussels and lakefront property values. Even after including water clarity and several potential confounding recreational and biophysical lake features in our models, the positive relationship between zebra mussel variables and property values remained. Our results highlight the need for further research into the welfare effects of invasive species and into public perceptions of invasive species, such as zebra mussels, that can be associated with both desirable and undesirable effects.

4.1. Introduction

Exotic invasive species have had massive ecological consequences in the United States. Over 40% of threatened or endangered species are at risk due to exotic species (Pimentel et al. 2005) and entire landscapes, ecological processes, and species assemblages have been altered due to invasion by exotics (Pimentel et al. 2005, Ricciardi and MacIsaac 2011). Not surprisingly, great economic costs are also associated with exotic invasions. The costs of invasive species have been estimated at $120 billion dollars annually in the United States based on lost production and their control (Pimentel et al. 2005).

Although these ecological and economic effects are well-documented, we have a poor sense of people’s perceptions of exotic invasive species. Surveys have provided us with conflicting information; for instance, respondents cite invasive species as ecologically detrimental (Limburg et al 2010), yet state that they value any personal economic or recreational benefit that may result from invasion (Garcia-Llorente et al. 2008, Limburg et al. 2010). Hedonic analyses are one method of understanding people’s preferences for invasive species through ‘revealed preferences’ inferred from the purchasing decisions made by property owners. However, hedonic analyses have not been frequently employed when estimating the economic effects of invasive species. In this study, we use multilevel hedonic valuation to investigate the association between the presence of an aquatic exotic invasive species, the zebra mussel (*Dreissena polymorpha*), and lakefront property values.

Of the few hedonic valuation studies that have documented the effects of exotic invasive species, all have estimated negative associations between these species and residential property values (Halstead et al. 2003, Holmes et al. 2006, Kaiser and Burnett 2006, Horsch and Lewis 2009, Zhang and Boyle 2010), suggesting that property owners have a preference against invasive species. If we look at aquatic systems in particular, which have proportionally more high-impact invasive species than terrestrial systems (Ricciardi and MacIsaac 2011), published hedonic studies have focused solely on the effects of nuisance exotic aquatic plants of the genus *Myriophyllum*, or watermilfoils (Halstead et al. 2003, Horsch and Lewis 2009, Zhang and Boyle 2010). In these studies, nuisance watermilfoil invasions were associated with declining property values, likely due to the suite of negative characteristics associated with this species (e.g., limited recreational activities due to the growth of dense mats that also provide habitat for mosquitoes and may negatively affect growth and reproduction of game fish and native aquatic plants (Halstead et al. 2003, Horsch and Lewis 2009).

Similar to exotic watermilfoils, zebra mussels can have many negative effects on lakes and users. They can reduce the availability of food and oxygen to other lake organisms (Pimentel et al. 2005) and result in decreased native mussel and phytoplankton abundance (Caraco et al. 1997, Fishman et al. 2010). This decrease in phytoplankton abundance can lead to an increase in water clarity and an associated shift to very high levels of benthic productivity (Higgins and Vander Zanden 2010) dominated by nuisance filamentous algae (Limburg et al. 2010). Zebra mussels also retain contaminants, resulting in biomagnification of these contaminants throughout the food web with particular harm to top predators (Mackie and Claudi 2010). In addition, zebra mussels have been linked to ‘major outbreaks’ of Type E Botulism, which can lead to high mortality rates in fish, birds, and amphibians (Mackie and Claudi 2010), and they are associated with increased toxic or harmful algal concentrations in low-nutrient lakes (Raikow et al. 2004, Knoll et al. 2008). Zebra mussels also reproduce rapidly and are often found at very high densities (Pimentel et al. 2005), leading to aesthetically displeasing and potentially injury-causing conditions within lakes and on surrounding beaches (Cantin 2009, Mackie and Claudi

2010). These high densities, along with the zebra mussel's affinity for hard substrates, can further affect lakefront property owners by infesting their boat hulls, water intakes, or plumbing structures (Mackie and Claudi 2010).

Despite these numerous negative ecological, recreational, and human health effects associated with this invasive species, the potential association between zebra mussels and property values is more ambiguous than that of the invasive watermilfoils. Nuisance filamentous algal blooms have been cited as economically detrimental by lakefront property owners (Limburg et al. 2010) and other associated effects of zebra mussels, such as their unsightly accumulation within and surrounding lakes, could negatively affect lakefront property values. On the other hand, zebra mussel presence has been associated with improved water clarity in a number of lakes (Johnson and Padilla 1996, Budd et al. 2001, Fishman et al. 2010, Kissman et al. 2010), which could increase lakefront property values. Water clarity is easily observed by potential lakefront property buyers (Michael et al. 2000), is positively associated with lakefront property values (e.g., Boyle et al. 1999, Michael et al. 2000, Gibbs et al. 2002), and was indicated as more economically valuable and important to lakefront property owners than the economic harm associated with zebra mussel-mediated benthic algal blooms (Limburg et al. 2010). Therefore, it is important to study water clarity and zebra mussels in concert in order to disentangle the relationships between these two variables and property values.

