LAKE HABITAT EFFECTS ON AGE-0 LARGEMOUTH BASS AND THE FACTORS INFLUENCING RIPARIAN PROPERTY OWNERS' PARTICIPATION IN SHORELINE CONSERVATION PROGRAMS

By

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ABSTRACT

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Lakes provide valuable ecosystem services to society such as drinking water, recreation, and food from fishing, but development of lake shorelines can degrade riparian habitats and lake ecosystems. Conservation of inland lake ecosystems and their fisheries requires an understanding of how ecosystem processes are affected by shoreline development. This dissertation investigates the effects of riparian and littoral habitats, which are rapidly changing as shorelines become more developed, on an economically and ecologically important fish species that uses these habitats, Largemouth Bass *Micropterus salmoides.* This dissertation first assesses whether the abundance of aquatic vegetation, which is often removed by shoreline property owners, affects the growth of Largemouth Bass during the summer and fall of the first year of their lives. This growth is important, because age-0 Largemouth Bass growth and mortality are predictors of recruitment into the fishery. I used open-bottomed mesocosm enclosures to conduct an experiment with three vegetation treatments (low coverage, vegetation edge, and high coverage), and found that age-0 Largemouth Bass consumed more fish prey and more prey overall in macrophyte edge and high macrophyte coverage treatments than those with low vegetation coverage. These increases in consumption led to increases in growth rates, which is an important predictor of increased recruitment.

Second, I evaluated catch, density, and recruitment of Largemouth Bass in 16 inland Michigan

lakes to determine whether macrophytes, large woody debris, and lake trophic status increased age-0 Largemouth Bass density or recruitment. Age-0 Largemouth Bass catches were higher at intermediate and high (40 – 100%) vegetation volumes in the water column, in areas near vegetation edges, near large woody debris, and areas having higher coverages of submersed aquatic vegetation. I estimated littoral age-0 and adult Largemouth Bass densities using independent habitat- and fish size-specific estimates of catchability. Using these density estimates, I found evidence that the ratio of age-0 to adult Largemouth Bass increased with trophic state and submersed aquatic vegetation, so efforts to improve Largemouth Bass recruitment should consider conserving submersed aquatic vegetation.

Third, I conducted a survey of Michigan's lakefront property owners to assess characteristics of shoreline properties and property owners that corresponded with higher willingness to participate in conservation programs. Respondents were significantly less likely to enroll in littoral area conservation easements to protect fish habitat and water quality if they indicated that they felt social pressure for manicured lawns and more likely to enroll if they had more years of formal education, shoreline frontage, naturally occurring riparian plants, ecological knowledge about lake shorelines, or if the lake had a more developed shoreline. Enrollment in riparian easements was significantly less likely if property owners indicated social pressure for manicured lawns, but was more likely if they had more years of formal education, naturally occurring riparian plants, or shoreline frontage. Small increases to conservation payments at low payment levels (e.g. \$100-\$500 year^{-1}) resulted in relatively large gains in enrollment; some respondents would enroll in littoral (29.8 % ± 2.2; mean ± SE) and riparian (24.4 % ± 2.1) easements even without payment due to the ecosystem services provided by these habitats.

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KEY TO ABBREVIATIONS

AICc	Akaike information criterion (corrected for sample size)
ANOVA	Analysis of variance
CV	Contingent valuation
LMM	Linear mixed model
GPS	Global positioning system
LWD	Large woody debris
MDEQ	Michigan Department of Environmental Quality
NCOA	National change of address
SAM	Spatial analysis in macroecology
SAV	Submersed aquatic vegetation
SD	Standard deviation
SE	Standard error
TSI	Trophic state index
USDOI	United States Department of Interior
USEPA	United States Environmental Protection Agency
USGS	United States Geological Survey
WTA	Willingness to accept
WTP	Willingness to pay
ZIP	Zero-inflated Poisson

INTRODUCTION

Michigan is home to over 6,000 inland lakes 10 acres or larger (EPA and USGS 2012). These inland lakes provide valuable ecosystem services to shoreline property owners and to the general public, such as the provision of clean drinking water, food from fish, regulation of flooding and climate, and generation of socio-cultural services such as recreational fishing and aesthetic value (Carson and Mitchell 1993; Finlayson et al. 2005; Tranvik et al. 2009). Recreational fishing in lakes provides tremendous value to Michigan. In 2011, 1.7 million recreational anglers fished Michigan’s inland lakes, Great Lakes, and rivers a total of 28 million days, providing $2.5 billion in retail sales, $4.2 billion in total economic impact, and $287 million in state and local tax revenues (US DOI et al. 2014). Of all the Great Lakes, rivers, and lakes in Michigan, fishing on inland lakes represents approximately 48% of total angler days (Lupi et al. 2001). Because of the value Michigan’s lakes and fisheries hold, it is critical to understand and address the threats that they face to conserve the ecosystem services they provide for the future. One of the major threats facing inland lake fisheries is fish habitat degradation associated with shoreline residential development (Jennings et al. 2003; Wehrly et al. 2012; Jacobson et al. 2016).

Fish habitats are the places fish occupy throughout their lives; fishes rely upon their habitat to provide conditions to grow, survive, and reproduce. Fish habitats are characterized by physical, chemical, and biological variables (Hudson 1992). Threats to fish habitat occur at multiple spatial scales. For example, a shoreline property owner hand-pulling “nuisance” aquatic vegetation in front of their property is an example of changes at the microhabitat scale (~2.5m), which is the finest habitat scale and the scale at which patches of vegetation and large woody debris (LWD) occur. A lake association applying herbicide is an example of removing aquatic plants at the lake scale. Increased nutrient runoff from the land that drains into the lake, causing abundant aquatic plant growth, is a watershed effect. Finally, climate change increasing the growing season for aquatic plants (Latifovic and Pouliot 2007; Hansen et al. 2016) is an example of a global effect that could change the coverage and density of aquatic vegetation in lakes. A challenge in managing changing lake ecosystems is understanding the mechanisms driving changes in ecosystem processes, identifying causal pathways among the processes of an ecosystem, and finally scaling up these factors to understand patterns in habitat among lakes and how they affect fishes.

Shoreline residential development of Upper Midwest lakes has rapidly expanded, with a 4.5-fold increase in human populations in lake-rich areas in the past century. Populations are expected to continue to rise due to overall population increase and the desirability of lakefront property (Peterson et al. 2003). This shoreline residential development affects fishes, because it is correlated with decreases to structural fish habitat in the littoral zone such as aquatic vegetation and LWD. Property owners impede the natural process of LWD recruitment to the lake by removing trees in the riparian and littoral zones to gain better access to the water and to improve their perceived aesthetics of the property (Christensen et al. 1996; Jennings et al. 2003; Francis and Schindler 2006; Marburg et al. 2006; Wehrly et al. 2012; Czarnecka 2016). Residential development on lake shorelines is also associated with decreased coverage of submersed and floating-leafed aquatic vegetation. Aquatic vegetation that is perceived to be a nuisance is removed by hand pulling, herbicide treatments, mechanical harvesting, and other methods (Radomski and Goeman 2001; Jennings et al. 2003).

This dissertation investigates the effects of changing littoral habitats in lake ecosystems on Largemouth Bass. Largemouth Bass are closely associated throughout their lives with the littoral habitats that humans degrade, such as such as aquatic vegetation and LWD (Miranda and Pugh 1997; Radomski and Goeman 2001; Jennings et al. 2003; Cross and Jacobson 2013; Middaugh et al. 2013). Largemouth Bass are also an ecologically important species that structures lake food webs (Carpenter et al. 1985). Finally, black basses such as Largemouth Bass are targeted by more anglers and recreational fishing effort in the United States than any other group of fishes (USDOI et al. 2014). The first goal of this dissertation is to investigate how removal of aquatic vegetation affects the growth of Largemouth Bass during their first summer and fall, when mortality is highest (Ludsin and DeVries 1997). Increased growth and survival during the first year (age-0) provides greater management options for Largemouth Bass sport fisheries by allowing for greater harvest (Beamesderfer and North 1995) and understanding of recruitment can help managers improve fishery quality (Allen and Pine 2000). The second goal is to quantify the relationships between age-0 Largemouth Bass, aquatic vegetation, and LWD in 16 Michigan lakes across a range of habitat conditions to determine whether effects of structural habitat identified at microhabitat scales influence population dynamics. A major driver of degradation in lake ecosystems is human activity (Radomski and Goeman 2001; Jennings et al. 2003; Wehrly et al. 2012; Cross and Jacobson 2013), so efforts to conserve fish habitat in lakes from human degradation for the benefit of lake ecosystems and society should start with understanding the human dimensions of this coupled human and natural system (Liu et al. 2007). The third goal of this dissertation is to use a survey of Michigan’s lakefront property owners to identify characteristics of lakefront properties and property owners that correspond to willingness to participate in littoral and riparian conservation programs on their properties to stop aquatic vegetation and LWD removal and benefit water quality.

The first chapter of this dissertation tests the impacts of aquatic vegetation (also called macrophyte) areal coverage and edge on age-0 Largemouth Bass diet and growth rates. I used experimental enclosures to rear age-0 Largemouth Bass in varying macrophyte coverages to test for the effects of macrophytes on the diet and growth rates of age-0 Largemouth Bass in an oligotrophic, glacial lake in Michigan. My hypothesis was that macrophytes support increased zooplankton, macroinvertebrate, and fish prey densities, resulting in increased age-0 Largemouth Bass consumption and growth. I predicted that increased prey densities in the presence of macrophytes would lead to selection against relatively low-energy zooplankton prey and for comparatively larger, high-energy fishes by age-0 Largemouth Bass. This increased piscivory should result in greater total consumption and increased growth of age-0 Largemouth Bass. Because diet and growth are related to overwinter survival and recruitment through size-selective mortality (Ludsin and DeVries 1997), assessment of the causal linkage between macrophytes and consumption and growth rates is important for understanding Largemouth Bass. Results from this study could be used by lake and fishery managers to inform macrophyte and fish habitat management to protect or increase Largemouth Bass recruitment rates by conserving aquatic vegetation in lakes.

The second chapter quantifies the effects of aquatic vegetation and LWD habitats on age-0 Largemouth Bass density at the microhabitat scale and determines whether differences in the amount of these microhabitat increases Largemouth Bass recruitment at the whole-lake, population level. I conducted electrofishing surveys on 16 glacial lakes in Michigan’s Lower

Peninsula that represented a range of aquatic vegetation coverages, productivity levels, and other habitat conditions. I hypothesized that age-0 Largemouth Bass catch would increase in microhabitats with intermediate (20 – 40%) vegetation coverage, near the edges of aquatic vegetation patches, and near LWD because these habitats may increase foraging rates or decrease mortality from predation (Wiley et al. 1984; Beckett et al. 1992; Olson et al. 2003; Sass et al. 2006). I hypothesized that age-0 Largemouth Bass catchability during electrofishing surveys would decline with the volume of vegetation in the water column, because vegetation decreases visibility and the ability to net fish during the survey (Bayley and Austen 2002). This may influence interpretation of age-0 Largemouth Bass catch data in high-vegetation habitats, such that actual densities are higher than previously reported. Finally, I hypothesized that the ratio of age-0 to adult Largemouth Bass would be increased by factors at both the whole lake scale (trophic status) and the cumulative effects of microhabitat abundance at the lake scale (mean distance to LWD and aquatic vegetation coverage) as these habitats potentially increase foraging and decrease predation mortality (Beckett et al. 1992; Wiley et al. 1984; Olson et al. 2003; Sass et al. 2006). Results from this research can be used to inform habitat management decisions regarding aquatic vegetation control and LWD restoration or removal as well as inform fisheries management choices regarding stock-recruitment relationships to benefit Largemouth Bass populations when recruitment limits their populations.

The third chapter determines characteristics of properties and property owners that influence the probability of enrollment with differing levels of financial incentives offered by the easement program. I then created estimates of the potential market supply of lakeshore property owners willing to enroll in natural shoreline easements to benefit fish, wildlife, and water quality. I accomplished these objectives by conducting a mixed-mode survey of shoreline property owners on Michigan's Lower Peninsula inland lakes to gather data assessing owners' demographic characteristics, knowledge, and opinions as well as information regarding their properties' shorelines. I modeled these variables' effects on the probabilities of enrolling in littoral and riparian conservation easements, and estimated the supply of properties for conservation easements using my easement enrollment models.

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CHAPTER 1: INFLUENCE OF AQUATIC MACROPHYTES ON AGE-0 LARGEMOUTH BASS GROWTH AND DIETS

Abstract

Macrophyte removal by lakefront property owners occurs on glacial lakes throughout the range of Largemouth Bass *Micropterus salmoides*, yet little information exists on how it affects recruitment of Largemouth Bass. We hypothesized that with greater prey availability in macrophytes, age-0 Largemouth Bass would increase consumption and growth. We conducted an experiment with age-0 Largemouth Bass in twelve 9.29-m^2 littoral mesocosms in glacial Chancellor Lake, MI during 30-day experimental periods in July, August, and September, 2014. We removed macrophytes from mesocosm substrates to produce low coverage, high coverage, and vegetation edge treatments and determined the effect of macrophytes on consumption and growth at differing age-0 Largemouth Bass densities (0.86 – 2.15 fish / m^2). When macrophytes were present, age-0 Largemouth Bass stomachs contained fewer zooplankton, more often contained terrestrial invertebrates, and less often contained aquatic macroinvertebrates than when macrophytes were absent. Age-0 Largemouth Bass consumed more fish prey in macrophyte edge and high macrophyte coverage enclosures stocked at moderate densities, resulting in total stomach content biomass increases. Age-0 Largemouth Bass from enclosures with macrophyte edge and high macrophyte coverages grew 9.7% (± 2.2 SD) and 8.3% (± 1.9) longer respectively, and fish in moderate stocking density, macrophyte edge or high macrophyte coverage treatments gained 109.3% (± 45.1) and 110.7% (± 45.0) more weight than their counterparts in low macrophyte coverage enclosures. These results demonstrate a causal linkage between macrophytes and age-0 Largemouth Bass consumption and growth. Fisheries managers seeking to increase consumption and growth rates in age-0 Largemouth Bass should consider

protecting and restoring macrophytes in littoral habitats to potentially improve recruitment.

Introduction

Fish habitats are being degraded as the result of human development along the shorelines of upper Midwest glacial lakes, threatening fish populations. Fish rely upon their habitat, which is characterized by physical, chemical, and biological variables (Hudson 1992), to provide conditions to grow, survive, and reproduce. Studies of land use change forecast that the densities of human development on lake shorelines will increase due to increasing human populations and the high desirability of lakefront property in the upper Midwest (Peterson et al. 2003; Wehrly et al. 2012). Shoreline development is shown to degrade habitat quality for many fish species through removal of large woody debris, terrestrial vegetation, and aquatic macrophytes (Schindler et al. 2000; Jennings et al. 2003). As a result of beneficial relationships between aquatic macrophytes and fish populations (Miranda and Pugh 1997; Middaugh et al. 2013), naturally-reproducing fish populations may benefit from management actions such as regulations restricting macrophyte removal. Therefore, it is necessary to better understand the impacts of littoral habitat changes such as macrophyte removal on fishes as lake and fishery managers seek to understand and manage fish habitats facing degradation.

Property owners remove unwanted or invasive macrophytes in a variety of ways including manual pulling, automated center-pivot machines, chemical treatment, and boat-mounted harvesters. Macrophyte removal is common in the littoral zones of glacial lakes, often resulting in losses of nearly two-thirds of the littoral vegetation near developed shorelines (Radomski et al. 2010). Although removal of macrophytes is often regulated by state agencies, little quantitative evidence is available to guide policies to achieve fisheries and lake management objectives. The presence of macrophytes is associated with increased abundance of zooplankton, aquatic macroinvertebrates, and prey fishes for gamefish (Beckett et al. 1992; Stansfield et al. 1997; Middaugh et al. 2013). However, the effects of macrophyte removal on growth, survival, and recruitment of many game fishes has not been thoroughly studied.

Largemouth Bass *Micropterus salmoides* are an important gamefish in lakes, and use a variety of habitats throughout their lives. Age-0 Largemouth Bass use littoral habitats as nursery grounds (Carpenter 1987). Growth rates of age-0 Largemouth Bass are particularly important to recruitment, because mortality is higher for small age-0 Largemouth Bass (Gutreuter et al. 1985; Miranda and Hubbard 1994; Ludsin and DeVries 1997; Post et al. 1998). Age-0 Largemouth Bass forage mainly on zooplankton (commonly Cyclopoida and Sididae), aquatic macroinvertebrates (Amphipoda, Chironomidae, and Ephemeroptera) and small or age-0 fishes such as Bluegill *Lepomis macrochirus* during July and August (Keast and Eadie 1985; Carpenter et al. 1987; Middaugh et al. 2013). Age-0 Largemouth Bass switch to a mainly piscivorous diet and consume zooplankton and aquatic macroinvertebrates secondarily during the late summer and fall (Keast and Eadie 1985; Carpenter et al. 1987; Olson 1996; Ludsin and DeVries 1997). High growth during the aquatic macroinvertebrate feeding stage results in larger age-0 Largemouth Bass individuals, which switch to an energy-rich piscivorous diet earlier and therefore continue to grow at higher rates than invertivorous individuals (Olson 1996).

Olson et al. (2003) found that age-0 Largemouth Bass captured prey at similar rates in habitats with and without artificial macrophytes, potentially due to their ability to navigate within the interstitial spaces of macrophytes. However, Valley and Bremigan (2002) found that age-0 Largemouth Bass in high coverages of aquatic plants experienced decreased encounter and forage rates when prey densities where similar in aquaria. Because abundance of aquatic macroinvertebrates and fish prey increases in macrophytes in a natural setting (Beckett et al. 1992; Wiley et al. 2011), it is still unclear whether age-0 Largemouth Bass experience increased encounter rates and consumption in macrophytes in a natural setting. If so, this would be consistent with the increased age-0 Largemouth Bass size and abundance seen to correspond with macrophytes in field surveys (Miranda and Pugh 1997; Middaugh et al. 2013). However, correlations between location of capture, diet, and growth (Miranda and Pugh 1997; Middaugh et al. 2013) depend upon the assumption that fish did not move between different habitats. Age-0 Largemouth Bass are known to disperse distances up to 500 m from the nest (Hessenauer et al. 2012), presumably using multiple habitats, so it is unclear how macrophyte coverage at the location of capture in field studies affected growth and diet. Field studies have found that consumption rates by age-2 and adult Largemouth Bass increase near the edges of macrophyte beds, due to the high prey densities (Beckett et al. 1992; Wiley et al. 2011) and greater visibility that increase encounters with prey (Smith 1995; Olson et al. 1998). However, it is not known whether age-0 Largemouth Bass consumption and growth are affected by macrophyte edge habitats.