In addition to the potential ecosystem service of improved water clarity, there are other services that may be associated with higher property values and also confounded with zebra mussel invasion. For instance, Horsch and Lewis (2009) and Zhang and Boyle (2010) argued that Eurasian watermilfoil is spread from lake to lake by recreational boaters and anglers. Furthermore, popular lakes are more likely to be visited, and thus infested, than less popular lakes (Horsch and Lewis 2009, Zhang and Boyle 2010). Both of these studies suggest that many of the amenities that make lakes popular are unobservable to researchers, and that these unobservable amenities are also likely correlated with lakeshore property values. Thus, ignoring these effects could lead to omitted variable bias in the estimated coefficients. This may be especially important because recreational boating is suspected as the most likely source of zebra mussel transfer among lakes (Johnson et al. 2001). To account for this potential confounding between zebra mussel invasion and lakefront property values, models should include recreational and biophysical lake characteristics that may make the lake more desirable for recreation.

There are many potential ecosystem services and disservices associated with zebra mussel invasion. In addition, there are a suite of features that could make a lake desirable for recreation and, thus, vulnerable to invasion. Therefore, it is difficult to predict the relationship between zebra mussels and lakefront property values. Furthermore, people's preferences toward and perceptions of zebra mussels and their economic and environmental effects are unknown. Thus, we did not expect to see the strong, negative relationship between zebra mussel invasion and property values that was found in previous hedonic valuation studies of other aquatic exotic invasive species.

4.2. Material and Methods

4.2.1 Lakefront property data

Lakefront property sales records were obtained, with paid access, from a real estate database maintained by Southwest Michigan Regional Information Center (SWMRIC 2007). These data include 303 single-family residential properties (excluding condominiums and apartments) sold between 2001 and 2005 that range in value from $49,000 to $1,654,000 located across a broad spatial extent (11 counties; Figure 4.1) All sales prices were converted to 2005 dollars using the consumer price index (CPI, Bureau of Labor Statistics 2008) (Leggett and Bockstael 2000, Horsch and Lewis 2009). Homes with nominal sales prices (e.g., $1) were removed from the dataset under the assumption that these houses were sold to family members for a token fee. In addition, homes with less than five feet of lake frontage were removed from the data set because these properties were likely those with shared deeded access rather than lakefront properties.

In addition to sales date, price, and location (i.e., longitude and latitude), the real estate database included structural characteristics and transaction information that we included in analyses (e.g., square footage, feet of water frontage, number of bedrooms and bathrooms; Table 4.1). Housing density around each property, the distance from each property to a city with a population of at least 10,000 people, and the percentage of wetlands surrounding the property were obtained using ArcGIS (ESRI version 9.3). Annual property tax, housing density, lot size, square footage, and water frontage were log transformed and percentage of wetlands was arcsine square root transformed to meet assumptions of normality.

4.2.2 Lake data

Zebra mussel presence and the number of years since established zebra mussel populations first invaded were determined for each lake using a national database of invasive species (USGS NAS 2012). This database provides information on the year that zebra mussels were first reported in each lake. We used these data to determine whether zebra mussels were present in each lake when each property was purchased and, if so, the number of years of invasion prior to the property sale.

Data on lake water clarity, as measured by Secchi disk depth, for the 33 lakes were collected during the summer months (July, August, and September) of 2001 to 2006 by researchers (Michigan State University), state biologists (Michigan Department of Natural Resources [DNR] and Department of Environmental Quality [DEQ]), and trained volunteers (Cooperative Lakes Monitoring Program [CLMP]). A summer sampling date was used because water clarity is typically at its lowest during the summer months due to increased incidence of algal blooms during the summer stratified period (Wetzel 2001). Additionally, this is the time of the year that many recreational activities take place. In all cases, we matched the sold date of the property to the single closest water clarity reading and, when readings were equally close, the Secchi disk reading taken prior to the date of sale was used (Michael et al. 2000). Eighty nine percent of properties were matched with a water clarity reading taken within two years of the property purchase date.

We also collected data on biophysical and recreational lake features that would make the lake desirable for recreation. In addition to water clarity, biophysical lake features included lake area and maximum lake depth because large, deep lakes are associated with both the presence of other aquatic invasive species (Johnson and Carlton 1996) and recreational boating (Reed-Anderson et al. 2000). Recreational lake features included the number of parking spaces at public boat launch sites on the lake and the number of times the lake had been stocked with sportfish, both of which have been associated with recreational boating in previous studies (Reed-Anderson et al. 2000, Horsch and Lewis 2009).

Maximum lake depth came from the same sources as the water clarity data. The number of parking spaces at the public access site was obtained through the Michigan DNR Public Boat Launch Directory (2013) and the number of sportfish stocking events was retrieved from the

Michigan DNR Fish Stocking Database (2013). Lake area, along with other lake characteristics included in the models (e.g., housing density surrounding the lake, presence of a public boat launch), were obtained using ArcGIS (Table 4.1). Lake-wide housing density, lake area, Secchi depth, the number of times the lake was stocked with sportfish, and the number of parking spaces at the public boat launch were log transformed to meet assumptions of normality and comparable variances.

4.2.3 Statistical analyses

Prior to analysis, we conducted a spatial autocorrelation analysis of lakefront property values to test whether unobservable neighborhood characteristics may be positively correlated with property sales price, potentially confounding the apparent relationship between sales price and zebra mussel presence. After finding no evidence of spatial autocorrelation beyond the spatial scale of the lake, we then estimated the association between zebra mussels and lakefront property values with multilevel hedonic valuation models. We use multilevel models because of the inherent hierarchical structure of the data driving property values; properties are nested on lakes with both individual property-level and lake-level predictor variables. We derived two sets of candidate models, one for each of two different metrics of zebra mussel invasion. The first set of models included zebra mussel presence or absence (n=303 properties, 33 lakes) and the second set of models included the number of years between zebra mussel invasion and when the property was sold (n=217 properties, 16 lakes). We estimated two sets (one set including zebra mussel presence/absence and the second set including time since zebra mussel invasion) of six models that included different predictor variables: 1) a best-fit model using both property and lake attributes (i.e., recreational and biophysical), 2) a model that included all property characteristics from (1) and recreational lake variables (i.e., fish stocking events and number of parking spaces at public boat launches), 3) a model that included all property characteristics from (1) and biophysical lake variables (i.e., water clarity, lake area, and maximum lake depth), 4) a model using only property characteristics from (1), 5) a fully saturated model that included all explanatory variables, and 6) a null or unconditional model. Thus, a total of 12 models were estimated.

For model selection, we used a multimodel inference analytical approach based on the Akaike information criterion for small samples (AIC*c*) rather than Neyman-Pearson hypothesis testing (Burnham and Anderson 2002). Models with relatively low AIC*c* values, as compared with other models, were considered the most parsimonious, striking a balance between bias and variance of model predictions. We assigned relative strengths of evidence to each candidate model according to AIC*c* weights and evaluated explanatory variables in terms of deviance, or overall variation, explained. All data analyses were conducted using R (http://www.r-project.org/, version 2.12.1).

4.3. Results

4.3.1 Model selection results: zebra mussel presence/absence

For the set of models including zebra mussel presence/absence, the model with the greatest strength of evidence (i.e., our ‘best’ model) explained 53% of the deviance in lakefront property values (Table 4.2). Property attributes explained most of the model deviance in lakefront property values (Figure 4.2), particularly square footage of the structure (%DE = 23.0), feet of lake frontage (%DE = 16.2), the proportion of land surrounding the property that is wetland (%DE = 11.6), and the number of full bathrooms (%DE = 9.0). For lake attributes, water clarity had the greatest support (%DE = 4.7), followed by zebra mussel presence (%DE = 2.8), and, finally, maximum lake depth (%DE = 1.8; Figure 4.2). All variables, including zebra mussel presence, had a positive relationship with lakefront property values, with the exception of the proportion of wetlands surrounding the property (Table 4.2).

The deviance explained for this ‘best’ model was 0.6% greater than that explained by the model that included biophysical lake features and property attributes; however the model with biophysical and property features did not have much support when compared to our best model (*w*AIC=0.10, ΔAIC_c=4.4). The model that included property and recreational lake variables also had little support when compared to our best model (*w*AIC<0.01, ΔAIC_c=22.1; Table 4.2), with a corresponding decrease of 6.3% in deviance explained. The deviance explained in lakefront property values decreased by 4.0% using the model with only property variables (*w*AIC<0.01, ΔAIC_c=11.3) and by 11.6% using the saturated model when compared to our model with the greatest strength of evidence (*w*AIC<0.01, ΔAIC_c=62.6; Table 4.2).

4.3.2 Model selection results: time since zebra mussel establishment

For the set of models that included time since zebra mussel establishment, the ‘best’ model explained 50% of the deviance in lakefront property values (Table 4.3). Again, property attributes explained most of the deviance in property values. Square footage of the structure and feet of water frontage explained about 16.0% and 13.6% of the deviance, respectively (Figure 4.3). The remaining property-level variables received a range of support, including the percentage of wetlands surrounding the property (%DE = 9.8), the number of full bathrooms (%DE = 4.2), and the presence of landscaping (%DE = 1.6). The best-supported lake attributes were time since zebra mussel establishment and lake water clarity, which explained 7.5% and 4.9% of the deviance in property values, respectively (Figure 4.3). All variables had a positive relationship with lakefront property values with the exception of proportion of wetlands surrounding the property (Table 4.3).