The goal of this study was to directly test the effects of macrophyte coverage and edge habitat on age-0 Largemouth Bass diet and growth rates. Our hypothesis was that macrophytes support increased zooplankton, macroinvertebrate, and fish prey densities, resulting in increased age-0 Largemouth consumption and growth. We predicted that increased prey densities in the presence of macrophytes would lead to selection against relatively low-energy zooplankton and for comparatively larger, high-energy fish prey by age-0 Largemouth Bass within each of three month-long periods studied (July, August, and September). We predicted that age-0 Largemouth Bass in macrophyte edge habitats would increase fish prey consumption, resulting in greater total consumption, improved condition, and increased growth.

Methods

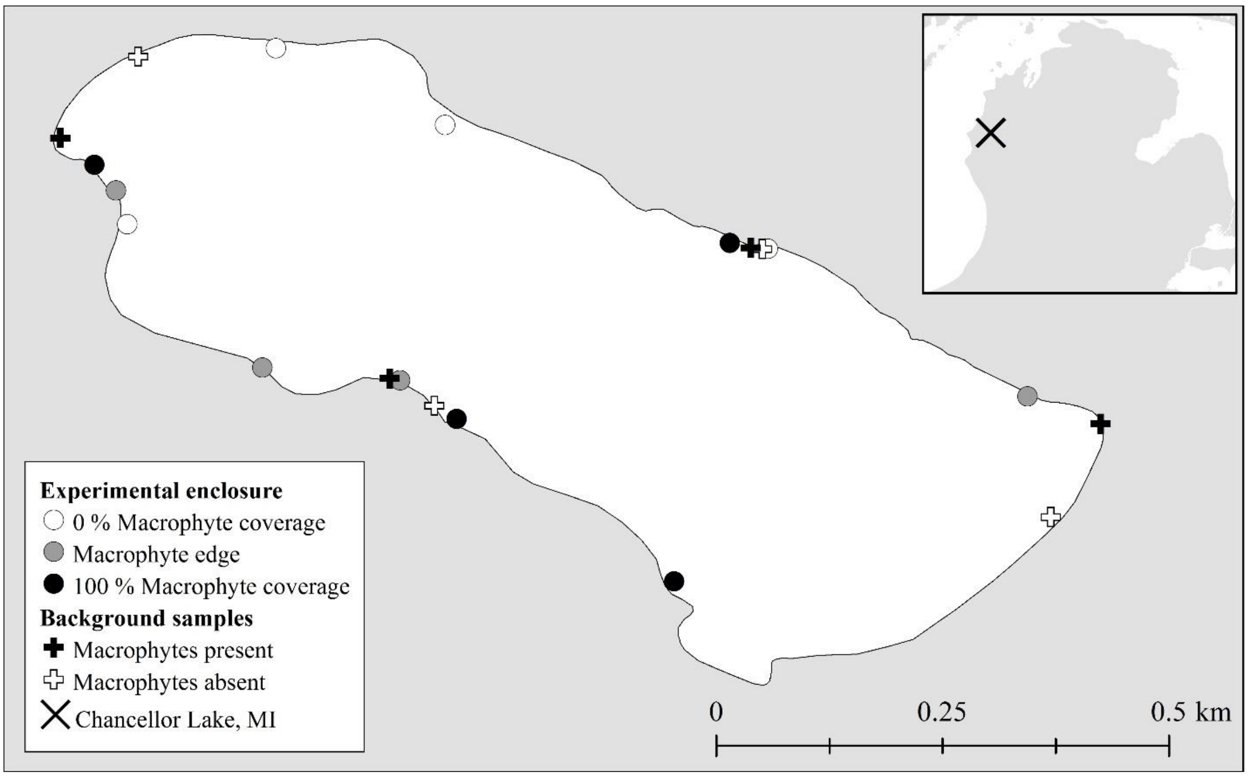

Figure 1.1. Locations of experimental enclosures with low vegetation coverage (white circles), macrophyte edge (grey circles), and high macrophyte coverage (black circles) as well as littoral sample sites outside the enclosures (background samples) with macrophytes absent (white crosses) and present (black crosses) in Chancellor Lake, MI.

Study Site

We conducted an experiment on age-0 Largemouth Bass in Chancellor Lake, Mason County, Michigan in 2014 (Figure 1.1). We chose Chancellor Lake due to its ~80% littoral coverage of macrophytes, our prior visual observations of high age-0 Largemouth Bass abundance, and lack of public access to minimize tampering with enclosures. Chancellor Lake is a 28-ha, oligotrophic glacial lake with summer Secchi depths of 6.5 m and a maximum depth of 17 m. It supports populations of Largemouth Bass, Northern Pike *Esox lucius*, Bluegill *Lepomis macrochirus*, Pumpkinseed Sunfish *Lepomis gibossus*, and Brown Bullhead *Ameirus nebulosus*.

Common macrophytes included emergent aquatic plants such as Pickerelweed *Pontederia cordata*, Softstem Bulrush *Schoenoplectus tabernaemontani*, and Three-way Sedge *Dulichium arundinaceum*; floating leaf macrophytes such as Yellow Water Lily *Nymphaea mexicana*; submersed fine leaf macrophytes such as *Chara* spp. and Northern Watermilfoil *Myriophyllum sibericum*; and submersed whole leaf macrophytes such as Illinois Pond weed *Potamogeton illinoensis*, Northern Water-nymph *Najas flexilis* and Big Leaf Pond Weed *Potamogeton amplifolius*.

Experimental design

Outdoor, partially enclosed mesocosms were used to experimentally test the effects of macrophytes on age-0 Largemouth Bass in a semi-natural setting that provided prey, macrophyte, and water quality conditions similar to those found in the littoral zone of the lake. Twelve mesocosms were constructed using 0.32-cm stretch mesh netting. Mesocosms were 3.048-m long on each side, and were open to the substrate on the bottom and to the water’s surface above (Figure 1.2). The netting was suspended from plastic pipe frames, which floated approximately 5 cm above the surface of the water and were lined with plastic panels to exclude turtles and other animals from the enclosure. The bottom of the netting was weighed down with lead weights and staked to the substrate to prevent escapement from the bottom of the enclosure. Visual checks using snorkeling equipment were conducted every 15 d for holes in the netting.

Figure 1.2. Age-0 Largemouth Bass were reared in experimental mesocosms with low macrophyte coverage (A), macrophyte edge (B), and high macrophyte coverage (C). Mesocosms enclosed fishes with mesh netting on the sides, but were open on the surface and bottom; floating plastic tubing and fencing minimized escape or entry by large fishes, turtles, and other animals.

Enclosures were sited at littoral locations interspersed along the perimeter of the lake. Criteria for site selection were: 1) maximum spatial separation between similar treatments; 2) preexisting, visually estimated macrophyte coverages matching the target coverages; and 3) property owner permission. Substrate was not part of site selection. The macrophyte edge mesocosms were bisected laterally by edge habitat separating high and low macrophyte coverages on either side (Figure 1.2B). Areas designated as low coverage in the macrophyte edge and low coverage treatments were scraped with a garden rake every 15 d during the experiment to limit regrowth. Average water depth (71 cm ± 12) was consistent among enclosures.

To prepare the enclosures, a 0.32-cm stretch mesh seine net was used to remove competitor or predator (> 2 cm) fishes from the mesocosm before stocking. We captured age-0 Largemouth Bass by seining throughout the littoral zone of the lake and stocked them the mesocosms for a period of approximately 30 d during three months (July: 3 July – 1 August 2014; August: 1

August – 31 August, and September: 1 September – 1 October). Each month, we removed all age-0 Largemouth Bass and added new fish from the lake. Each mesocosm was stocked with a high (20 individuals in July, 16 in August, and 16 in September) or moderate (10, 8, and 8) density of Largemouth Bass for each month, and densities were randomly assigned each month. These densities were determined based on previous studies (Garvey et al. 1998) and the range of densities observed during seining. Fish captured from the lake were randomly assigned to one of twelve enclosures or assigned to a random subsample of at least 30 fish that was set aside to record total length (to the nearest 0.1 cm) and wet weight (to the nearest 0.01 g). This subsampling minimized handling stress to fish in the experiment while providing a population-level estimate of mean length and weight at the beginning of each trial. Enclosures were also visually inspected every 15 d for presence of potential fish predators (e.g. Brown Bullhead) which, when found, were subsequently removed by angling or seining. Replicates in which we discovered other predatory fishes or that had holes in the netting were removed from the analysis. After each month, age-0 Largemouth Bass were removed from the enclosures by seining (0.32-cm stretch mesh) and enumerated. We seined each mesocosm at the end of each month until we had three consecutive hauls with no age-0 Largemouth Bass (Garvey et al. 1998). Each age-0 Largemouth Bass captured at the end of the experiment was measured for its final total length and weight, euthanized with MS-222, and preserved in a freezer for later stomach content analysis in the laboratory. Differences in total length were tested by comparing the final total lengths of each fish. Differences in weight were calculated by subtracting the population-level estimate of age-0 Largemouth Bass weight at the start of the trial from each individual's final weight.

We analyzed the stomach contents of each age-0 Largemouth Bass after the trial was completed by dissecting and removing their stomachs. Zooplankton, macroinvertebrate, and fish in the stomach were enumerated and identified to Family (zooplankton and macroinvertebrates) or species (fish) when possible. The length of the first 30 diet items in each taxonomic group in each stomach was recorded and used to estimate weight for those taxa. Diet item lengths were measured to estimate dry mass using length-weight regressions from the literature (Dumont et al. 1975; Benke et al. 1999; Sabo et al. 2002; Caballero et al. 2004; Jimenez et al. 2011; J. Watkins, L. Rudstam, and K. Holeck unpublished data). Dry mass for fish diet items was calculated based upon a length-wet weight relationship derived from complete and intact age-0 Largemouth Bass diet items in this study and assuming dry mass to be 25% of wet weight (Whitledge and Hayward 1997).

Habitat assessment

We measured macrophyte coverage and water quality characteristics to relate to fish growth. We assessed macrophyte coverage with five evenly-spaced 0.09–m^2 quadrats placed within each mesocosm. We visually estimated the percent coverage of each macrophyte species within each quadrat from above the water surface. We then calculated the average macrophyte coverage of each of the five quadrats to obtain an estimate of percent macrophyte coverage in the entire mesocosm. We measured dissolved oxygen, temperature, chlorophyll α, and total phosphorous within each enclosure at the end of each month to account for potential water quality effects on growth. Oxygen and temperature were measured at the surface and substrate using a YSI ProODO optical dissolved oxygen meter. Chlorophyll α and total phosphorous were measured from water samples by the Michigan Department of Environmental Quality to account for potential differences in primary productivity among enclosures.

The aquatic macroinvertebrate community was sampled at the end of each month at two stratified random sites within each enclosure using an Ekman dredge (0.1125 m^2). Benthos and substrate recovered with the dredge were filtered over a 595-µm sieve; particles retained in the sieve were preserved in 95% ethanol and then transported to the laboratory for aquatic macroinvertebrate enumeration. Aquatic macroinvertebrates were identified to Family and enumerated from each sample using a dissecting microscope, and this count was used as an index of abundance.

The zooplankton community in each mesocosm was sampled at the end of each experimental period. An 80-µm mesh Wisconsin-style zooplankton net (mouth diameter = 0.125 m) was towed from the bottom of the mesocosm on one side to the top of the mesocosm on the other side, producing a depth-integrated sample. This procedure was completed three times at 0.75-m intervals within each of the mesocosms, and the contents were preserved in 95% ethanol. Zooplankton in samples were identified to Family and enumerated using a dissecting microscope.

To assess potential differences between habitats within (mesocosms) and outside (background sites) the enclosures, we sampled water chemistry, zooplankton, macroinvertebrate, and fish in mesocosms and at background sites throughout the lake at the end of each month. Stratified random samples were collected at four sampling locations dispersed evenly around the lake, because wind influences lake water circulation and potentially biological communities such as the zooplankton upon which age-0 Largemouth Bass prey (Jackson et al. 2001). At each of the four sampling locations, a sample site with macrophytes present and a sample site with macrophytes absent were identified a random distance and direction within 100 m of the location (Figure 1.1). At each site, water samples were collected, preserved, and analyzed as described above. One benthic macroinvertebrate sample was collected with an Ekman dredge and one zooplankton sample was collected using the same towing pattern as described above. Seine hauls were also conducted at each site to assess age-0 Largemouth Bass and prey fish densities in the littoral zone of Chancellor Lake. For fish density calculations, we assumed that the area searched was the distance between the ends of the seine net multiplied by the length of the seine haul.

Statistical analysis

We tested our hypotheses regarding age-0 Largemouth Bass length, weight, stomach content dry mass, and number of stomach content items using linear mixed models (LMM) in R using the *lmer* package (Bates et al. 2015), with fixed-effects terms (macrophyte treatment, stocking density, and month) and random effects (for each of twelve enclosures). We tested our hypotheses for occurrence of diet items with logit regressions using the *glm* package (R Core Team 2013). We selected model variables using reverse selection for all main and interaction effects, determined variable coefficients to be statistically significant at $\alpha = 0.05$, and conducted *post hoc* Tukey’s tests using the *glht* package (Hothorn et al. 2008).

We compared chemical and physical habitats and prey densities inside and outside of the mesocosms to determine the similarity of these two habitats for purposes of extending conclusions drawn from this mesocosm study to natural systems. We did this by fitting an LMM as described above for each dependent habitat variable with fixed effects (macrophyte coverage, whether site was mesocosm or background, and month) and random effects (each site).

Results

A total of 153 age-0 Largemouth Bass were recovered from the enclosures across all 3 months (Table 1.1). During the experiment, problems such as the discovery of a hole in the netting or a fish predator in the enclosure were identified in three enclosures during July and in four enclosures during September; these enclosures were removed from statistical comparisons for those months to avoid potential predation, immigration, and emigration effects. In the remaining 29 intact replicates, overall recovery rates of age-0 Largemouth Bass were 39%, with recovery rates of 46% (July), 32% (August), and 38% (September) during each month. During July in one of the high vegetation coverage mesocosms, 20 age-0 Largemouth Bass were stocked and 29 were removed. The most likely explanation for this increase is that some fish avoided capture during initial seining when clearing the enclosures, as this enclosure initially contained an extraordinarily large number (45) of age-0 Largemouth Bass before the trials began. No holes were detected in this enclosure. Model results presented below did not differ in coefficient sign or significance when using a randomly subsampled 20 of the 29 age-0 Largemouth Bass from this enclosure, so all 29 fish were included in statistical analysis.

Table 1.1. Numbers of age-0 Largemouth Bass stocked and recovered in twelve experimental mesocosms in Chancellor Lake, Michigan with varying macrophyte treatments across three months. Mean (SD) is reported for each treatment group. Replicates with potential fish predators inside or holes in the netting were removed from analysis and are indicated by "NA".

	July		August		September	
Macrophyte treatment	Fish stocked	Fish recovered	Fish stocked	Fish recovered	Fish stocked	Fish recovered
Low coverage	10	0	8	1	16	0
Low coverage	10	9	16	12	16	0
Low coverage	20	NA	16	11	8	NA
Low coverage	20	9	8	1	8	5
Low coverage treatments	*15.0 (6.8)*	*6 (5.2)*	*12.0 (4.6)*	*6.3 (6.1)*	*12 (4.6)*	*1.7 (2.9)*
Macrophyte edge	10	NA	8	3	16	7
Macrophyte edge	20	3	16	5	8	4
Macrophyte edge	10	10	16	6	8	8
Macrophyte edge	20	3	8	0	16	NA
Edge treatments	*15.0 (6.8)*	*5.3 (4.0)*	*12.0 (4.6)*	*3.5 (2.6)*	*12 (4.6)*	*6.3 (2.1)*
High coverage	20	7	16	3	16	NA
High coverage	10	NA	8	1	16	NA
High coverage	10	4	16	0	8	2
High coverage	20	29	8	3	8	7
High coverage treatments	*15.0 (6.8)*	*13.3 (13.7)*	*12 (4.6)*	*1.8 (1.5)*	*12 (4.6)*	*4.5 (3.5)*
Grand Mean	*15 (5.2)*	*8.2 (8.5)*	*12 (4.2)*	*3.8 (4.0)*	*12 (4.2)*	*4.1 (3.2)*

Habitat assessment

Actual macrophyte coverages in low macrophyte coverage treatments (3.9% ± 6.7; mean ± SD unless reported otherwise), macrophyte edge treatments (41.7 ± 16.1), and high macrophyte coverage treatments (58.3% ± 17.6) differed (Table 1.2; F = 301.20; df = 2, P <0.001). The relative frequencies of macrophytes by growth forms (emergent, floating leaves, submersed with finely-divided leaves, and submersed with whole leaves) were similar among enclosures in the macrophyte edge and high coverage treatments based on an ANOVA estimating the interaction effects of growth form and treatment (F = 0.91; df = 1; P = 0.34).

Table 1.2. Macrophyte percent coverages in each mesocosm across July, August, and September for four structural categories of aquatic macrophytes (emergent, floating leaves, submersed with finely-divided leaves, and submersed with whole leaves).

Target macrophyte coverage	Emergent	Floating leaf	Submersed fine leaf	Submersed whole leaf	Total macrophyte coverage
Low coverage	0	0	7.3	0.1	7.4
Low coverage	0	0	0.1	2.5	2.7
Low coverage	0	0	0	0.8	0.8
Low coverage	0	0	1.9	0.3	2.3
Low coverage treatments	*0 (0)*	*0 (0)*	*2.3 (3.4)*	*0.9 (1.1)*	*3.3 (2.9)*
Macrophyte edge	57.3	0	0	0	57.3
Macrophyte edge	23.7	2.1	0	0.8	26.6
Macrophyte edge	34.3	0	0	4.3	38.7
Macrophyte edge	9.9	0	0	28.8	38.7
Edge treatments	*31.3 (20.1)*	*0.5 (1.1)*	*0 (0)*	*8.5 (13.7)*	*40.3 (12.7)*
High coverage	61	2.8	0	8.5	72.3
High coverage	54.3	0.7	0	2.8	57.8
High coverage	13.9	21.3	0	10	45.2
High coverage	5.7	8.7	0	45.7	60
High coverage treatments	*33.7 (9.3)*	*8.4 (13.3)*	*0 (0)*	*16.8 (19.6)*	*58.8 (11.1)*
Grand mean	*21.7 (24.1)*	*3 (6.3)*	*0.8 (2.1)*	*8.7 (14.2)*	*34.1 (25.7)*

All physical and chemical water quality parameters in the enclosures were within the survival and growth tolerance for age-0 Largemouth Bass (Stuber et al. 1982) throughout the duration of the experiment, and there were no differences between treatments. In the enclosures, water column surface temperatures were 22.0 °C ± 3.0, water column bottom temperatures were 22.0 °C ± 3.0, water column surface dissolved oxygen concentrations were 9.4 mg/L ± 1.1, and water column bottom dissolved oxygen concentrations were 9.3 mg/L ± 1.3. Concentrations of chlorophyll α (1.2 µg/L ± 0.4) and total phosphorus (0.01 mg/L ± 0.01) in the enclosures were at levels consistent with Chancellor Lake’s oligotrophic classification (Wetzel 2001). Results of

ANOVA tests for differences between enclosures by macrophyte treatment after accounting for month did not reveal significant differences for surface water temperatures (*F* = 0.18; df = 2; *P* = 0.83), bottom water temperatures (2.42; 2; 0.11), bottom dissolved oxygen concentrations (2.533; 2; 0.10), surface dissolved oxygen concentrations (1.31; 2; 0.29), chlorophyll α (0.05; 2; 0.96), or total phosphorus (1.21; 2; 0.31).