This ‘best’ model explained 2.5% more of the deviance in lakefront property values than the model that included only property attributes and 14.0% more deviance than the saturated model; with neither model receiving much support when compared to this best model (wAIC=0.04, ΔAIC_c=10.4 and wAIC<0.01, ΔAIC_c=70.2, respectively; Table 4.3). The model including property and biophysical lake variables had weak support compared to our model with the greatest strength of evidence (wAIC=0.01, ΔAIC_c=10.4; Table 4.3), and a decrease of over 1.8% in the deviation explained. The model with property and recreational variables also had little support (wAIC=0.01, ΔAIC_c=10.4) and a decrease of 3.1% in the deviation explained when compared to our best model.

4.4 Discussion

Contrary to previous hedonic valuation studies of exotic invasive species, we did not find a negative relationship between property values and zebra mussel invasion. In fact, properties on zebra-mussel invaded lakes sold for an average of $367,891 and properties on uninvaded lakes sold for an average of $202,582. However, because there have been no previous hedonic valuation studies of lake zebra mussel invasions, we have little theoretical justification for concluding that zebra mussel invasions are directly related to higher property values. In fact, we pre-supposed that our zebra mussel variables could be confounded with, or serve as a proxy for, other desirable lake features. To account for this, we included a set of recreational (fish stocking events, number of parking spaces at public boat launches) and biophysical (water clarity, lake area, and maximum lake depth) variables in our models. In addition, we also examined the relationships between each of these variables and zebra mussel presence, time since zebra mussel establishment, and property values.

Deeper water clarity has been associated with zebra mussel invasion (Budd et al. 2001, Fishman et al. 2010), and we know that water clarity is valuable to lakefront property owners (e.g., Limburg et al. 2010). However, for our study lakes, water clarity in zebra mussel-invaded lakes was similar to the lakes that were zebra mussel-free (Table 4.4). Further, using only invaded lakes, time since zebra mussel invasion was not correlated with water clarity ($r = 0.07$, $p>0.05$). Thus, we have little evidence that confounding of zebra mussels and water clarity is the reason for our positive relationship between zebra mussels and lakefront property values.

We included two additional biophysical variables in our models, lake area and maximum lake depth, because large, deep lakes have been identified as desirable sites for recreational boating (e.g., Reed-Anderson et al. 2000, Bossenbroek et al. 2007), and recreational boating is the most likely vector of zebra mussel transfer among lakes (Johnson 2001, Bossenbroek et al. 2007). A significantly greater number of larger, deeper lakes in our study had established zebra mussel populations ($p<0.05$ for each; Table 4.4) and lake area was positively correlated with the length of time since zebra mussels were first established in the lake ($r = 0.75$, $p<0.001$). Lake area and depth were also positively associated with property values ($r = 0.67$ and 0.53, $p<0.001$ and <0.01, respectively). Thus, we have sufficient evidence to indicate that lake area and maximum lake depth have the potential to be confounded with both zebra mussel presence and property values and could be contributing to the positive relationship between the two variables.

However, the inclusion of these potential confounding variables in our models did nothing to diminish the explanatory power of the zebra mussel variables.

Finally, we considered two additional variables that can serve as proxies for lake recreational interest: the number of fish stocking events and the number of parking spaces at public access sites (Reed-Andersen et al. 2000). For our study lakes, those with more parking spaces and more fish stocking events had higher rates of zebra mussel establishment ($p<0.01$ for each; Table 4.4). However, only parking availability was positively associated with the length of time since zebra mussels were established ($r = 0.78$, $p<0.001$) and, most importantly, lakefront property values ($r = 0.53$, $p<0.01$). Therefore, we have evidence that the amount of parking at public boat launches could also be confounded with both metrics of zebra mussel invasions and lakefront property values. However, we see that the inclusion of these recreational variables in our models did not undermine the explanatory power of the metrics of zebra mussel invasions.

In addition to these potentially confounding variables, zebra mussels may serve as a proxy for a different desirable recreational lake feature that is not captured in our models (e.g. hard lake bottom substrates that are preferred by both zebra mussels [Mackie and Claudi 2010] and property owners). On the other hand, the positive relationship that we found between zebra mussel invasion and lakefront property values could represent a real preference of property owners for invaded lakes. We know little about peoples' attitudes toward zebra mussels and it is possible that a portion of the public may believe that zebra mussel establishments are beneficial due to their association with improved water clarity (Strayer 2009, Limburg et al. 2010). When questioned about invasive species in general, almost 20% of respondents in one survey were open to the introduction of invasive species if it meant economic or recreational benefit for themselves (Garcia-Llorente et al. 2008). Further, there is a reported disconnect between lakefront property owner's perceptions of invasive species and the ecosystem services with which they may be associated. In one survey, lakefront property owners cited invasive species as one of the greatest threats to their home lake, yet placed a high value on the improvement in water clarity that occurred post-zebra mussel invasion (Limburg et al. 2010).

Even with this known preference of property-owners for good lake water clarity (Michael et al. 2000, Gibbs et al. 2002, Limburg et al. 2010), we have no direct evidence to suggest that home-buyers would prefer to purchase homes on zebra mussel-invaded lakes. Further, the lack of public awareness and understanding of this species (Strayer 2009) suggests that home-buyers may not detect zebra mussel presence in the lake prior to buying a property. Nor may they fully understand the ecosystem 'disservices' that could be associated with living on an invaded lake, such as nuisance filamentous algal blooms (Higgins and Vander Zanden 2010, Limburg et al. 2010), unsightly and potentially injurious shell build ups along lake shorelines (Cantin 2009, Mackie and Claudi 2010), or infestation of boat hulls and water intake structures (Mackie and Claudi 2010). Further, anecdotal evidence suggests that the public may still view zebra mussel invasion as a localized, lake-level problem with little realization of the broader ecological and economic impacts (Strayer 2009). Our study emphasizes the need for further research into public, and particularly lakefront property owners', perceptions of zebra mussels and the underlying mechanisms driving the positive relationships we found between zebra mussels and property values.

4.5 Conclusions

We know that many of the ecological and economic consequences of zebra mussel invasions are detrimental. Yet, we found a positive relationship between zebra mussels and lakefront property values. Further, this relationship could not be explained by associated ecosystem services (improved water clarity) or confounded recreational (available parking at public boat launches) and biophysical (lake area and depth) lake variables. Therefore, we must conclude that there is either another confounding variable that we failed to account for *or* that the positive relationship between zebra mussels and property values is real.

Unfortunately, we have little understanding of the public's, and particularly lake property owners', perceptions of zebra mussels. We know that people may perceive some exotic invasive species as valuable due to their actual ecological and economic benefits (Garcia-Llorente et al. 2008, Davis et al. 2011). For example, a number of fish species (e.g., rainbow trout, Atlantic salmon) have been introduced in North America outside of their native ranges for their recreational and commercial value (Copp et al. 2005). Exotic honeysuckle species provide critical habitat for native birds that are, in turn, responsible for maintaining local and regional plant communities through seed-dispersal and pollination (Gleditsch and Carlo 2011). Exotics may even benefit ecological restoration efforts when they are used as more specialized and effective biological controls of destructive invasive species (Hoddle 2004) or as ecosystem engineers at disturbed sites to allow for recolonization by native species (D'Antonio and Meyerson 2002). Therefore, just because in the case of zebra mussels we know that there are many ecosystem disservices associated with their establishment, it is important to also recognize their potential to provide ecosystem services and, as a result, their potential to be valued for these services. An important, but missing, piece of the puzzle linking zebra mussels and property values is an understanding of peoples' perceptions of the services provided by this aquatic exotic invasive species.

4.6 Acknowledgements

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APPENDIX

APPENDIX 4

4.1 TABLES

Table 4.1. Property- and lake-level variables included in analyses and the expected association between each variable and property values based on previous studies. ? indicates that no previous studies have included this variable in models and/or the expected association is ambiguous. Wetland = palustrine scrub/shrub, forested, and emergent wetlands.

Variables	**Description**	**Median**	**SD**	**Expected Association**
SP	Sold price in US dollars	249,469	229,703	
Property Attributes				
ACD	=1 if any type of air conditioning, 0 if none	1	0.47	+
BD	Number of bedrooms	3	1.12	+
DC[a]	Straight line distance (m) to nearest city with population > 10,000	22,707.09	7,774.08	-
FB	Number of full bathrooms	2	0.83	+
LSD	=1 if any landscaping, 0 if none	1	0.49	+
HD[b]	Number of houses within 150 meter radius	12	6.55	+
SF	Square footage of the house	1500	840.48	+
WF	Feet of lake frontage	63	112.97	+
WT[c]	Percent of wetlands within 1 kilometer radius	10.83	6.79	?
Lake Attributes				
AR	Lake area (ac)	333.62	903.76	+
FS	Number of times lake was stocked with sportfish since 1990	9	17.79	+
HDL[b]	Number of houses per kilometer of shoreline	27.89	11.57	+
MX	Maximum lake depth (m)	16.15	6.91	+
PK	Number of parking spaces at the public access site	15	106.63	-
WC	Water clarity reading (m)	2.90	1.10	+

Table 4.1 (cont'd)

Variables	**Description**	**Median**	**SD**	**Expected Association**
ZMT	Number of years between the year zebra mussels were reported as established in the lake and the year the property sold	8	3.10	?
ZM	=1 if report of zebra mussels established in lake by the year the property sold, 0 if no report	1	0.46	?