We sampled potential prey in the mesocosms (low and high macrophyte coverage) and at background sites (macrophytes present or absent) to determine whether prey density inside the mesocosms was similar to natural conditions in the lake. Mean zooplankton density in the enclosures was 0.08 individuals/L ± 0.04. An ANOVA comparing zooplankton densities at high and low macrophyte coverages inside mesocosms and at background sites provided no evidence for statistically significant differences between mesocosm and background site abundances (*F* = 1.32; df = 1; *P* = 0.26). Mean aquatic macroinvertebrate densities in the mesocosms were 839.1 individuals/m^3 ± 499.3. There was also no evidence that aquatic macroinvertebrate densities differed by location inside or outside mesocosms (*F* = 2.13; df = 1; *P* = 0.16) at high or low macrophyte coverages. We were unable to reliably sample prey fish abundances inside the enclosures, as small (< 2 cm) fish were able to escape seining through the mesh netting on the sides of the enclosures. However, we visually observed prey-sized (< 5 cm) fishes such as *Lepomis* spp. and Cyprinids throughout the study in most of the mesocosms as well as during seining for age-0 Largemouth Bass, meaning that fish were available as prey for the age-0 Largemouth Bass.

We evaluated differences in prey resources to determine whether they were comparable among low macrophyte coverage, high macrophyte coverage, and macrophyte edge treatments. ANOVA results indicated that total zooplankton densities significantly differed by macrophyte treatment ($F = 9.73$; df = 2; $P < 0.01$), and Tukey's *post hoc* comparisons provided evidence for higher zooplankton densities in macrophyte edge (0.08 individuals/L ± 0.02) and high coverage treatments (0.112 individuals/L ± 0.53) than low macrophyte coverage treatments (0.05 individuals/L ± 0.02). There was no evidence that densities of aquatic macroinvertebrates differed among macrophyte treatments ($F = 0.09$; df = 2; $P = 0.91$). Densities of prey fish outside the mesocosms in habitats with macrophytes were 2.32 individuals/m^2 ± 1.65 and 0.39 individuals/m^2 ± 0.68 in habitats without macrophytes. This difference was not statistically significant ($t = 2.32$, df = 6, $P = 0.06$), but is biologically significant because it means that prey densities outside the mesocosms increased by a factor of five when vegetation was present.

Stocking densities of age-0 Largemouth Bass in the enclosures (0.86 – 2.15 fish/m^2) were higher than densities estimated from seine hauls in the littoral zone of the lake on 27 June (0.09 fish/m^2 ± 0.11) and 30 July 2014 (0.02 fish/m^2 ± 0.02). However, repeated seining of one enclosure before stocking for the experiment produced up to 45 age-0 Largemouth Bass (4.843 fish/m^2), providing evidence that age-0 Largemouth Bass densities in the enclosures were within natural ranges.

Stomach content analysis

Of the 152 stomachs analyzed, only 3 fish had empty stomachs. The most frequent diet items consumed by age-0 Largemouth Bass (Table 1.3) were zooplankton (55.2% ± 32.3), with common taxa including Copepoda (42.1 % ± 30.8) and Cladocera (12.4 % ± 19.0). Aquatic macroinvertebrates were the next most common diet item (24.8 % ± 25.2), with common aquatic macroinvertebrates including larval Diptera (16.0 % ± 17.5) and Odonata (3.7 % ± 12.7). Terrestrial invertebrates made up a smaller portion of the diet (14.4% ± 21.7), with the most common being adult Diptera (8.3 % ± 17.3) and Hemiptera (5.5 % ± 10.7). Fishes were the smallest fraction of the diet items consumed by number (3.3 % ± 13.5), indicating that feeding events on fish were relatively rare in comparison to other items; fish consumed by age-0 Largemouth Bass belonged to Percidae (0.5% ± 2.6) and Centrarchidae including Largemouth Bass and *Lepomis spp.* (2.2% ± 10.8).

Table 1.3. Summary of stomach contents identified as zooplankton, aquatic macroinvertebrates, terrestrial invertebrates, and fish from age-0 Largemouth Bass in enclosures by differing macrophyte treatments and age-0 Largemouth Bass stocking densities for 30 d. Data are combined across July, August, and September and presented as percent by number (SD), percent occurrence, and mean dry weight (mg) for each macrophyte coverage.

	Percent by number			Percent occurrence			Stomach content dry weight		
Vegetation treatment	Low	Edge	High	Low	Edge	High	Low	Edge	High
Zoop.	71 (26)	45 (32)	50 (33)	100	86	84	1 (1)	0 (2)	0 (1)
Aquatic macro.	25 (23)	24 (22)	26 (29)	100	92	76	2 (3)	2 (4)	2 (7)
Terrest. inverts.	4 (9)	25 (28)	14 (19)	31	63	56	0 (1)	2 (3)	2 (4)
Fish	0 (2)	6 (17)	4 (15)	2	22	16	8 (59)	89 (181)	68 (179)

Age-0 Largemouth Bass stomach contents were also analyzed for to determine the importance of diet items as expressed by percent occurrence (Table 1.3), which indicates the proportion of fish consuming a particular diet item. Zooplankton were present in most age-0 Largemouth Bass stomachs in the macrophyte edge (86% of stomachs) and high coverage (84% of stomachs) and all fish stomachs from low macrophyte coverage treatments (Table 1.3). More age-0 Largemouth

Bass from low than high coverages fed on zooplankton, indicating that more age-0 Largemouth Bass were zooplanktivorous when macrophytes were absent. Aquatic macroinvertebrates were also found in most stomachs. Fewer stomachs (76%) from fish in high vegetation coverage treatments contained aquatic macroinvertebrates than macrophyte edge (92% of stomachs) and low (100%) treatments (Table 1.3). Age-0 Largemouth Bass in macrophyte edge (63% of stomachs) and high macrophyte coverage (56%) treatments were more likely to have eaten terrestrial invertebrates, likely as a result of increased emergent and floating leaf vegetation in macrophyte edge and high macrophyte coverage treatments. Fish prey were consumed by relatively few age-0 Largemouth Bass (Table 1.3). Tukey's tests provided evidence that Age-0 Largemouth Bass in macrophyte edge treatments were more likely to have been piscivorous (22% of stomachs) than those in low macrophyte coverage (2% of stomachs) treatments (difference = 20.3%; $P = 0.01$) and some evidence for increased piscivory in high (16% of stomachs) over low macrophyte coverages (difference = 14.2%; $P = 0.07$). Increased piscivory in high macrophyte coverages was not correlated with age-0 Largemouth Bass length ($Z < 0.001$; df = 149; $P > 0.99$), providing evidence that vegetation determined piscivory across the length range of age-0 Largemouth Bass in our enclosures. Overall, age-0 Largemouth Bass consumed similar numbers of Percid (14) and Centrarchid (15) fishes. Of the Percid diet items, 13 (93 %) were only able to be identified as *Etheostoma* spp. due to morphological similarity and partial digestion, with Johnny darter *Etheostoma nigram*, Iowa darter *Etheostoma exile*, and Rainbow darter *Etheostoma caeruleum* observed during seining. The heavy inclusion of *Etheostoma* spp. in the diets indicates piscivory on benthic fishes is an important component of age-0 Largemouth Bass diets. Of the Centrarchid diet items, 14 (93%) were age-0 Largemouth Bass and 1 (7%) was *Lepomis* spp., indicating predation on littoral fishes from throughout the water column.

Whereas zooplankton were the most common diet item in age-0 Largemouth Bass stomachs, fishes constituted the large majority when assessed by biomass (Table 1.3). Zooplankton contributed relatively little (1%) to the overall mass of prey consumed (0.6 mg ± 1.3). Zooplankton mass in the stomach contents differed by macrophyte coverage (F = 5.86; df = 2, 148; P < 0.01), and was significantly lower for high macrophyte coverage and macrophyte edge treatments than in low macrophyte coverages (Table 1.3). Zooplankton dry mass in stomachs also differed by age-0 Largemouth Bass stocking density (F = 12.84; df = 1, 148; P < 0.01), and was lower in treatments with high stocking density (difference = 0.7 mg; P < 0.01). Aquatic macroinvertebrates provided a relatively small proportion (3.5%) of the total consumption, averaging 2.1 mg ± 4.9 dry mass, and did not differ by macrophyte coverage (F = 0.05; df = 2, 6; P = 0.95). Terrestrial invertebrates also provided a relatively small proportion (2.7%) of total consumption, averaging 1.6 mg ± 3.0, and this did not differ by macrophyte coverage (F = 4.05; df = 2, 6; P = 0.08). Fishes contributed the largest proportion (93%) of dry mass to the average age-0 Largemouth Bass diet (56.0 mg ± 155.2). Fishes in the diet were best-estimated by an LMM including macrophyte coverage treatment (F = 5.26; df = 2, 146; P = 0.01), age-0 Largemouth Bass stocking density (F = 14.37; df = 1, 146; P < 0.01), and the interaction of macrophyte coverage and stocking density (F= 4.48; df = 2, 146; P = 0.01); Tukey's tests indicated higher weights of fish diet items from age-0 Largemouth Bass in mesocosms with moderate stocking densities and either macrophyte edge or high macrophyte coverage. Fish weights in the diets of age-0 Largemouth Bass in moderate stocking density treatments were similar at macrophyte edge and high macrophyte coverage treatments (difference = 5.1 mg; P > 0.99).

We compared total stomach content dry mass to macrophyte treatment, stocking density, and month (Table 1.4). An LMM predicting total stomach content dry mass provided evidence for significant main effects of macrophyte treatment (F = 5.34; df = 2; P < 0.01) and stocking density (14.79; 1; <0.01), as well as the interaction between these variables (4.44; 2; 0.01). A Tukey's test provided evidence that treatments with moderate stocking density and either high macrophyte coverage or macrophyte edge had higher total stomach content weights than other treatments, indicating an increase in consumption due to macrophytes. There was no greater stomach content mass in macrophyte edge than high macrophyte coverage, moderate stocking density treatments (difference = -6.14 mg; P > 0.99) or high stocking density treatments (-9.91 mg; > 0.99), meaning that there did not appear to be a decline in consumption by age-0 Largemouth Bass from macrophyte edge to high macrophyte coverages. After removing Largemouth Bass in the stomach contents from the analysis due to their artificially high densities in the mesocosms, the fish and total stomach contents from age-0 Largemouth Bass in moderate stocking density, macrophyte edge treatments were still greater than other treatments, but not significantly different.

Table 1.4. Summary of dry weights (mg) of all stomach contents from age-0 Largemouth Bass in enclosures with differing macrophyte treatments and age-0 Largemouth Bass stocking density for 30 d. Mean (SD) dry weights are combined across July, August, and September; values followed by a common superscript are not significantly different ($\alpha = 0.05$) from other treatments at different macrophyte coverage or stock density.

	Macrophyte coverage			
	Low	Macrophyte edge	High	Total
High stock density	15.9 (74.1) ^{z}	18.3 (65.5) ^{z}	28.2 (111.9) ^{z}	21.5 (88.9)
Moderate stock density	4.9 (2.6) ^{z}	165.7 (224.4) ^{y}	171.8 (254.3) ^{y}	123.1 (211.6)
Total	12.2 (60.3)	93.5 (181.0)	72.6 (179.5)	60.3 (155.6)

Growth

Age-0 Largemouth Bass total lengths (Figure 1.3) were analyzed to determine if there were significant differences in length based upon macrophyte treatment, stocking density, and month. Age-0 Largemouth Bass lengths at the end of each month were 4.47 cm ± 0.68 (July), 5.66 cm ± 0.94 (August), and 7.00 cm ± 0.96 (September). An LMM estimating age-0 Largemouth Bass lengths only included significant main effects for macrophyte treatment (F = 5.27; df = 2, 148; P < 0.01) and month (F = 102.35; df = 2, 148; P < 0.01); all other factors and interactions were insignificant or could not be tested due to sample size. Age-0 Largemouth Bass total lengths were no longer in macrophyte edge than high macrophyte coverage treatments (difference = 0.08 cm; SE = 0.17; Z = 0.54; P = 0.89), whereas fish from both macrophyte edge (difference = 0.54 cm; SE = 0.17; Z = 3.14, P = 0.01) and high macrophyte coverage treatments (difference = 0.46 cm; SE = 0.17; Z = 2.72; P = 0.02) were larger than fish from low macrophyte coverages. As a proportion of total length, these estimates indicate that fish were 9.7% ± 2.2 longer in macrophyte edge treatments and 8.3% ± 1.9 longer in high macrophyte coverage treatments than their counterparts in low macrophyte coverage treatments across July, August, and September. Therefore, age-0 Largemouth Bass growth increased with macrophyte coverage across the range of coverages in our study.

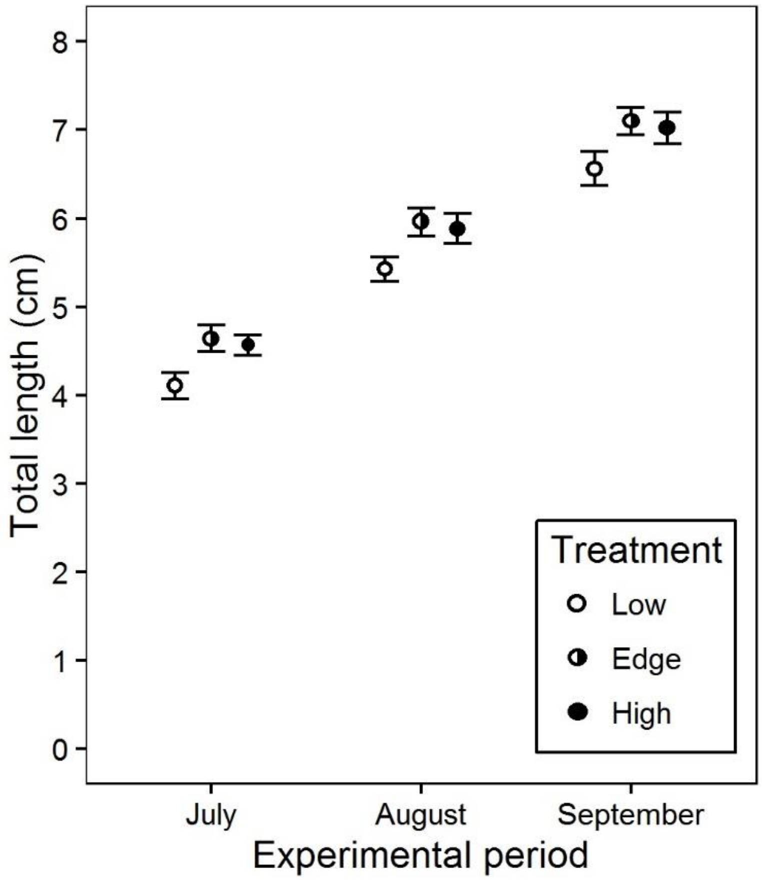

Figure 1.3. Total lengths of age-0 Largemouth Bass at the end of July, August, and September for treatments of low macrophyte coverage, macrophyte edge, high macrophyte coverage across all stocking densities. Points indicate average length and bars indicate SE as estimated by a linear mixed model.

We analyzed data on the percent increase in age-0 Largemouth Bass weights to determine differences based upon macrophyte coverage, stocking density, and month (Figure 1.4). Age-0 Largemouth Bass at the end of each month weighed 1.08 g ± 0.59 (July), 2.25 g ± 1.17 (August), and 2.68 g ± 1.20 (September). An LMM estimating the percent increase in age-0 Largemouth Bass weights over each month was fitted to the data, and only included significant main effects of macrophyte coverage (F = 3.93; df = 2, 147; P = 0.02), stocking density treatment (F = 5.12; df = 1, 127; P = 0.03), and month (F = 38.43; df = 2, 147; P < 0.01). All other factors and interactions were insignificant or could not be tested due to sample size. Age-0 Largemouth Bass weight increases were similar for macrophyte edge and high macrophyte coverage treatments (difference = 1.3%; SE = 44.2; $Z = 0.031$; $P > 0.99$), whereas fish from both macrophyte edge (difference = 109.3%; SE = 45.1; $Z = 2.42$; $P = 0.04$) and high macrophyte coverage treatments (difference = 110.7%; SE = 45.0; $Z = 2.46$; $P = 0.04$) gained significantly more weight than fish from low macrophyte coverages. In addition to macrophyte coverage affecting age-0 Largemouth Bass weight gain, fish in moderate density treatments gained more weight than those in high density treatments (difference = 90.4%; SE = 40.0; $Z = 2.26$; $P = 0.02$). Therefore, weight gain was density-dependent. Age-0 Largemouth Bass weight gains, standardized as a percentage of total weight, decreased over time, with greater growth in July than August (difference = 113.6%; SE = 43.2; $Z = 2.63$; $P = 0.02$) or September (difference = 436.5%; SE = 49.8; $Z = 4.98$; $P < 0.01$) as well as greater growth in August than September (difference = 322.3%; SE = 56.3; $Z = 5.74$; $P < 0.01$).