[a] Based on the 2000 U.S. Census.

[b] The sum of all structures (e.g., residential structures, garages, sheds, condominium) identified using aerial photographs; thus, any error due to this procedure affects all lakes equally (Stedman and Hammer 2006).

[c] Land use/cover was based on data from the National Oceanic and Atmospheric Administration's Coastal Change Analysis Program (C-CAP).

Table 4.2. The zebra mussel presence/absence (ZM) candidate models examining the relationships between lake-level (not shaded) and property-level (shaded) variables and lakefront property values. Signs (+/-) show the direction of the association between the variable and lakefront property values. Models were ranked based on AIC$_C$ and include information on the number of parameters (k), maximum log-likelihood (LL), change in AIC$_C$ for each model as compared to the model with the greatest strength of evidence (ΔAIC$_C$), model weights (*w*AIC), the percentage of deviance, or overall variation, explained (%DE), and change in %DE when compared to the model with the greatest strength of evidence (Δ%DE). Variable abbreviations are as in Table 4.1. Prop=property, bio=biophysical, rec=recreational. Note: number of fish stocking events was highly correlated with number of parking spaces at the public access, so only the former of the two was included in the Property & Recreation model.

Model	AR	FS	HDL	MX	PK	WC	ZM	ACD	BD	DC	FB	HD	LSD	SF	WF	WT	LL	ΔAICc	*w*AIC	%DE
Best				+		+	+				+			+	+	-	-91.0	0.0	0.9	53
Prop & Bio	+			+		+	+				+			+	+	-	-92.2	4.4	0.1	52
Prop Only							+				+			+	+	-	-98.8	11.3	0.0	49
Prop & Rec		-					+				+			+	+	-	-103.1	22.1	0.0	47
Saturated	+	-	+	+	+	+	+	+	+	+	+	+	+	+	+	-	-113.5	62.6	0.0	41
Null																	-197.3	190.2	0.0	0

Table 4.3. The time since zebra mussel invasion (ZMT) candidate models examining the relationships between lake-level (not shaded) and property-level (shaded) variables and lakefront property values. Signs (+/-) show the direction of the association between the variable and lakefront property values. Models were ranked based on AIC_c and include information on the number of parameters (k), maximum log-likelihood (LL), change in AIC_c for each model as compared to the model with the greatest strength of evidence (ΔAIC_c), model weights (*w*AIC), the percentage of deviance, or overall variation, explained (%DE), and change in %DE when compared to the model with the greatest strength of evidence (Δ%DE). Variable abbreviations are as in Table 4.1. Prop=property, bio=biophysical, rec=recreational. Note: number of fish stocking events was highly correlated with number of parking spaces at the public access, so only the former of the two was included in the Property & Recreation model.

Model	AR	FS	HDL	MX	PK	WC	ZMT	ACD	BD	DC	FB	HD	LSD	SF	WF	WT	*k*	LL	ΔAICc	*w*AIC	%DE
Best						+	+				+		+	+	+	-	10	-84.6	0.0	0.95	50
Prop & Bio	-			+		+	+				+		+	+	+	-	12	-87.6	10.4	0.01	48
Prop Only							+				+		+	+	+	-	9	-88.8	6.2	0.04	47
Prop & Rec		-					+				+		+	+	+	-	10	-89.8	10.4	0.01	47
Saturated	+	+	-	+	-	+	+	+	+	+	+	+	+	+	+	-	19	-108.1	70.2	0.0	36
Null																	3	-168.3	202.7	0.0	0

Table 4.4. Relationships among the variables (i.e., water clarity, recreational features, and biophysical features) that are potentially confounded with zebra mussels and property values. ZM=zebra mussels, Sig=significance, *na* = not applicable

		ZM Present?			ZM Time Established		Water Clarity		Sold Price	
	Symbol	Yes	No	Sig	*r*	Sig	*r*	Sig	*r*	Sig
Lake area (natural log)	AR	6.27	5.38	**	0.75	***	-0.16		0.67	***
Lake Maximum Depth	MX	17.84	13.92	*	0.21		0.35	*	0.53	**
Number of Parking Spaces (natural log)	PK	3.23	2.35	**	0.78	***	-0.16		0.53	**
Fish Stocking Events (natural log)	FS	2.49	1.27	***	-0.04		-0.02		0.19	
Mean Sold Price (natural log)	SP	12.63	12.13	*	0.56	*	0.34	*	*na*	
Water Clarity (natural log)	WC	0.91	0.89		0.07		*na*		0.34	*

p-value <0.05*, <0.01**, <0.001***

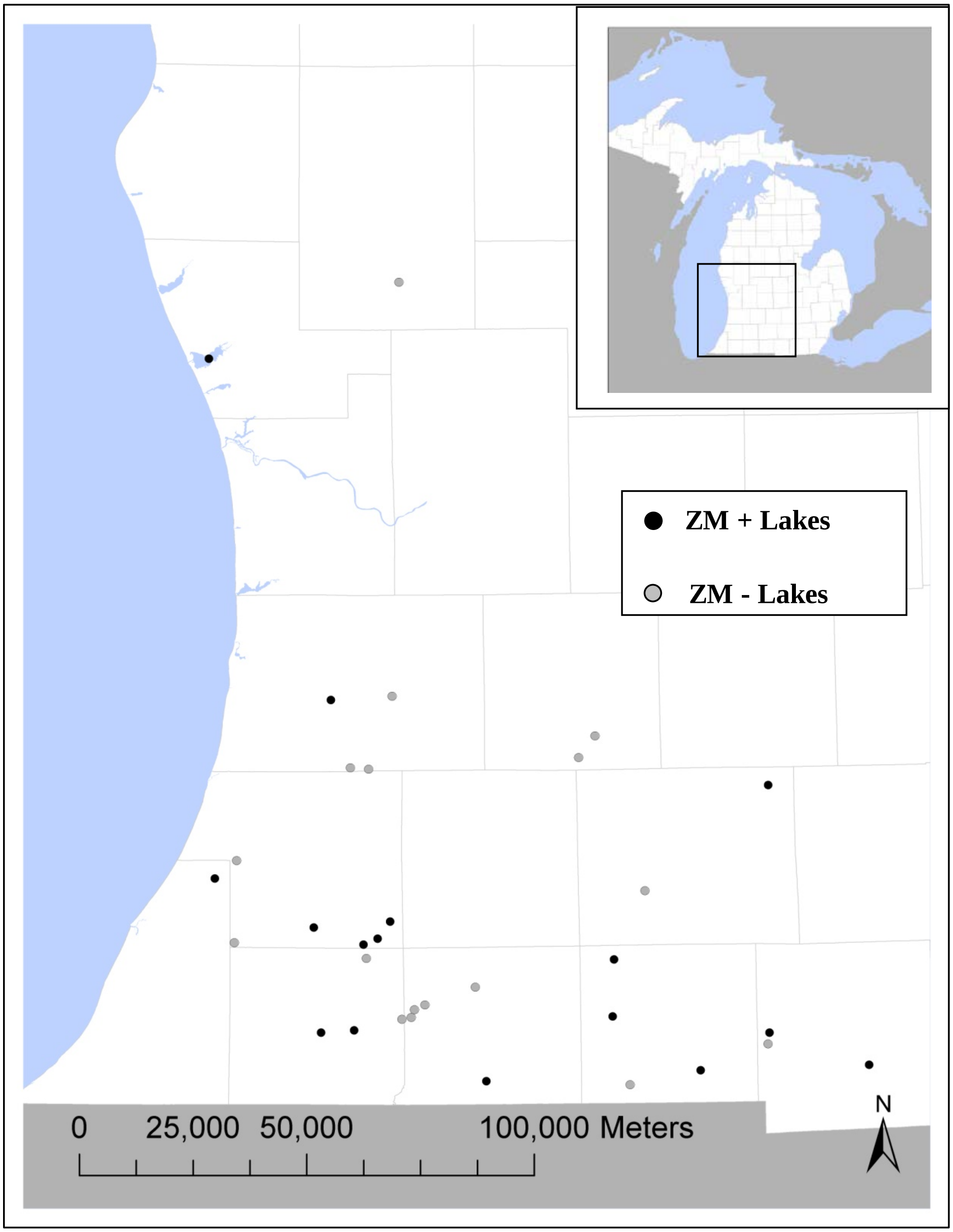

Figure 4.1. Map of our study extent, including 33 lakes (16 with established zebra mussel populations) in 11 Michigan, USA counties.