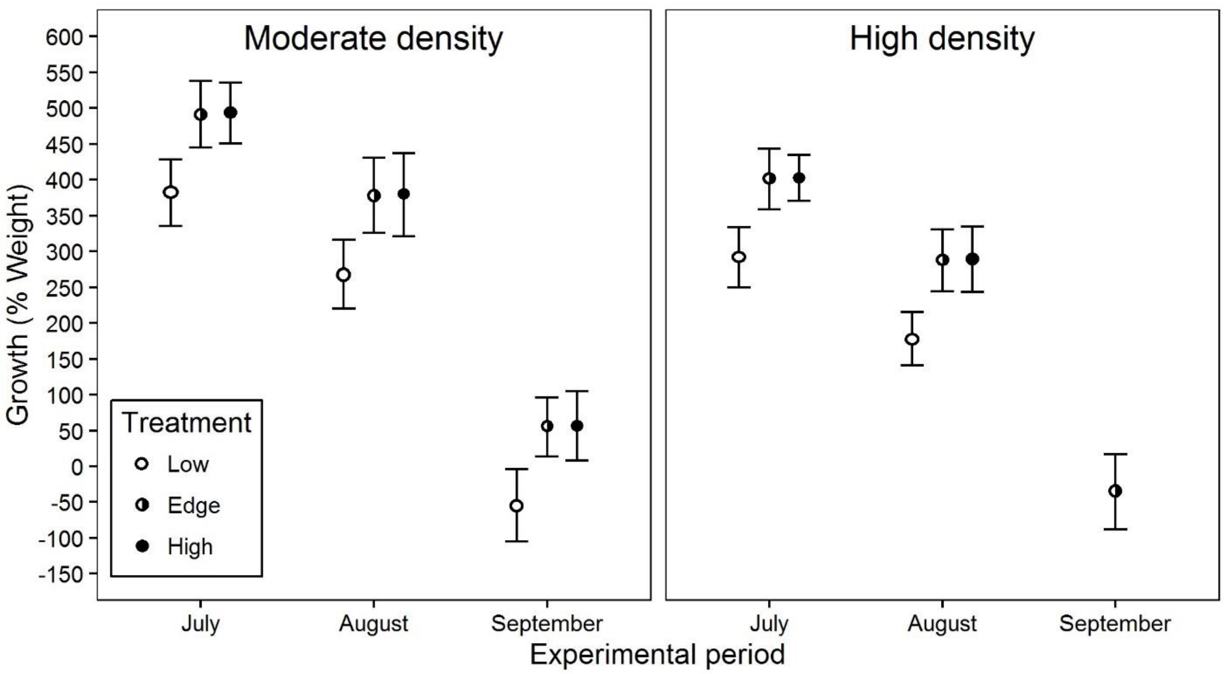

Figure 1.4. Percent change in weights of age-0 Largemouth Bass at the end of each month for treatments of low macrophyte coverage, macrophyte edge, and high macrophyte coverage treatments at moderate (0.86 – 1.08 fish/m^2) and high (1.72 – 2.15 fish/m^2) stocking densities over July, August, and September. Points indicate average percent change in weight and bars indicate SE as estimated by a linear mixed model; lack of data in high density, September trials limited ability to calculate some estimates.

Discussion

Although correlations between macrophytes, fish diets, and growth have been shown in larger-scale field studies (Miranda and Pugh 1997; Middaugh et al. 2013), it has not been shown that the quantity of macrophytes in a lake can cause diet and growth responses in fish. This critical, causal linkage between macrophyte coverage and increased age-0 Largemouth Bass consumption and growth is important, because consumption and growth directly influence recruitment (Ludsin and DeVries 1997). Our study demonstrates that age-0 Largemouth Bass reared in habitats with macrophytes and macrophyte edges experienced increased consumption and growth rates, and provides support for conservation of macrophytes to improve Largemouth Bass recruitment in a temperate oligotrophic lake. We found that age-0 Largemouth Bass in our mesocosm experiment consumed more prey in enclosures with macrophytes present, presumably due to increased prey abundance. Specifically, they had diets with fewer zooplankton, more terrestrial invertebrates, and more fishes. Fish from macrophyte edge and high macrophyte cover enclosures stocked at moderate densities had greater total consumption across all months. Growth of age-0 Largemouth Bass corresponded with increased consumption, as fish from enclosures with macrophytes grew ~9% longer than fish that lived in macrophyte-free enclosures. Similarly, fish in moderate stocking density enclosures with macrophytes gained about twice the weight of their counterparts in macrophyte-free enclosures. Our finding that high macrophyte coverage and macrophyte edge habitats increased consumption and growth implies that macrophytes may benefit recruitment, because growth increases recruitment (Ludsin and DeVries 1997). Fishery and lake managers can use this information to make decisions regarding macrophyte and fishery management in north temperate lakes.

Comparing mesocosm and littoral habitats

To interpret the results of this mesocosm study in the context of lake ecosystems and facilitate their application to fishery and lake management, we assessed similarities and differences in water quality and prey densities between the environment inside and outside of our enclosures. We did not detect differences between enclosures and mesocosms in sampled water chemistry, physical parameters, zooplankton, aquatic macroinvertebrates, and our observations of prey fishes. Zooplankton, aquatic macroinvertebrates, terrestrial invertebrates, and prey fishes demonstrated that they were able to move freely within the mesocosms, so their vulnerability to predation inside the enclosures was likely similar to levels outside the enclosures. Age-0 Largemouth Bass stocking densities in the enclosures were above average, but within the range, of age-0 Largemouth Bass observed in the littoral zone in Chancellor Lake.

Stomach content analysis

Fish prey increased greatly in the diets of age-0 Largemouth Bass in macrophyte edge and high macrophyte coverages at moderate stocking densities, providing more energy for growth to age-0 Largemouth Bass in these habitats. Representing over 90% of the diet by mass, the consumption of fishes was the major determinant of overall consumption trends, which showed the same pattern as fish prey. Although we did not measure prey fish densities in the enclosures directly, results from our seining surveys in the lake provided some evidence for increased prey fish abundance in areas with macrophytes present, and other studies have found increased age-0 fish densities in macrophytes (Bryan and Scarnecchia 1992; Wiley et al. 2011). Given that some prey fish were able to pass through the mesh and migrate into and out of the enclosures and that prey fish densities are higher in macrophytes, we conclude that it is likely that prey fish densities were higher in the macrophyte edge and high macrophyte treatments. These increased densities likely explain the increased consumption by age-0 Largemouth Bass that we observed. If prey density is similar, age-0 Largemouth Bass are able to forage at similar rates when vegetation is present or absent (Olson et al. 2003), so increased prey density in macrophytes likely resulted in increased consumption. Our finding that fish prey increased with macrophytes is consistent with a field study by Middaugh et al. (2013), who found that age-0 Largemouth Bass captured from habitats with submersed aquatic vegetation coverages greater than 22% consumed twice as many fish prey. However, Miranda and Pugh (1997) found that consumption of fish prey declined in lake coves with higher macrophyte coverages (> 30%) in the southern United States. The field studies of Middaugh et al. (2013) and Miranda and Pugh (1997) are indirect, as they rely on coarse assessments of macrophyte coverage and assume that age-0 Largemouth Bass have not migrated between dissimilar habitats. Because our study confined fish to specific habitats, it shows that increased macrophytes led to increased piscivory and consumption over the range of coverages tested.

Age-0 Largemouth Bass stomachs contained more terrestrial invertebrates in macrophyte edge and high macrophyte coverage treatments. Although this effect was relatively small compared to fish diet items, it still existed and likely contributed to increased total consumption and growth. Previous studies have found a positive association between terrestrial invertebrates with emergent and floating leaf aquatic plants due to the habitat these aquatic plants provide (Toft et al. 2003). This increased abundance of terrestrial invertebrates in emergent and floating leaf macrophytes is likely to explain increased terrestrial invertebrate consumption by Largemouth Bass in our enclosures. An alternative hypothesis for increased terrestrial invertebrate consumption could be that the enclosures lacked sufficient prey for the age-0 Largemouth Bass, and this resource limitation required the fish to expand their diet to include terrestrial invertebrates (Sass et al. 2006b). However, this alternative hypothesis is unlikely because age-0 Largemouth Bass consumption of other diet items also increased in enclosures where terrestrial invertebrates increased, providing evidence that increased prey abundance in macrophytes is the more likely cause for increased terrestrial invertebrate consumption.

We expected to detect increased aquatic macroinvertebrate consumption due to increased abundance in mesocosms with macrophyte edges and high macrophyte coverages. Previous studies have found that benthic macroinvertebrate densities increase in benthic (Beckett et al.

1992) and epiphytic (Gerking 1957) habitats with macrophytes (Crowder and Cooper 1982). However, we did not find increases in aquatic macroinvertebrate densities in the mesocosms, which is likely due to our sampling methodology. Our Ekman dredge was sometimes unable to penetrate through dense macrophyte stems and roots, resulting in the likelihood of us undersampling the aquatic macroinvertebrates community in dense macrophyte habitats. Regardless, we did not detect increased aquatic macroinvertebrate consumption by age-0 Largemouth Bass in mesocosms with macrophytes present. Garvey et al. (1998) found that aquatic macroinvertebrate consumption declined with an increased abundance of fish prey and Olson (1996) found that increased size led to increased piscivory through ontogenetic development. Therefore, the increased size of fishes in enclosures with macrophytes and the increased fish consumption likely created a positive feedback that reduced macroinvertebrate consumption in these enclosures despite greater availability.

Greater foraging opportunities existed in the macrophyte edge and high macrophyte coverage, moderate stocking density treatments, which is supported by the increases we found in the total biomass of diets in those treatments. Although zooplankton densities were higher in enclosures with macrophyte edges and high macrophyte coverages, age-0 Largemouth Bass stomachs contained less zooplankton biomass, providing evidence of intentional avoidance of zooplankton. Consumption of higher-energy fish prey items increased for age-0 Largemouth Bass in the macrophyte edge and high macrophyte coverage, moderate stocking density treatments. These conclusions are consistent with results from studies of age-0 Largemouth Bass in aquaria and 0.5-m deep outdoor pool microcosms (Garvey et al. 1998), which found that increased fish prey availability resulted in increased fish consumption and decreased zooplankton consumption. Our results are also consistent with the findings of Middaugh et al. (2013), who found that age-0 Largemouth Bass sampled from lakes have greater fish prey stomach contents when captured in habitats with greater than 22% macrophyte coverage and total stomach content weights from sites with greater than 60% macrophyte coverage.

Previous research has found that adult Largemouth Bass (Smith 1995) and age-2 Largemouth Bass use macrophyte edge habitats to increase encounter rates with potential prey items and therefore increase consumption. Our results were unable to discern differences between the high macrophyte coverage and macrophyte edge treatments, but fish from edge treatments had higher growth than those with low vegetation. If consumption and growth were linearly related to the fraction of area with macrophytes, we would have expected the edge habitat mesocosms to be intermediate to the high macrophyte coverage treatments. Alternatively, instead of a linear increase, it could be that consumption and growth peak at intermediate densities and decrease at higher vegetation coverages (Valley and Bremigan 2002, Miranda and Hubbard 1994). This would also potentially explain the lack of difference between edge and high macrophyte treatments. We cannot differentiate between the edge effect and intermediate density hypotheses with our study design. Future research should use an experimental design with similar vegetation coverage but differing amounts of edge habitat, similar to Smith (1995), to further explore this relationship.

Growth

While stomach contents provide a snapshot of feeding activity, growth rates provide an integrated index of feeding over time. The growth rates observed in age-0 Largemouth Bass over time were consistent with the patterns seen in diets; age-0 Largemouth Bass grew more quickly in habitats with macrophyte edge and high macrophyte coverages with lower densities of intraspecific competitors. These results are also consistent with findings from field surveys that found age-0 Largemouth Bass were longer when macrophytes were present (Miranda and Hubbard 1994; Middaugh et al. 2013). Miranda and Hubbard (1994) found both increased length and abundance of age-0 Largemouth Bass when vegetation was present, providing additional evidence that the increased growth rates we observed in our study could correspond with mitigation of size-selective mortality (Miranda and Pugh 1997) and increased recruitment (Miranda and Hubbard 1994; Ludsin and DeVries 1997).

Future Research

The increased piscivory we observed in enclosures with macrophytes corresponded with increased growth rates in age-0 Largemouth Bass. Although previous field research has identified correlations between age-0 Largemouth Bass diet, size, and macrophyte coverage (Middaugh et al. 2013), results from our study show that increased macrophytes and macrophyte edge habitats led more directly to increased piscivory. We were unable to continue our study overwinter to directly determine the impacts of macrophytes on recruitment. Other studies have shown greater overwinter mortality for small individuals (Miranda and Hubbard 1994; Ludsin and DeVries 1997; Post et al. 1998) and that high growth during the summer and fall results in increased overwintering age-0 Largemouth Bass size distributions (Ludsin and DeVries 1997). Since overwinter mortality represents a recruitment bottleneck for age-0 Largemouth Bass (Ludsin and DeVries 1997), increased age-0 Largemouth Bass growth rates from macrophytes should translate to greater recruitment. Future research should test the hypothesis that gains in age-0 Largemouth Bass growth from increased macrophyte coverages result in decreased overwinter mortality and increased recruitment at the whole-lake scale in north temperate lakes such as Chancellor Lake.

Management Implications

This research demonstrates a critical, causal connection between increased macrophyte habitats and increased age-0 Largemouth Bass consumption and growth rates, which are likely to benefit recruitment. Macrophyte removal at large and sometimes whole-lake scales occurs throughout the range of Largemouth Bass, and our results indicate that it can limit age-0 Largemouth Bass consumption and growth and thus potentially recruitment in a north temperate lake. We recommend that managers seeking to improve age-0 Largemouth Bass consumption, growth, and recruitment protect existing macrophytes and restore macrophytes to maximize coverage in locations where they have been removed in lakes.

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CHAPTER 2: INFLUENCES OF TROPHIC STATE, AQUATIC VEGETATION, AND LARGE WOODY DEBRIS ON AGE-0 LARGEMOUTH BASS DENSITY

Abstract

Fisheries scientists and managers require knowledge of fish-habitat relationships to understand and potentially mitigate the effects of habitat degradation on fish population dynamics. However, these relationships are difficult to assess due to the relatively coarse scale at which fisheries data are often collected, a problem for species such as Largemouth Bass that relate to structural microhabitats such as aquatic vegetation or large woody debris. Specifically, there is a lack of information about age-0 Largemouth Bass microhabitat selection and the effects of habitats at multiple scales on Largemouth Bass recruitment. We evaluated habitat selection and recruitment for Largemouth Bass in 16 inland Michigan lakes to determine the influence of vegetation, littoral large woody debris, and lake trophic state. We conducted nighttime electrofishing surveys to assess age-0 and adult Largemouth Bass fish catches and densities at the microhabitat scale. We modeled age-0 and adult Largemouth Bass catches to assess habitat selection and found evidence for higher catches at intermediate and high (40 – 100%) vegetation densities, near vegetation edges, near large woody debris, and in higher coverages of submersed aquatic vegetation. We independently estimated size- and habitat-specific catchability rates to account for bias in electrofishing gear that affects interpretation of catch data. Catchability increased with fish length, but decreased with the volume of vegetation in the water column. We used habitat maps, habitat-specific catchability rates, and model predictions of catch to estimate age-0 and adult Largemouth Bass average littoral densities. The best model predicted that the ratio of age-0 to adult Largemouth Bass increased with trophic state and average amount of submersed aquatic vegetation. Our results demonstrate the need for the conservation of large woody debris and aquatic vegetation to increase local abundance and lake-level recruitment to potentially benefit

Largemouth Bass fisheries.

Introduction

Residential development of Upper Midwest lake shorelines is rapidly increasing (Peterson et al. 2003), and affects fish habitats (Christensen et al. 1996; Radomski et al. 2001; Jennings et al. 2003; Wehrly et al. 2012). Fish habitats are the places that fish occupy throughout their lives and fishes rely on their habitats to grow, survive, and reproduce. Fish habitats are characterized by physical, chemical, and biological conditions (Hudson 1992). The physical aspect of fish habitat includes structural habitats such as aquatic vegetation that grows in lakes and large woody debris (LWD) that falls naturally into lakes or is transported by streams into lakes. Shoreline property owners impede the recruitment of LWD to the lake by removing trees in the riparian and littoral zones to improve their visibility and access to the water (Christensen et al. 1996; Jennings et al. 2003; Francis and Schindler 2006; Marburg et al. 2006; Wehrly et al. 2012; Czarnecka 2016). Residential development on lake shorelines is also associated with decreased coverage of submersed and floating-leafed aquatic vegetation, because the aquatic vegetation that some people consider a nuisance is removed by hand pulling, herbicide treatments, and mechanical harvesting (Radomski and Goeman 2001; Jennings et al. 2003; Chapter 3). These changes affect fish microhabitats, the finest scale habitat features that fish use such as a patch of aquatic vegetation or a piece of LWD. Cumulative effects to microhabitats can affect fish populations (Jennings et al. 1999; Radomski and Goeman 2001; Sass et al. 2006b) and potentially their fisheries. In Michigan, recreational fisheries support a $4.2B industry (USDOI et al. 2014) and 48% of fishing trips occur on inland lakes (Lupi et al. 2001), so it is important to understand the effects of shoreline development on inland lake fishes and fisheries.

Michigan's inland lakes support populations of Largemouth Bass *Micropterus salmoides,* an ecologically important species that structures lake trophic dynamics (Carpenter et al. 1987) and a highly sought after sportfish (Lupi et al. 2001). Naturally-reproducing Largemouth Bass fisheries require successful recruitment, whereby fish hatch, grow, and survive until they are large enough to be captured by the fishery. Successful recruitment provides greater management options as more individuals are available for harvest by sport fisheries (Beamesderfer and North 1995) and understanding of recruitment can help managers improve fishery quality by setting regulations to adjust harvest (Allen and Pine 2000). Survival and growth during the first year are major factors that determine Largemouth Bass recruitment success, because their relatively small size and energetic reserves make age-0 Largemouth Bass are more susceptible to predation and starvation than in later life history stages (Ludsin and DeVries 1997; Post et al. 1998). Age-0 fishes must minimize predation risk while also foraging to avoid starvation and survive to age-1, and aquatic vegetation may influence both foraging rates and predation risks (Werner et al. 1983a; Valley and Bremigan 2002; Sass et al 2006a). For example, age-0 Largemouth Bass are less susceptible to predation when aquatic vegetation is present, but more susceptible near the edges of macrophytes beds where predators can see farther through the water and so have increased encounter rates (Smith 1995; Olson et al. 2003; Sass et al. 2006a). In aquarium experiments, age-0 Largemouth Bass feeding rates were reported to be similar when vegetation was present or absent (Olson et al. 2003), but declined at higher vegetation densities (90 plants/m^2; Valley and Bremigan 2002).

Field surveys have supported the hypothesis that age-0 Largemouth Bass select intermediate vegetation coverages that minimize the ratio of daily mortality rate to growth rate (Werner et al.

1983a), with age-0 Largemouth Bass densities peaking between 10-40% vegetation coverage (Miranda and Pugh 1997). However, Middaugh et al. (2013) did not detect a decline in consumption or growth at high macrophyte coverages, instead finding that piscivorous consumption was greater above 24% submersed aquatic vegetation (SAV) coverage and total consumption was greater above 61% SAV coverage. While consumption increased at relatively high SAV coverages, Middaugh et al. (2013) found weak ($R^2 = 0.05$) evidence that age-0 Largemouth Bass catch per unit effort declined above 8% SAV coverage. So, consumption may not be the only factor determining age-0 Largemouth Bass catch rates.