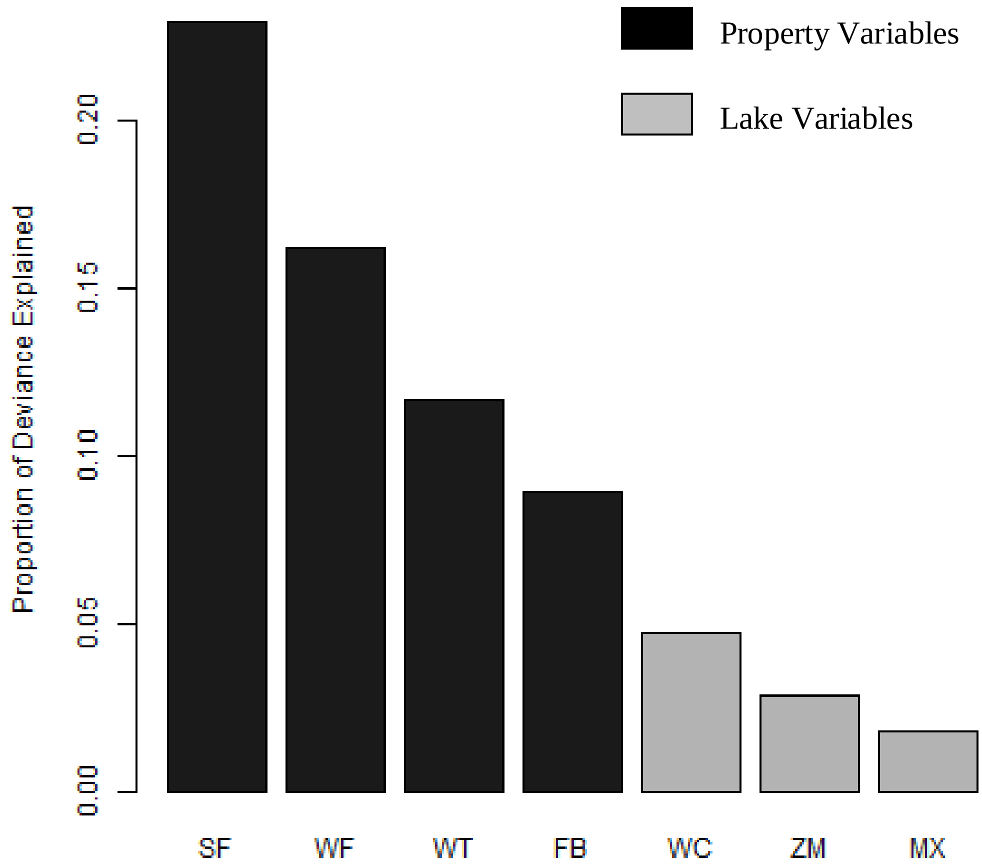

Figure 4.2. Proportion of deviance in property values explained by property and lake predictor variables in the best model that included zebra mussel presence/absence. Variable abbreviations are as in Table 4.1.

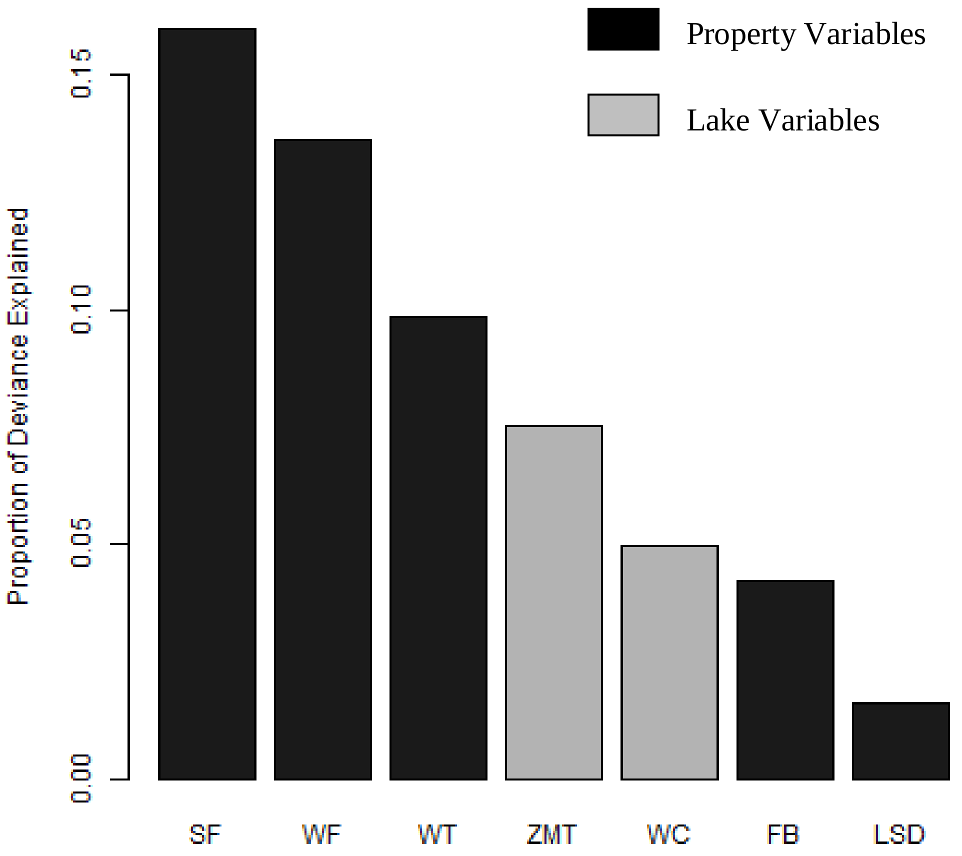

Figure 4.3. Proportion of deviance in property values explained by property and lake predictor variables in the best model that included time since zebra mussel invasion. Variable abbreviations are as in Table 4.1.

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