Most field studies to date that have found age-0 Largemouth Bass decline at high macrophyte coverages (Miranda and Pugh 1997; Middaugh et al. 2013) have not corrected for differing catchabilities of their gears in areas of relatively high macrophyte coverage. Catchability is known to decline due to visibility and ability to net fish during electrofishing (Bayley and Austen 2002) and during seining due to vegetation fouling the gear (Pierce et al. 1990). Therefore, an information gap exists as to whether apparent declines in age-0 Largemouth Bass at high vegetation coverages are a result of declining catchability. The answers that fill this information gap regarding microhabitat use and selection may depend upon the scale of analysis. Assessing microhabitat selection and fish densities requires finer resolution (6.25 m^2 in this study) than the 300 -140,000 m^2 scale used in previous studies (e.g. Miranda and Pugh 1997; Middaugh et al. 2013), because the microhabitats we hypothesized age-0 Largemouth Bass use are structured on finer scales.

LWD may also influence age-0 Largemouth Bass predation risk, growth from foraging, and ultimately recruitment. Adult Largemouth Bass select sites near LWD for nests, presumably due to increased ability to defend the nest and thus increased hatching success (Lawson et al. 2011; Weis and Sass 2011; but see Wagner et al. 2006). Age-0 Largemouth Bass experience lower predation in LWD and use it as refuge (Miranda and Hubbard 1994; Sass et al. 2006; Sass et al. 2012). While predation rates may be lower in LWD, age-0 Largemouth Bass growth rates may also be lower (Gaeta 2011; Sass et al. 2012). However, mechanisms for this decreased growth are unclear, and other studies (Gaeta et al. 2014) have found similar growth rates and abundances before and after LWD levels declined. In summary, LWD could serve as a refuge from predation, but its effects on growth rates are unclear and potentially negative. Therefore, we cannot predict whether age-0 Largemouth Bass maximizing growth and minimizing predation should select for habitats with LWD and we do not know whether recruitment is influenced by LWD.

Lake-scale habitat characteristics such as overall productivity may also determine average age-0 Largemouth Bass densities at the whole-lake level. Largemouth Bass recruitment is influenced by productivity in the water column, which provides greater zooplankton, macroinvertebrate, and fish prey availability (Hanson and Leggett 1982; Hanson and Peters 1984; Pace 1986; Bachmann et al. 1996; Allen et al. 1999; Garvey et al. 2002; Brauns et al. 2007). With greater prey availability, age-0 Largemouth Bass have the ability to feed more effectively and grow more quickly (Keast and Eadie 1985). Decreased prey abundances may also lead to greater predation risk. For example, age-0 Largemouth Bass could increase use of high predation-risk habitats while seeking to minimize the ratio of predation risk to foraging returns (Werner et al. 1983a; Gilliam and Fraser 1987). Additionally, when foraging opportunities are scarce, age-0

Largemouth Bass might use higher-risk feeding strategies such as focusing limited information processing abilities on foraging rather than on potential predators (Milinksi 1984). All of these mechanisms likely combine to increase Largemouth Bass recruitment in more productive lakes.

The goal of our study was to quantify the effects of habitat on age-0 Largemouth Bass density at the microhabitat scale and to determine whether cumulative increases in microhabitats influenced stock-recruitment relationships at the whole-lake, population level. To achieve this goal, we developed models of microhabitat-scale age-0 and adult Largemouth Bass catch, converted estimates of catch to density using habitat-specific catchability coefficients, and tested whether the ratios of recruits to adults among lakes in Michigan with a range of habitats were influenced by microhabitat coverage and overall lake productivity. We hypothesized that age-0 Largemouth Bass catch would be highest in microhabitats with intermediate (20 – 40%) vegetation coverage, near the edges of aquatic vegetation patches, and near LWD. We hypothesized that age-0 Largemouth Bass catchability would decline with the amount of vegetation in the water column, and that this would influence interpretation of age-0 Largemouth Bass catch data in high-vegetation habitats such that relative abundance would be higher than previously described in the literature. Finally, we hypothesized that the ratio of age-0 to adult Largemouth Bass would be increased by both whole lake factors (trophic status) and the cumulative effects of microhabitat (LWD and aquatic vegetation metrics). Results from this research can be used to inform habitat management decisions by riparian property owners, nonprofit organizations, and natural resource agencies regarding aquatic vegetation control and LWD conservation. Additionally, this research can inform fisheries management to benefit Largemouth Bass populations by informing choices that are influenced by stock-recruitment relationships.

Methods

Largemouth Bass surveys

We surveyed Largemouth Bass in each of sixteen Michigan lakes (Table 2.1) once between 28 September to 1 November, 2014 and once between 8 September to 30 September, 2015. Lakes were chosen based on size (< 140 ha), presence of Largemouth Bass in prior surveys by the Michigan Department of Natural Resources, and to achieve a broad range of habitat conditions for trophic state and vegetation coverage variables. Nighttime surveys were conducted with a bow-mounted boat electrofisher using direct current at a rate of 60 pulses per second and averaging between 6-12 A. Electrofishing transects to collect Largemouth Bass were started at evenly spaced intervals or at the end of the previous transect in cases of overlap; the number of transects varied based on avoiding overlapping transects, time limitations, and equipment failure. We electrofished by motoring in a zig-zag fashion between the 1.5-m contour and the shoreline (hereafter, “littoral zone”). We recorded the electrofishing boat’s transect path with a Trimble GeoXT GPS (Trimble Navigation Ltd., Sunnyvale, California) to later determine which areas were surveyed. Technicians attempted to capture every Largemouth Bass they saw by scooping the fish with dip nets. We recorded GPS coordinates for each scoop with fish, and captured fish were placed in separate livewell compartments corresponding to the scoop and GPS coordinates. We used the electrofishing transect paths to create a map of electrofished areas for each transect as a measure of our survey effort. We considered the area within 3 m of our transect path on either side to be the electrofished area, because we estimated this to be the effective range our technicians’ nets.

Table 2.1. Lakes surveyed for Largemouth Bass and summary habitat statistics hypothesized to affect Largemouth Bass catch. Mean (SD) vegetation volume, emergent vegetation coverage, submersed aquatic vegetation (SAV) coverage, and distance to large woody debris (LWD) were assessed for the littoral (0 – 1.5 m) area of each lake and surface temperatures were recorded prior to the first electrofishing survey each night in 2014 and 2015, respectively. Lake productivity measured by trophic state index (TSI) for Michigan lakes.

Lake Name	Surface area (ha)	Littoral area (ha)	TSI	Vegetation volume (%)	Emergent vegetation coverage (%)	SAV coverage (%)	Distance to LWD (m)	Temperature (2014, 2015; °C)
Big Blue	135.8	27.4	36.9	14 (24)	7 (21)	32 (42)	169 (124)	12.1, 22.3
Big	86.1	33.6	38.8	33 (27)	14 (25)	61 (41)	213 (99)	11.0 20.5
Chief	47.8	27.0	42.8	16 (24)	14 (21)	5 (20)	228 (95)	9.8, 19.3
Ford	73.6	23.6	33.7	27 (33)	10 (24)	44 (43)	283 (56)	17.5, 22.8
Gun	94.6	31.7	35.6	32 (28)	30 (26)	5 (17)	153 (98)	14.2, 21.4
Harper	33.6	19.3	35.3	10 (17)	6 (13)	42 (39)	98 (80)	15.7, 23.6
Hicks	64.6	25.4	53.6	63 (27)	45 (30)	29 (35)	252 (85)	10.3, 19.7
Hogback	21.7	10.9	44.2	62 (35)	55 (38)	17 (30)	300 (0)	NA, 14.8
Idlewild	42.1	22.3	38.2	15 (22)	10 (20)	37 (40)	142 (99)	11.4, 21.3
Little Bass	22.2	11.2	36.3	14 (18)	7 (13)	36 (36)	56 (54)	11.2, 21.1
Loon	37.4	13.6	42.3	34 (35)	28 (33)	24 (33)	176 (108)	9.4, 18.6
Meauwataka	34.4	7.4	35.8	39 (38)	21 (28)	31 (32)	163 (107)	11.8, 20.3
North	40.4	19.7	39.7	13 (17)	3 (9)	41 (33)	213 (98)	20.1, 24.0
Pine	67.4	37.6	36.0	4 (13)	21 (39)	19 (33)	93 (66)	12.2, 21.2
Reed/Rainbow	38.2	19.2	35.0	29 (33)	21 (27)	35 (33)	136 (88)	15.6, 21.4
Todd	33.1	10.8	43.2	65 (27)	44 (36)	47 (37)	220 (104)	9.9, 19.2

After each transect, we measured the length of each Largemouth Bass we captured and removed scales from a random subsample of potential age-0 Largemouth Bass (< 15 cm) to determine age (DeVries and Frie 1996). Our age-length data showed that at 10.1 cm, 50% of Largemouth Bass were age-0 and 50% were age-1, so all Largemouth Bass less than 10.1 cm whose scales were not analyzed (227) were assumed to be age-0 and Largemouth Bass 10.1 cm or greater were assumed to be age-1 or older. Based upon our sample of fish with known ages, this assumption incorrectly classified 2% of age-0 Largemouth Bass as age-1 and 3% of Largemouth Bass classified as age-0 were actually age-1. We created a 2.5 x 2.5-m raster grid in ArcMap (Environmental Systems Research Institute, Redlands, California) for 2014 and 2015 surveys, where each cell represented the sum of age-0 Largemouth Bass captured in its area and only grid cells in the electrofished littoral area were assigned a value. We assumed that Largemouth Bass greater than 19.9 cm could be sexually mature (Laarman and Schneider 1985) and so were considered adults; we created similar raster grids representing the total number of adults present in each searched grid cell in 2014 and 2015. These count data from grid cells searched by electrofishing were used to model Largemouth Bass catches using habitat covariates (as described below).

Habitat surveys

We mapped littoral aquatic vegetation in each lake during September, 2014 after vegetation had reached peak growth (MDEQ and USGS 2008). We visually classified aquatic vegetation from a boat during daytime as percent coverage of emergent vegetation (EMG) and submersed aquatic vegetation (SAV). We also visually estimated the average vegetation height as a proportion of the water column. Aquatic vegetation patches were mapped with a GPS as polygons representing patches of similar coverage and height for each vegetation type by driving a boat along the edge of each vegetation patch. We calculated the average proportion of the water column with vegetation (hereafter "vegetation volume" or VEGVOL) by multiplying the coverage by the height for each vegetation type in a cell and summing these values. We calculated a measure of the squared vegetation volume ($VEGVOL^2$) to test for nonlinear effects in vegetation volume by multiplying vegetation volume by itself and dividing by 100 for comparable scale. We also calculated a metric of vegetation edge habitat (VEGEDGE) measuring the maximum range in vegetation volume for a grid cell and the eight cells with which it shared an edge or corner.

While conducting vegetation surveys, we mapped the location of the center of each piece of

LWD (> 3 m length or 0.5 m diameter) that we observed in the littoral zone for later comparison to Largemouth Bass catch. We used the cost-distance function in ArcGIS to calculate the shortest distance that a fish could swim through the water to the nearest piece of LWD (LWDDIST). We coded all distances greater than 300 m to LWD as 300 m, because fish densities at the microhabitat level are unlikely to have been affected by LWD at distances farther than the average distance that age-0 Largemouth Bass disperse from their nest (300 m; Hessenauer et al. 2012).

We assessed overall lake productivity using a Trophic State Index (TSI) specific to Michigan lakes (MDEQ and USGS 2008); trophic state indices convert total phosphorus, chlorophyll α, and Secchi depth into a single metric of lake trophic condition and are well-correlated with the abundance of zooplankton, macroinvertebrates, and fishes that age-0 Largemouth Bass consume (Hanson and Leggett 1982; Hanson and Peters 1984; Pace 1986; Bachmann et al. 1996; Allen et al. 1999; Garvey et al. 2002; Pinto-Coelho et al. 2005; Brauns et al. 2007). We collected water samples for total phosphorus and chlorophyll α analysis in July 2014 and during each fall electrofishing survey per MDEQ and USGS protocol (2008), and calculated the average concentration of total phosphorus and chlorophyll α across all measurements. We measured Secchi depth in each lake during daylight hours in September 2014 (MDEQ and USGS 2008).

Largemouth Bass catch models

We created separate models predicting age-0 and adult Largemouth Bass catch in grid cells searched by our electrofishing surveys based upon habitat covariates. We modeled age-0 and adult Largemouth Bass catches using a zero-inflated Poisson (ZIP) regression (Zeilies et al.

2008). ZIP models predict the absence or potential presence of individuals using a logit model, and in instances where individuals are potentially present, a Poisson regression model estimates the count (Zeilies et al. 2008). We used ZIP regression because our catch models needed to account for excess zeroes with respect to the expected Poisson distribution due potentially to changing recruitment among lakes and years. Counts of were predicted by habitat covariates measured at two scales: the whole lake scale (TSI and surface temperature) and grid-cell (EMG, SAV, VEGVOL, VEGVOL^2, VEGEDGE, and LWDDIST). We conducted all model selection in this study using Aikaike's information criterion corrected for sample size (AICc; Burnham and Anderson 2002). Predictions of all models in this study within 10 AICc points of the best-fitting model (Burnham et al. 2011) were model-averaged based on their weight (w_i; Burnham and Anderson 2002). We tested for correlation among variables and removed those that were highly correlated (Pearson's $r > 0.7$; Geiger et al. 2010), with the exception of VEGVOL and VEGVOL^2, which were highly correlated ($r = 0.94$). We checked the residual errors of both age-0 and adult catch models for spatial autocorrelation measured by Moran's I values at distances between 0 and 1000 m in each lake to investigate concerns about statistical independence of catches in nearby cells using the Spatial Analysis in Macroecology program (SAM; Version 4.0; Rangel et al. 2010).

Catchability estimation

We estimated patterns in catchability of Largemouth Bass by size class and amount of vegetation using a mark-recapture experiment; these catchability estimates were later used to estimate density of age-0 and adult Largemouth Bass. We created an enclosure using a seine-style net (1-cm mesh) in a rectangular shape approximately 26 m long and 10 m wide. Floats at the surface and weights at the bottom prevented escape above or below the net and we visually inspected the net for contact with the bottom during deployment. We marked Largemouth Bass from our electrofishing surveys with a fin clip and stocked them in the enclosure. Then, we conducted four electrofishing passes down the middle of the net pen throughout the night. After two electrofishing passes, Largemouth Bass from the most recent electrofishing survey transect were marked and added to the net pen to increase the number of fish available for capture. We measured lengths and classified the Largemouth Bass stocked and captured in the enclosure as small (< 15 cm) or large (≥ 15 cm) for models of catchability. The total number of Largemouth Bass available for capture and number captured during each transect was summed across the transects conducted at each lake, each year, by size class. We divided the number of fish captured in each size class by the number available and by the fraction of enclosure area searched to calculate catchability for small and large Largemouth Bass. We created a set of candidate linear regression models with size class and vegetation volume as potential predictors for catchability, and used model-averaging to predict catchability based on size class and vegetation.

Largemouth Bass density and recruitment

We estimated density of age-0 and adult Largemouth Bass in each littoral grid cell in the lake to facilitate interpretation of our catch models after accounting for catchability bias and to enable modeling of stock-recruit relationships among lakes. To accomplish this, we first applied our models of age-0 and adult catch to each cell of the littoral zone. For these predictions of catch, we substituted the average lake surface temperature value recorded during our surveys (16.9°C) among all lakes in the study for the values measured the night of each survey. Using the same temperature value for predicting catch in all lakes standardized for the declines in catch that we experienced later in the fall as surface temperatures declined. Predicted catch for each grid cell was then divided by predicted catchability based on the vegetation volume in that cell and size class. This produced a point estimate of age-0 and adult Largemouth Bass density (#/m^2) in each cell. Visual comparison of these density estimates plotted against habitat covariates provided information about the effect size of each habitat covariate and interpretation of the covariate's effect on density after accounting for catchability bias. We predicted the average density of Largemouth Bass in each littoral cell and calculated the average fish density among cells in each lake to estimate average lake-wide age-0 and adult densities each year.

We used these fish densities to analyze the ratio of age-0 to adult Largemouth Bass (i.e. recruits per adult stock, R:S) with the assumption of a density independent mortality (Hayes et al. 1996). To do this, we fit a linear mixed model to predict R:S using the *lme4* package (Bates et al. 2015) in R (R Core Team 2013) with fixed effects for variables at the whole lake-level (mean EMG, mean SAV, mean VEGVOL, mean $VEGVOL^2$, mean VEGEDGE, and mean LWDDIST) and a random effect (year).

Results

We caught a total of 670 age-0 and 1,494 adult Largemouth Bass during nighttime electrofishing surveys in 2014 and 2015 after electrofishing 687,244 m^2 of the littoral zone in 16 Michigan lakes (Table 2.2). Hogback Lake was not surveyed in 2014 due to equipment failure.

Table 2.2. Age-0 and adult Largemouth Bass caught from inland Michigan lakes during nighttime electrofishing transects in 2014 and 2015. Area searched is the sum of littoral area within 3 m of the boat's path during electrofishing transects for each lake.

	2014			2015		
	Age-0 catch	Adult catch	Area searched (m^2)	Age-0 catch	Adult catch	Area searched (m^2)
Big Blue	2	36	16,131	29	19	10,269
Big	21	38	26,506	67	15	14,981
Chief	12	31	48,575	21	33	33,238
Ford	2	72	26,188	26	57	20,631
Gun	5	101	19,231	14	72	13,938
Harper	1	96	25,850	12	57	21,200
Hicks	40	17	43,913	67	20	21,113
Hogback	NA	NA	NA	34	20	17,250
Idlewild	13	22	25,031	22	35	19,594
Little Bass	1	75	19,700	18	56	16,438
Loon	7	40	12,825	16	37	9,481
Meauwataka	2	76	23,500	6	62	13,713
North	27	83	14,581	77	32	9,763
Pine	2	53	53,838	14	42	43,969
Reed/Rainbow	3	90	15,550	15	65	12,625
Todd	67	17	18,250	27	25	19,375
Total	205	847	389,669	465	647	297,575

Largemouth Bass catch models

We modeled age-0 Largemouth Bass catch using habitat covariates, and eight models were within ten AICc points of the highest ranked model (Table 2.3). The highest ranked models included count model coefficients for vegetation volume and vegetation volume squared, temperature, vegetation edge, distance to LWD, submersed aquatic vegetation, and trophic state index as well as zero inflation model coefficients for year and lake name. Age-0 Largemouth Bass catch increased with vegetation volume (VEGVOL), but when also accounting for the negative coefficient on $VEGVOL^2$, catch was high when vegetation occupied 40-80% of the water column and peaked near 60% in every model. Age-0 Largemouth Bass catch also increased with temperature across the range observed (9.4 - 24.0 °C) in every model. In the five most likely models ($\sum w_i$ = 0.920), higher age-0 Largemouth Bass catches were predicted near edges of vegetation patches, where the range of vegetation volumes among cells was greater. In some models, age-0 Largemouth Bass were caught at higher numbers near LWD ($\sum w_i$ = 0.877) and areas with more submersed aquatic vegetation (0.477). Spatial autocorrelation was low (all Moran's I << 0.2; Cooper et al. 2016) in all age-0 catch models, so we did not attempt to correct for spatial autocorrelation.

Table 2.3. Top-ranked zero-inflated Poisson models to estimate density of age-0 Largemouth Bass in the littoral zones of 16 Michigan lakes. Count model coefficients were vegetation volume (VEGVOL; % water column), the square of vegetation volume ($VEGVOL^2$), temperature (TEMP; °C), submersed aquatic vegetation coverage (SAV; %), trophic state index (TSI), distance to the nearest piece of large wood debris (LWDDIST; m), and maximum range of vegetation volume (VEGEDGE) in adjacent cells (% water column). Zero-inflation model coefficients (lake and year) are not shown.

Rank	ΔAICc	Weight	Intercept	VEGVOL	$VEGVOL^2$	TEMP	VEGEDGE	LWDDIST	TSI	SAV
1		0.282	-3.162	0.025	-0.021	0.074	0.004	-0.001		0.002
2	0.285	0.244	-3.164	0.027	-0.023	0.077	0.005	-0.001		
3	1.020	0.169	-1.962	0.027	-0.023	0.066	0.005	-0.001	-0.025	
4	1.133	0.160	-2.149	0.025	-0.022	0.066	0.004	-0.001	-0.021	0.002
5	2.919	0.065	-3.42	0.028	-0.025	0.079	0.005			
6	4.491	0.030	-1.68	0.029	-0.025	0.063			-0.034	
7	4.584	0.028	-3.346	0.026	-0.023	0.075				0.002
8	5.112	0.022	-3.088	0.027	-0.023	0.075		-0.001		

We also fitted candidate zero-inflated Poisson models to predict adult Largemouth Bass catch in sixteen Michigan lakes (Table 2.4); the top-ranked model provided evidence that adult Largemouth Bass catch was highest at intermediate vegetation volumes (highest catches were predicted between 40 – 80%), because catch increased with VEGVOL but decreased with $VEGVOL^2$. In the top-ranked model adult Largemouth Bass catch increased near vegetation edges, increased with submersed aquatic vegetation coverage, increased closer to LWD, decreased with trophic state, and decreased with colder temperatures (Table 2.4). Three candidate models were within one AICc point of the top-ranked model. The sign and magnitude of all coefficients were the same among top models when included, indicating that the models were robust to the addition of variables. Spatial autocorrelation was low (all Moran's I << 0.2; Cooper et al. 2016) in all adult Largemouth Bass catch models, so spatial autocorrelation was not incorporated into models explicitly.

Table 2.4. Top-ranked zero-inflated Poisson models to estimate density of adult Largemouth Bass in the littoral zones of 16 Michigan lakes. Count model coefficients were vegetation volume (VEGVOL; % water column), the square of vegetation volume (VEGVOL^2), temperature (°C), submersed aquatic vegetation coverage (SAV; %), trophic state index (TSI), distance to the nearest piece of large wood debris (LWDDIST; m), and maximum range of vegetation volumes (VEGEDGE) in adjacent cells (% water column). Zero-inflation model coefficients (lake and year) are not shown.

Rank	ΔAICc	Weight	Intercept	VEGVOL	VEGVOL^2	TEMP	VEGEDGE	LWDDIST	TSI	SAV
1		0.876	-0.525	0.016	-0.013	0.062	0.005	-0.001	-0.068	0.005
2	-4.62	0.087	-3.112	0.015	-0.013	0.067	0.005	-0.001		0.005
3	-6.33	0.037	-0.42	0.017	-0.014	0.06	0.005		-0.073	0.005

Catchability estimation

We captured a total of 15 small Largemouth Bass of the 228 stocked while electrofishing in the enclosures and 376 of 1,356 large Largemouth Bass. We calculated catchability for replicates with five or more small (11 replicates) or large (29) Largemouth Bass available for capture. Mean length in small (8.4 cm) and large (27.1 cm) size classes and vegetation volume in the enclosure were used to estimate catchability; the models within 10 AICc points of the highest ranked models (Table 2.5) showed that catchability declined with size and vegetation volume. For example, weighted model averages produced estimates of 12.6% ± 7.6 (mean ± SE) and 5.2% ± 9.0 catchability for small Largemouth Bass in 0% and 100% vegetation volumes, while catchability for large Largemouth Bass was 49.1% ± 3.9 and 39.6% ± 6.6, respectively.

Largemouth Bass were distributed throughout the enclosures; although we did not formally quantify Largemouth Bass distribution in the enclosures, their density appeared to be 20-40% higher near the edges of enclosures with low vegetation coverage. This violated our assumption of even distribution in the enclosures. As a result, our estimates of the number of Largemouth Bass in the searched area of the enclosure that assumed an even distribution are likely overestimates. Because we divided the number of fish caught by the number of fish expected to be in the searched area, catchability was likely underestimated. The uneven distribution of Largemouth Bass was only observed in enclosures with low vegetation coverage, so underestimates of catchability are only expected in habitats with less vegetation.

Table 2.5. Coefficients and model weights for highest ranked linear regression models predicting catch for potential age-0 and adult Largemouth Bass in an enclosure based upon mean length of each size class and aquatic vegetation volume.

Rank	ΔAICc	Weight	Intercept	LENGTH	VEGVOL	LENGTH*VEGVOL
1		0.530739	-0.072	0.02		
2	0.73	0.368859	-0.027	0.019	-0.001	
3	3.33	0.100402	-0.038	0.02	-0.001	0.00001

Largemouth Bass density and recruitment

We plotted predicted density of age-0 Largemouth Bass in littoral grid cells for all lakes in 2014 and 2015 (Figure 2.1) to supplement interpretation of habitat covariates in Table 2.3 and evaluate densities after accounting for catchability differing with vegetation volume. Figure 2.1 shows model estimates of density using the distributions of littoral zone habitats available in the 16 lakes we studied, so that the effects of all variables in the weighted models are considered simultaneously. For example, Figure 2.1 shows how VEGVOL, $VEGVOL^2$, and other variables in the weight-averaged models combined to produce a relationship where predicted age-0 Largemouth Bass density was highest at intermediate vegetation volumes (40 – 60%), but still about four times greater at high (60 – 100%) vegetation volumes than low coverages (0 – 20%). Figure 2.1 also shows that age-0 Largemouth Bass densities increased with greater submersed aquatic vegetation coverages. The pattern between trophic state and age-0 Largemouth Bass density is inconsistent across the range of trophic states (Figure 2.1), meaning the other covariates appear to have more influence on age-0 Largemouth Bass density at the microhabitat scale than trophic state index. The relatively weak relationship between trophic state and age-0 Largemouth Bass density among grid cells is also evidenced by the relatively low weight ($\sum w_i$ = 0.359) of models that include it. The inconsistent pattern between trophic state and age-0 Largemouth Bass density is due to the nonlinear effects of the ZIP model and the effects of "lake" as a categorical variable for excess zeroes in the catch data. Figure 2.1 shows small increases to predicted density of age-0 Largemouth Bass in cells with larger vegetation edges. The relationship between LWD and age-0 Largemouth Bass density among cells is relatively flat (Figure 2.1), so LWD seems to have relatively less effect than aquatic vegetation.

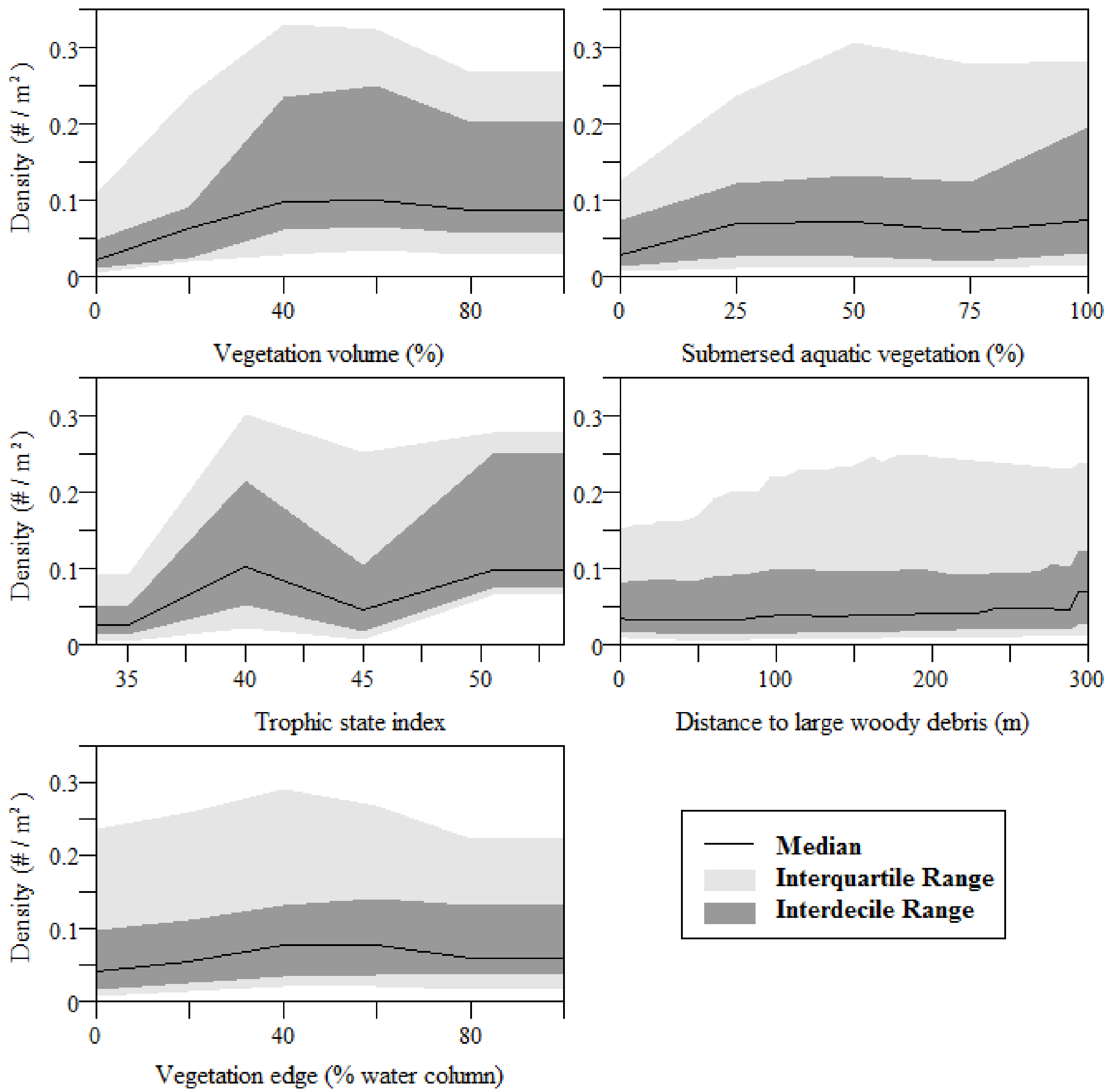

Figure 2.1. Model-averaged, estimated density of age-0 Largemouth Bass abundance in 2.25 m^2 littoral zone grid cells for 16 Michigan lakes plotted against vegetation volume (% water column), submersed aquatic vegetation coverage (%), trophic state index, distance to the nearest piece of large woody debris (m), and maximum range of vegetation volume (vegetation edge) in adjacent cells (% water column).

The three top-ranking linear mixed models predicting the ratio of recruits to adult stock (R:S; Table 2.6) included fixed effects predicting R:S increases with trophic state, SAV, emergent vegetation, vegetation volume, and vegetation volume squared, and decreases in R:S with the average distance to LWD. Figure 2.2 illustrates predicted R:S based on fixed effects (SAV and trophic state) for the highest-ranked model and shows that while both variables affect R:S, trophic state has about twice the effect of SAV across the range of these variables. R:S increased with trophic state in all top-ranked models and with submersed aquatic vegetation in most ($\sum w_i$ = 0.63) top-ranked models. While density of age-0 and adult Largemouth Bass decreased with trophic state, adult Largemouth Bass decreased more quickly, explaining why R:S increased with trophic state. Coefficients in potential models showed evidence for positive relationships between R:S and mean emergent vegetation ($\sum w_i$ = 0.06), vegetation volume (0.07), and vegetation volume squared (0.06) and a negative relationship with mean distance to LWD. However, the small relative weight of these models indicates that these relationships are much less likely to be the best predictors of R:S. We found no negative coefficients on mean vegetation volume squared, and thus no evidence that R:S plateaued or declined at higher vegetation volumes.

Table 2.6. Coefficients and model weights for highest ranked linear mixed models predicting the ratio of fall age-0 to adult (> 19.9 cm) Largemouth Bass in sixteen Michigan lakes based on lake trophic state index (TSI), mean submersed aquatic vegetation coverage (SAV; %), mean emergent vegetation coverage (EMG; %), mean vegetation volume (VEGVOL; %), mean vegetation volume squared ($VEGVOL^2$), and mean distance to large woody debris (LWDDIST; m).

Rank	ΔAICc	Weight	Intercept	TSI	Mean SAV	Mean EMG	Mean VEGVOL	Mean $VEGVOL^2$	Mean LWDDIST
1		0.526	-35.902	0.918	0.126				
2	1.179	0.292	-29.993	0.87					
3	4.942	0.044	-32.47	0.778	0.14	0.08			
4	5.325	0.037	-24.756	0.677			0.08		
5	5.816	0.029	-31.722	0.779	0.114		0.056		
6	5.860	0.028	-25.194	0.709				0.08	
7	5.926	0.027	-32.126	0.8	0.118			0.057	
8	7.406	0.013	-28.079	0.802		0.037			
9	9.965	0.004	-35.203	0.873	0.122		0.007		0.007

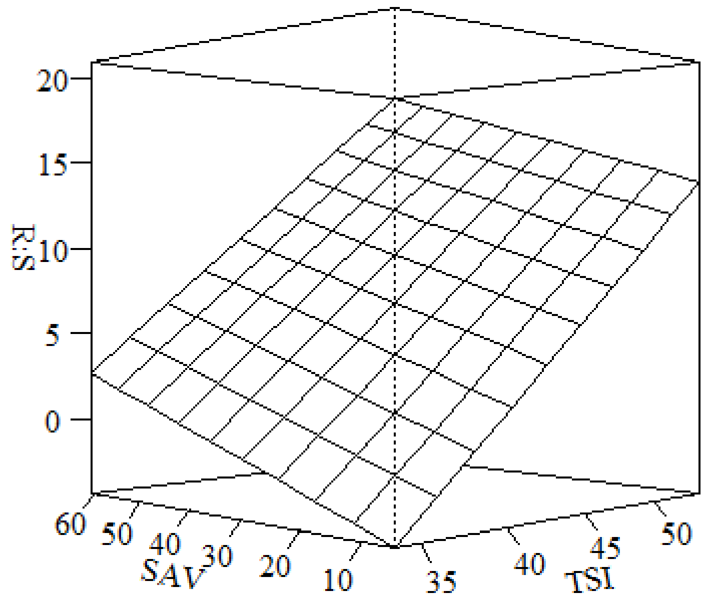

Figure 2.2. Predicted ratio of fall age-0 to adult (> 19.9 cm) Largemouth Bass (R:S) in sixteen Michigan lakes based on fixed effects for lake trophic state index (TSI) and mean submersed aquatic vegetation coverage (SAV; %) from the top-ranked linear mixed model predicting the ratio of age-0 to adult Largemouth Bass (R:S).

Discussion

We sought to estimate the density of age-0 Largemouth Bass in relation to aquatic vegetation, LWD, and lake trophic status, and then use these relationships to quantify age-0 Largemouth Bass habitat selection and stock-recruitment relationships with respect to these habitats. Our results provided evidence for the highest age-0 Largemouth Bass densities in intermediate (40 – 60%) vegetation volumes and higher age-0 Largemouth Bass densities at high (60-100%) vegetation volumes, near vegetation edges, near LWD, and in higher coverages of SAV. At the whole lake, population scale, increases in the ratio of recruits to adult Largemouth Bass in Michigan inland lakes correlated strongly with increases in overall lake productivity (trophic state) and SAV coverage.

We found that densities of age-0 Largemouth Bass peaked near 60% vegetation volume, and were higher at 60 – 100% than 0-40% vegetation volume. Furthermore, we also found that age-0 Largemouth Bass catch and density increased with SAV coverage. Together, these findings provide evidence that age-0 Largemouth Bass densities are higher at high aquatic vegetation coverages than described in the existing literature. For example, electrofishing surveys of coves in a southern United States reservoir, with no sampling bias compensation, found that vegetation coverages of 10-40% had the highest catch per unit effort of age-0 Largemouth Bass, and that catch at high vegetation coverage was similar to or lower than that at low coverage (Miranda and Pugh 1997). Similarly, seining surveys in Indiana lakes found evidence that age-0 Largemouth Bass catch per unit effort was lower at SAV coverages above 8% (Middaugh et al. 2013). While our results are consistent with Miranda and Pugh (1997) at low vegetation levels, we provide evidence that age-0 Largemouth Bass densities do not decline to the extent previously reported in field studies at high vegetation volumes (Miranda and Pugh 1997; Middaugh et al. 2013) and that both catch and density increase with SAV coverage. Our ability to compensate for bias in our sampling method is the main reason for our differing conclusions; Hoyer and Canfield (1996) used rotenone in a highly efficient sampling method (Bayley and Austen 2002) and reported a linear increase in age-0 Largemouth Bass abundance with the percentage of the lake volume containing aquatic vegetation in Florida lakes.

Our data do not provide information as to the mechanisms underlying the observed patterns between age-0 Largemouth Bass density and aquatic vegetation, but our results are consistent with the theory that fish choose habitats with intermediate vegetation to optimize foraging rates (Crowder and Cooper 1982; Werner et al. 1983b). Age-1 growth rates (Cheruvlil et al. 2005) and age-0 Largemouth Bass feeding rates decline at higher vegetation densities (90 plants/m^2) due to higher search times (Valley and Bremigan 2002), but are similar between aquaria with low (35% coverage) and no vegetation (Olson et al. 2003). Nohner et al. (Chapter 1) found that age-0 Largemouth Bass consumption, piscivory, and growth rates were similarly high at medium (42%) and high (59%) vegetation coverages and significantly lower at 4% vegetation coverages. Nohner et al. (Chapter 1) assumed that consumption and growth were high at these coverages in a Michigan lake due to fish foraging effectively within the interstices of the naturally occurring vegetation (Lynch and Johnson 1989). In addition to foraging rate, predation risk also determines habitat selection (Werner and Hall 1983a; Gilliam and Fraser 1987). The literature suggests that age-0 Largemouth Bass maximize the ratio of foraging returns to predation risk by avoiding habitats with low or no vegetation due to increased predation risk (Werner et al. 1983a; Miranda and Pugh 1997; Olson et al. 2003; Sass et al. 2006a Middaugh et al. 2013). Therefore, age-0 Largemouth Bass should occur in the highest densities at intermediate vegetation coverages (35-60%), lower densities in high vegetation coverage (60 – 100%), and lowest densities in areas with low (< 35%) or no vegetation; this pattern is almost identical to what we observed in our age-0 Largemouth Bass density estimates.

Our finding that age-0 Largemouth Bass density increased near vegetation edges is the first evidence of such a pattern for this life-history stage. Adult Largemouth Bass use edge habitats to utilize increase foraging rates due to the high abundance of prey in vegetation (Bachmann et al. 1996; Allen et al. 1999; Garvey et al. 2002) and increased visibility, mobility, and prey encounter rates in the open water (Lynch and Johnson 1989; Smith 1995). Previous research has shown that age-2 Largemouth Bass growth rates increased when edge habitat was created by cutting channels in the aquatic vegetation of a Wisconsin lake (Olson et al. 1998), but Olson et al. (1998) did not address age-0 Largemouth Bass, so it is difficult to determine its implications to this life history stage. Fishes are hypothesized to occupy habitats that minimize the ratio of predation to returns from foraging (Werner et al. 1983a; Gilliam and Fraser 1987), so if age-0 Largemouth Bass do experience increased growth rates by occupying edge habitats, those increases would need to outweigh increased predation risk in those habitats (Smith 1995; Sass et al. 2006a). Future research on age-0 Largemouth Bass foraging should investigate the gains to growth from increased foraging in vegetation edge microhabitats and potential effects to recruitment. Despite the observed selection for vegetation edge habitats by age-0 Largemouth Bass, we do not recommend management approaches to increase these habitats such as harvesting of channels in vegetation (e.g. Olson et al. 1998), because we observed a weak relationship between vegetation edge and recruitment and a linear increase in the ratio of recruits to adult Largemouth Bass.

Our data supported the hypothesis that age-0 Largemouth Bass densities increase near LWD, but the effect size in relation to other factors such as vegetation volume was relatively small and we did not find evidence that more LWD corresponded to greater recruitment. Our data do not allow us to conclude why age-0 Largemouth Bass densities increased near LWD, which may be important for understanding and determining the circumstances in which LWD protection or restoration would be beneficial for Largemouth Bass recruitment. Age-0 Largemouth Bass were potentially using LWD as a refuge from predators because predation rates are lower in LWD (Sass et al. 2012). While the effects of LWD to predation rates are known, the effects of LWD on age-0 Largemouth Bass growth rates may be positive (Sass et al. 2012) or negative (Gaeta et al. 2011). Age-0 Largemouth Bass' use of LWD may have been mediated by other available habitats; Wills et al. (2004) found that LWD attracted black bass when aquatic vegetation was absent, but not when it was present due to an apparent preference for aquatic vegetation. Aquatic vegetation was present in all lakes and greater than 10% of littoral volume in most (88%) of the lakes in our study, so age-0 Largemouth Bass' use of LWD and potential benefits to recruitment (R:S) may have been decreased by aquatic vegetation that provided refuge from predation and foraging opportunities.

We found that more age-0 Largemouth Bass were produced per adult in more eutrophic lakes. This was likely due to increased productivity and forage, which otherwise might limit growth rates and mitigate predation rates (Werner and Hall 1983a; Miranda and Hubbard 1994; Hoyer and Canfield 1996; Post et al. 1998; Allen et al. 1999; Post 2003). Our data cannot discern between mechanisms, but the literature provides hypotheses for understanding how increased productivity could benefit Largemouth Bass recruitment. Age-0 Largemouth Bass feed on zooplankton, macroinvertebrates, and fishes, whose abundance increases with trophic state (Hanson and Leggett 1982; Hanson and Peters 1984; Pace 1986; Bachmann et al. 1996; Allen et al. 1999; Garvey et al. 2002; Brauns et al. 2007). Therefore, as trophic state and forage abundance increase, age-0 Largemouth Bass have the ability to feed more effectively and grow more quickly (Keast and Eadie 1985). In addition, in lakes with low productivity, the decreased prey abundances may lead to greater predation risk. A lack of forage may lead age-0 Largemouth Bass to increase use of high predation-risk habitats as fish seek to minimize the ratio of predation risk to foraging returns (Werner et al. 1983a; Gilliam and Fraser 1987). When foraging opportunities are scarce, age-0 Largemouth Bass might use higher-risk feeding strategies such as focusing limited information processing abilities on foraging rather than on potential predators

(Milinksi 1984). Furthermore, size-specific predation (Werner and Hall 1983a; Miranda and Hubbard 1994) and cannibalism (Post 2003) on smaller individuals could decrease the abundance of age-0 Largemouth Bass when growth rates are limited by overall productivity (Miranda and Hubbard 1994; Hoyer and Canfield 1996; Post et al. 1998; Post 2003).

Corroborating our results, recruitment to age-1 in Tennessee impoundments (Maceina and Bettoli 1998) and Alabama lakes (Allen et al. 1999) was attributed to primary productivity in the water column that led to greater prey availability, growth, and survival. However, some studies (Hoyer and Canfield 1996; Garvey et al. 2002) have failed to detect a linear pattern between trophic state and age-0 Largemouth Bass recruitment. Garvey et al. (2002) attribute the observed decoupling of recruitment from trophic state to age-0 Largemouth Bass switching prey from more energetically profitable Gizzard Shad *Dorosoma cepedianum* to less profitable alternatives. This switching occurred because in more eutrophic systems, age-0 Gizzard Shad grow quickly and are too large for age-0 Largemouth Bass to consume. However, Gizzard Shad were not present in the lakes we studied, so we did not observe this decoupling of Largemouth Bass recruitment and lake trophic state. Compensatory mortality at high densities has been observed in other lakes, as predation rates are higher when age-0 Largemouth Bass are more abundant (Post et al. 1998), but we did not find evidence of this pattern.

We found that in addition to trophic status, recruitment increased across the range (5 – 61%) of mean SAV coverages in our lakes, which was consistent with a survey of Florida lakes (Hoyer and Canfield 1996). However, Pothoven et al. (1999) failed to detect a decline in age-0 Largemouth Bass abundance after herbicide vegetation removal, potentially because the dense growth form of the Eurasian watermilfoil that was removed often has very small interstices and may have limited foraging (Lynch and Johnson 1989; Valley and Bremigan 2002). Because age-0 Largemouth Bass consumption and growth are greater (Chapter 1) and predation risk is lower in habitats with SAV (Sass et al. 2006a), age-0 Largemouth Bass may use vegetation refugia both to increase returns from foraging and to avoid predation mortality. An alternate explanation for increased survival in lakes with more SAV could be that age-0 Largemouth Bass are completing diel migrations between vegetated and unvegetated microhabitats (Shoup 2003) to maximize the ratio of growth from foraging against risk of predation over time (Werner et al. 1983a). While our data cannot determine the mechanisms underlying age-0 Largemouth Bass growth and survival, our finding that the recruitment increased linearly with SAV leads us to recommend conserving littoral SAV coverage up to at least the maximum of the range (60% total coverage) that we studied coverage to benefit recruitment.

The focus of this research was age-0 Largemouth Bass due to the importance of this life history stage to Largemouth Bass fisheries (Beamesderfer and North 1995; Allen and Pine 2000), but it was also important to have an index of adult spawning stock to calculate R:S for each lake. R:S allowed us to standardize the density of recruits we observed by an index of the expected amount of eggs hatched in the lake to infer changes to post-hatch, per-recruit survival based on habitat covariates (Post et al. 1998; Hayes et al. 1996). Therefore, we also created a statistical model of adult Largemouth Bass littoral densities predicted by habitat covariates within and among our study lakes. Adult Largemouth Bass density model coefficients concurred with existing literature, providing evidence that littoral adult Largemouth Bass catches and densities were higher in intermediate vegetation volumes (Wiley et al. 1984; Olson et al. 1998; Pothoven et al.

1999), near vegetation edges (Smith 1995; Olson et al. 1998) and near LWD (Sass et al. 2006b; Sass et al. 2012; Gaeta et al. 2014). Adult Largemouth Bass are thought to use inshore habitats more often during the fall and the evening and thus fall electrofishing during the nighttime is regarded as good indicator of relative population size (Hall 1986; Coble 1992; Bayley and Austen 2002). However, we did observe numerous adult Largemouth Bass escaping our sampling gear in instances where the electrofishing boat was accidentally driven into deeper (>1.5 m) waters than targeted by our protocol. Therefore, our adult catch model is only useful for estimating the relative abundance of adult Largemouth Bass that occupied the littoral zone during sampling and as a relative index of the population.

We corrected for bias in catch based on fish size and habitat-specific estimates of catchability to provide unbiased estimates of age-0 Largemouth Bass densities in habitats with varying vegetation coverage (Bayley and Austen 2002). When independently estimating catchability, we observed slightly (20 – 40%) higher densities of fish near the edges of vegetation-free enclosures. If these observations were accurate, we likely underestimated catchability and overestimated densities of Largemouth Bass by a similar magnitude in open water. If this were the case, the difference between actual age-0 Largemouth Bass densities in habitats with no and high SAV coverage would be greater, strengthening our conclusions that age-0 Largemouth Bass selected for habitats with aquatic vegetation, that SAV increases recruitment, and that managers seeking to improve recruitment should conserve SAV up to 60% littoral coverage.

Our research should inform efforts to manage habitats to improve Largemouth Bass recruitment. The common application of herbicides and use of other techniques to reduce aquatic plants in inland lakes may harm Largemouth Bass recruitment, especially if SAV will be removed below 60% littoral area coverage. However, our findings that both age-0 and adult Largemouth Bass aggregate in microhabitats with moderate to high vegetation volumes (including emergent vegetation), near aquatic vegetation edges, and near LWD reinforces the need to also conserve these habitats. Aquatic vegetation and LWD are often removed by shoreline property owners, leading to a negative relationship with shoreline dwelling densities (Christensen et al. 1996; Radomski and Goeman 2001; Jennings et al. 2003; Francis and Schindler 2006; Marburg et al. 2006; Wehrly et al. 2012; Czarnecka 2016; Chapter 3). Therefore, efforts to improve Largemouth Bass recruitment should seek to convince shoreline property owners to protect and restore these critical habitats. Additionally, natural resource managers can use low lake productivity or low littoral SAV coverages as indicators to diagnose potential reasons for low recruitment and to potentially adjust fishery regulations (Allen and Pine 2000) in the context of anticipated low recruitment in systems with these conditions. Due to the numerous, negative effects to fishes of lake eutrophication identified in the literature (e.g., Lee et al. 1991; Carpenter et al. 1999; Tammi 1999; Jeppesen et al. 2000, Cross and Jacobson 2013) and the declining relationship that we found between adult Largemouth Bass and trophic state, we strongly recommend against managing approaches that seek to increase trophic state based upon our results.

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CHAPTER 3: LAKEFRONT PROPERTY OWNERS' WILLINGNESS TO ACCEPT EASEMENTS FOR CONSERVATION OF WATER QUALITY AND HABITAT

Abstract

Lakes provide valuable ecosystem services such as food, drinking water, and recreation, but shoreline development can degrade riparian habitats and lake ecosystems. Easement contracts for specific rights on a property can encourage conservation practices for water quality, fish habitat, and wildlife habitat, yet little is known about the easement market. We surveyed inland lake shoreline property owners in Michigan to assess supply of two conservation easements (in riparian and in littoral zones) and to identify property and property owner characteristics influencing potential enrollment. Respondents were significantly less likely to enroll in littoral area easements if they indicated social pressure for manicured lawns and more likely to enroll if they had more formal education, shoreline frontage, naturally occurring riparian plants, ecological knowledge, or if the lake had a more developed shoreline. Riparian easement enrollment was significantly less likely if property owners indicated social pressure for manicured lawns, but was more likely if they had more formal education, naturally occurring riparian plants, or shoreline frontage. When payments were low, marginal gains in enrollment were relatively high. Some respondents would enroll in littoral (29.8 % ± 2.2; mean ± SE) and riparian (24.4 % ± 2.1) easements even without payment. Estimated mean willingness to accept values were $1365 (littoral) and $6956 (riparian). Targeting high-probability property owners with large shoreline frontages, more formal education, and high riparian plant coverages and conducting education programs to increase ecological knowledge and change social norms regarding manicured riparian lawns could increase conservation outcomes for water quality or habitat.

Introduction

Inland lakes provide valuable ecosystem services to shoreline property owners and to the general public. These services include the provision of clean drinking water and food from fish and wild rice, regulation of flooding and climate, and generation of socio-cultural services such as recreational and aesthetic value (Carson and Mitchell 1993; Finlayson et al. 2005; Tranvik et al. 2009).

Production of these ecosystem services relies on ecologically functional lakes and watersheds, which are in many cases being degraded by human activities such as agriculture, residential development, and removal of terrestrial and aquatic vegetation that alter aquatic and terrestrial ecosystems. Residential development along lake shorelines in the Upper Midwest United States has increased and is expected to continue increasing in the future (Peterson et al. 2003; Stedman and Hammer 2006; Baker et al. 2008). As a result of this development, riparian habitats (the land adjacent to a water body) along lake shorelines have been altered to consist of more impervious surfaces (Arnold and Gibbons 1996), fewer trees, more mowed grass lawns, and fewer plants (Elias and Meyer 2003), contributing to water quality declines (Nürnberg and LaZerte 2004). Furthermore, shoreline development has resulted in changes to littoral habitats (the nearshore waters that are shallow enough to allow plant growth) such as decreases in native plant and large woody habitat abundance due to direct human removal and increases in the number of docks (Radomski et al. 2010). This degradation of riparian and littoral habitat has resulted in declines in abundance of fish (Helmus and Sass 2008), birds (Lindsay et al. 2002; Newbrey et al. 2005), and amphibians (Woodford and Meyer 2003; Henning and Rembsburg 2009) that rely on these habitats throughout their lives. The increased runoff of nutrients from developed shorelines has also contributed to reduced water quality in lakes through eutrophication (Nürnberg and LaZerte 2004; Garrison et al. 2000).

Degradation of riparian and lake ecosystems also influences humans. The recreational value and desirability of lakes is closely tied to water quality, as users prefer to visit, fish, and otherwise use lakes with clearer water (Ribaudo and Piper 1991; Lupi and Feather 1998; Eiswerth et al. 2008; Keeler et al. 2015) and are willing to pay for improved water quality (Jordan and Enlnagheeb 1993; Netusil et al. 2014) and fish habitat (Ekstrand and Loomis 1975). A similar effect is seen in shoreline property values, with property values falling in less clear lakes (David 1968; Michael et al. 2000; Gibbs et al. 2002) and owners valuing natural shorelines for their aesthetics (Michael et al. 2000).

While shoreline development can degrade riparian habitats and lake ecosystems, some property management choices made by individual property owners can mitigate the negative impacts of development. Best management practices such as minimizing impervious surfaces and maintaining vegetation in riparian buffer zones reduce overland runoff, thereby minimizing shoreline property erosion, nutrient loading, and sedimentation in the lake (Carpenter et al. 1998). Further best management practices include providing important structural habitats for fishes and other aquatic animals in the littoral zone by allowing aquatic vegetation to grow naturally instead of removing it, not blocking growth with mats, not killing it with herbicides (Amato et al. 2012) and by allowing fallen trees to remain in the lake. By applying best management practices, shoreline property owners can choose to mitigate the adverse impacts they might otherwise have on the lake.

Natural resource managers, policy makers, and nonprofit organizations can influence property owner decisions regarding the health of riparian and littoral habitats. Regulations limiting the minimum size of a lakeshore property parcel, impervious surface coverage, terrestrial and aquatic vegetation removal, building locations, and placement of docks are common tools used to protect littoral and riparian habitats by state natural resource agencies and local units of government (Jacobson et al 2015). Another common strategy for increasing use of conservation practices is education and outreach, whereby information is provided with the intent of encouraging shoreline property owners to voluntarily utilize conservation practices due to the benefits such practices would provide such as increased water quality, fish and wildlife habitat, and aesthetic quality. Finally, both governments and non-profit organizations can use payments to incentivize adoption of conservation practices. For example, land trusts purchase specific rights from property owners through conservation easements, which often require the adoption of various conservation practices. Governments may encourage adoption of conservation practices for lakeshore properties through tax incentives, such as the Shoreline Incentive Program offered by Burnett County, Wisconsin, through which property owners receive an initial payment of US$250 and an annual tax incentive of US$50 to maintain a shoreline buffer with native riparian vegetation.

Easement and incentive programs are increasingly common tools for encouraging conservation practices on lakeshore properties, yet little is known about the market for adopting these practices. The potential supply of lakeshore property owners willing to enroll in incentive programs to preserve lake ecosystem health using riparian and nearshore easements across a range of financial incentive levels is unknown; and literature estimating the supply does not exist. As a result of this knowledge gap, it is difficult for resource managers, government agencies, and non-profit organizations to determine the feasibility of conservation easements as a strategy to protect water quality and fish and wildlife habitat.

In addition to determining the feasibility of natural lakeshore easements, resource managers, government agencies, and non-profit organizations require information about how characteristics of property owners and properties affect an individual property owner's probability of enrolling in an easement. Existing research demonstrates that shoreline conservation may be influenced by characteristics of the lakefront property and property owner. For instance, some property owners feel that native vegetation and woody habitat impede recreation, raise safety concerns, and block views of the lake (Jorgensen et al. 2005). Lakefront property owner beliefs about the ability of lakes to withstand shoreline modification, benefit from conservation actions, and the consequences of shoreline development have been reported to be important predictors of conservation actions (Jorgensen and Stedman 2006; Shaw et al. 2011; Amato et al. 2015). However, the same relationship was not found for formal education (Welle and Hodgson 2011), potentially because formal education does not necessarily include lessons in ecology. Whereas the number of activities that occur on a shoreline property isn't a good predictor of sense of place (Jorgensen and Stedman 2006), the amount of time spent on a lakefront property (Jorgensen and Stedman 2006), social norms regarding property management (Shaw et al. 2011), and recreation on a lake are directly related to conservation actions such as willingness to make payments to improve water quality (Welle and Hodgson 2011). However, there is a gap in understanding about how these property and property owner attributes relate to the probability of accepting a payment for a conservation easement on their property.

The goal of this study was to estimate the potential supply of lakeshore property owners willing to enroll in natural shoreline easements in Michigan's Lower Peninsula and to determine characteristics of properties and property owners that influence the probability of enrollment. We accomplished this goal by conducting a mixed-mode survey of owners of shoreline properties on Michigan's inland lakes to gather data characterizing owners and their properties, modeling these variables' effects on the probabilities of enrolling in littoral and riparian conservation easements, and estimating the supply of properties for conservation easements based on our models.

Methods

Survey Instrument

We conducted a mixed-mode internet and mail survey of people owning properties on inland lakes in Michigan's Lower Peninsula regarding their willingness to enroll in conservation easements on their property. The survey used a contingent valuation (CV) method to estimate the financial incentives needed by property owners to voluntarily enroll in an easement and the supply of conservation easements on lakefront properties. The CV approach elicits property owners' stated preferences using survey questions and is commonly used to estimate the value of non-market goods. The CV method is well-suited to situations where the phenomena of interest cannot be observed from existing behaviors (e.g., the potential supply of easements on lakes currently without easement programs). For these reasons, CV methods are commonly used to estimate the value of nonmarket goods and services (Ekstrand and Loomis 1975; Shultz et al. 1990; Jordan and Enlnagheeb 1993).

We tailored our CV survey questions to Michigan property owners based on state property rights laws for lakes to ensure the plausibility of the survey choice scenario as property owners considered enrollment in an easement (Arrow et al. 1993). In general, shoreline property owners in Michigan have the right to remove riparian and littoral aquatic vegetation on their properties at their discretion and remove deadfall trees from the water in front of their property. Therefore, conservation easements are sometimes used to protect lakeshore habitats by requiring application of best management practices. We used this policy tool as the payment method to elicit shoreline property owners' willingness to accept (WTA) conservation easements for conservation practices to protect riparian and littoral fish and wildlife habitat and water quality.

Our survey estimated WTA values for easements requiring application of conservation practices using separate questions for two different areas of shoreline properties to improve water quality, fish habitat, and wildlife habitat; one easement addressed practices in the riparian zone and the other addressed the littoral zone (Appendices D.1 – D.11). We used dichotomous choice questions to elicit WTA, because this survey structure has the best incentive properties to elicit a truthful and accurate response (Kolstad 2000; Haab and McConnell 2002; Boyle 2003); specifically, our dichotomous choice questions provided the respondent an opportunity to receive payment for a good (an easement) at a given price that they could accept or reject as they would in a market. The easements we offered required application of conservation practices for water quality and fish and wildlife habitat on the land and water using fixed zones, which are more easily interpreted, implemented, and enforced than alternatives based on hydrological characteristics such as the depth-to-water index (Tiwari et al. 2016).

A concern with regard to CV methods is hypothetical bias, whereby survey questions that the respondent thinks are only hypothetical will elicit only hypothetical answers that may not correspond to how they would act in a real market (Bohm 1972; Murphy et al. 2005). However, if respondents believe that a question is consequential to them (i.e. they believe it could affect the economic utility they gain), economic theory predicts that they will have a strategic incentive to answer truthfully and accurately (Carson and Groves 2007) and empirical results support this theory (Vossler and Evans 2009; Herriges et al. 2010). We provided incentive for truthful responses by using statements of consequentiality to minimize hypothetical bias; our consequentiality statement indicated that results from the survey would be "made available to policymakers and other organizations as a guide for future decisions about incentive programs." We have anecdotal evidence that at least some respondents believed their decisions were consequential for policy, as we received two follow-up calls from respondents wishing to enroll in any resulting program.

Prior to the CV questions, respondents saw graphics and answered questions about their property in the littoral and riparian zones. These questions helped inform respondents about the economic good that the CV questions would later evaluate. The survey also contained a page with interactive questions describing the easement programs in illustration and text. Each CV question appeared on its own page with additional summary information about the good (Appendices D.7 – D.10). Introductory information for the littoral easement stated that the "purpose is to improve habitat and increase the numbers of fish and aquatic wildlife; property owners must allow all native plants in the water to grow naturally out 50 feet into the lake (can treat invasive plants); owners must allow any branches that fall in the lake to remain in the lake; and the conditions apply along 50% of the shoreline." The exact wording of the final part of the CV question for the littoral zone was, “Would you accept this voluntary offer of $X per year to allow aquatic plants and fallen tree branches in the water along 50% of your shoreline?” The payment amounts (X) offered in the CV questions were randomly assigned as $100, $500, $1,000, $5,000, and $10,000 and were based on qualitative research and data from our pilot study of shoreline property owners discussed below. For the riparian easement, the purpose was “to improve habitat for fish and wildlife to benefit their populations, stabilize your shoreline, and improve water clarity in the lake”. Property owners were required to allow all native plants on the land within 50 feet of the shoreline to grow naturally; native grass and shrub seeds as well as tree saplings that a naturalist might grow would be provided for optional planting; property owners were allowed to trim branches above a height of four feet to improve visibility to the lake; and these conditions applied along 50% of the shoreline. The exact wording of the final part of the CV question for the riparian zone was, “Would you accept this voluntary offer of $X per year to allow native plants to grow naturally on the land along 50% of your shoreline?” The survey stressed that the easements were voluntary to distinguish them from other types of easements (e.g. utility easements) which may not be voluntary. As a follow-up to each CV question, we also asked if the respondent would be willing to enroll in such a program, even if there was no payment.

The survey included questions about shoreline property owners’ environmental attitudes, ecological knowledge, and formal education to potentially explain variation in WTA based upon these characteristics. Previous research has indicated that greater ecological knowledge may relate to a greater likelihood of conserving native vegetation on shoreline properties (Jorgensen and Stedman 2006). Three separate questions on our survey asked respondents to rate on a 5-point Likert scale their agreement with statements that how they maintain their shoreline property affects the number of fish, the water quality, and the amount of wildlife in and around their lake, with those that strongly disagreed (coded as 1) having low knowledge and those that strongly agreed (5) having high knowledge. Each property owner's average response across these statements was used as an index of ecological knowledge. We asked respondents what their highest level of education was among the following categories and converted responses to years: some high school (10 y), high school graduate (12 y); Associate's degree (14 y); Bachelor's degree (16 y); Master's degree (18 y); beyond a Master's degree (20 y).

As social norms such as mowing the lawn and maintaining certain landscaping aesthetics may also predict conservation actions (Shaw et al. 2011), we asked shoreline property owners to respond whether they agree with a statement that "it is important to me that my neighbors maintain a manicured lawn and shoreline," and we used this as an indicator of a social norm held by the respondent. This was measured on a Likert scale from 5 (strongly agree) to 1 (strongly disagree).

The easements proposed to shoreline property owners may be interpreted as limits on their rights to manage their property in a way that allows them to derive utility from the property through recreational activities and other uses. We asked respondents to indicate which of nine ways their household used the land on their shoreline property (i.e. bird or wildlife watching; campfire; eating or cooking outdoors; hunting; landscaping or gardening; recreational equipment storage; relaxation; yard games/children playing; and other) and which of nine ways they used the water and shoreline of their property (i.e., boat storage or access; boating or motorized watersports; fishing; hunting; non-motorized water activities; swimming; view of the lake; wildlife viewing;

and other). We summed the number of uses for water and for land and used this as an equally weighted indicator of the number of each property owner's uses for the land and water.

In addition to the indices of land and water use, we also created an index of the amount of time that owners and their guests spent at the property in 2014. To do this, respondents indicated the frequency of visits per year (never, 0 d; rarely, 1-5 d; occasionally, 6 – 30 d; and commonly, >30 d) by people in six categories (you; spouse or partner; other immediate family; other relatives; friends; and renters); the number of people in each category was not included. These number-of-day values were summed across all categories to create an estimate of time spent at the property. The survey also contained a question about the number of times owners fished in their lake during 2014 (including from a boat, shoreline, or otherwise). While recall bias may have affected these recreational and time use answers, the indices serve as relative measures of activity and are thus useful in our statistical models predicting willingness to accept conservation easements.

In addition to survey questions focusing on property owner characteristics, we also used the survey to collect information about characteristics of the property to assess whether property attributes influenced willingness to participate in conservation easements. Property owners provided estimates of the percent coverage of trees, shrubs, uncut grass, wetland plants, mowed grass, and areas with no plants in the riparian area (within 50 feet of the shoreline); we calculated the percent naturally occurring vegetation coverage by dividing the summed tree, shrub, uncut grass, and wetland plants by the sum of the areas with vegetation coverage responses.

Invasive aquatic plant species are common in Michigan's inland lakes, and management to remove them occurs throughout the state. When invasive species, commonly aquatic plants, are present, property owners may perceive them to be a nuisance and remove them, thus being less willing to enter into an agreement that they perceive limits their invasive plant management options. Although our proposed littoral easement specifically allowed for removal of invasive species, we included the presence of invasive species in the lake in our WTA models to test whether their presence still affected probability of accepting the easement. We asked shoreline property owners whether invasive species were present in their lake, with responses being interpreted as an index of the probability of presence for “yes” (1), “no” (0), and “I don’t know” (0.5) responses.

The size of the shoreline property is also likely to impact the utility that shoreline property owners perceive they are losing when entering either the proposed littoral or riparian easement. The survey included a question assessing an easily-reported metric of property size, shoreline frontage, which is the length of shoreline on the property. Focus groups and cognitive interviews (per Kaplowitz et al. 2004) showed that shoreline property owners almost always know this distance due to the high property values associated with shoreline frontage, and frontage response categories (0 – 15 m, 15 – 30 m, 30 – 61 m, and > 61 m) were selected to achieve a roughly equal distribution of shoreline frontages based on data from our pilot study described below.

In addition to gaining information about the shoreline properties of respondents through the survey, we also used publicly available data to characterize their properties. To determine the proximity between owners’ permanent and lake addresses where the two differ, we calculated the driving distance between the mailing address listed in each recipient's tax records and the coordinates of the random point used to select their shoreline property for the survey. Driving distances were calculated using Google Maps (Google, Mountain View, California 2015) and Macro Recorder 5.8.0.0 (Jitbit Software, Edinburgh, United Kingdom 2011).

The willingness of property owners to enroll in conservation easements may also be related to the extent to which the shoreline has been developed on their lake. We calculated riparian land cover development at the whole-lake scale to determine whether probability of enrollment was affected by development. We used the most recent National Land Cover Dataset (NLCD; Homer et al. 2015) to estimate the proportion of each lake's shoreline classified in developed categories (low, medium, or high intensity developed, open space, barren land, cultivated crops, and pasture or hay). For this purpose, shoreline land cover was defined as the 30 x 30-meter pixels adjacent to the lake in the NLCD dataset; this is the smallest resolution available and is similar to the recommended 30.5-m building setback recommended by the Michigan Department of Environmental Quality (MDEQ 2015).

The survey was pretested in accordance with recommendations from Dillman (2007) by six groups: professionals experienced in survey design (6 individuals), resource managers that may use the information (5), two lakeshore property owner focus groups (22), individual cognitive interviews with lakeshore property owners (7) and a pilot survey (269). During the pretesting, we evaluated performance against Fowler's (1995) criteria that the survey was consistently understood and that respondents were able to answer the survey questions as well as the additional criterion that the economic good in question, the conservation easement, was clearly described and identified (Carson et al. 2003). After each pretest, the survey was modified to address any deficiencies in the criteria above; deficiencies were identified through direct feedback and observations of confusion or inability to answer. The survey was reviewed by researchers familiar with survey design and by managers with the Michigan Department of Environmental Quality and the Department of Natural Resources. Following these reviews, a focus group with twelve lakeshore property owners from across the study region was conducted by participants taking the survey individually and then discussing the survey as a group. Then we held one-on-one cognitive interviews (Kaplowitz et al. 2004) with seven lakeshore property owners on a lake in Bath, MI, which in the southern region of the state. Next, we used a focus group of ten property owners on a lake near Fountain, MI, which is in the northern region of the study to improve representation of geographically diverse lakeshore properties. Finally, a web-based pilot survey that also allowed open-ended comments about the survey was sent to members of 10 organizations of lakefront property owners (i.e. lake associations) across the state that provided a total of 269 responses. Pilot survey respondents answered similar CV questions over a range ($100 – $20,000) of payments, which informed selection of payment levels for the final survey.

Survey Population

Our survey targeted heads of households for properties on inland lakes of Michigan's Lower Peninsula. We generated random geographic locations along the shoreline of all inland lakes greater than 4 ha using the National Hydrography Dataset Plus Version 2 (US Environmental Protection Agency (USEPA) and US Geological Survey (USGS 2012) and ArcGIS version 10.2 (Environmental Systems Research Institute, Redlands, California 2016). We conducted a stratified random sample of these points to identify potential sample sites to send surveys; the strata were by county with number of sample sites drawn in proportion to the length of shoreline in that county. We then used publicly available, spatial datasets of property parcels provided by counties to acquire mailing addresses for lakefront property owners at each sample site (Figure 3.1). Next, we created a potential sample of 1,101 lakeshore property owner addresses by overlaying the sampling points and parcel databases. After checking addresses against a National Change of Address (NCOA) database for bad/insufficient address, we removed 10 potential addresses, resulting in a sample of 1,091 presumed shoreline property owners in our study region.

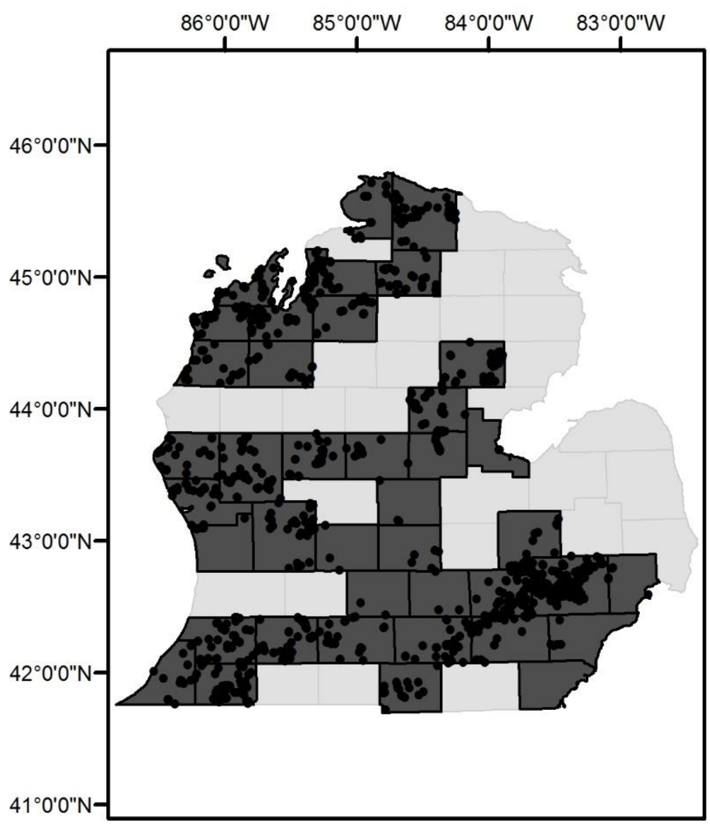

Figure 3.1. Michigan counties where sampling was possible (dark grey) or impossible (light grey) based upon existence of publicly available parcel data and locations of lakefront properties surveyed (points). Density of surveyed lakefront properties was proportional to the length of shorelines on lakes greater than 4 ha in each county across the landscape.

Survey Implementation

An invitation to complete the survey online, including a $1 bill as incentive, was mailed to lake shoreline property owners 12 August 2015, followed by two reminder postcards on 19 August and 16 September 2015. All survey mailings were conducted using pre-canceled stamps at a non-profit rate, therefore we did not receive returned mail from incorrect or unoccupied addresses which may have been ineligible for the study. A paper copy of the survey with a postage-paid return envelope was mailed 6 October 2015 to addresses from which a response had not yet been received, and the survey was closed 31 December 2015.

Statistical Model

We used two separate random utility models (Haab and McConnell 2002) to estimate the probability of respondents agreeing to the littoral and riparian conservation easements we proposed. Random utility models are based upon the logic that utility derived from a dichotomous choice is a function of the choice's attributes (e.g. easement requirements, financial incentives) and the desire of the respondent to maximize their utility. The model is based upon the premise that the probability of a "yes" response to the offer is the probability the respondent thinks they are better off accepting the agreement and the incentive payment, where α is a vector of parameter coefficients, z_j is a vector of attributes of the respondent and their property, β is a coefficient for the natural logarithm of the payment, t_j is the easement payment amount, and ε_j is random error (Haab and McConnell 2002):

$$\mathrm{P}(yes_j) = \mathrm{P}(\alpha z_j - \beta \ln t_j + \varepsilon_j > 0) \qquad (1)$$

Applying this model to our data, we fitted a logit regression (per Haab and McConnell 2002) predicting the probability of a "yes" response:

$$P\left(yes_j\right) = \left(1 + e^{-(\alpha z_j - \beta \ln t_j)}\right)^{-1} \quad (2)$$

We tested the hypotheses that each parameter influenced probability of enrollment in a conservation program based upon parameter estimates for β and each parameter in α. All hypothesis tests were considered statistically significant at $P < 0.05$. We used parameters recovered from the logit models to estimate mean WTA values according to Haab and McConnell (2002), which represent the mean value at which respondents would receive equal utility rejecting or accepting the offer.

Results

Descriptive statistics

We mailed survey invitations to a total of 1,091 NCOA-verified addresses and received 528 unique survey responses after removing duplicates (19) and refusals (1), resulting in a response rate (RR2; AAPOR 2008) of 48.4%. Response rates did not differ significantly between property owners by latitude, longitude, or lake size.

Mean parameter values describing shoreline properties and property owners are provided for property owners that completed both littoral and riparian easement questions (Table 3.1). While the average respondent's permanent address was over 120 km from their lake property, 57.3% lived less than 10 km from their lakefront property. The average education of respondents was greater than 15 years (some college education). Invasive species were commonly reported, with 255 (50%) property owners reporting invasive species were present in their lake, 168 (33%) reporting they were absent, and 82 (16%) that did not know. Respondents reported that the average riparian buffer on their properties and the littoral zone adjacent to their properties were slightly more than half covered by naturally occurring plants. Property owners that agreed that it was "important to me that my neighbors maintain a manicured lawn and shoreline" reported a significantly greater ($P < 0.005$) proportion of their lawns were mowed (62% ± 36; mean ± SD) than those that disagreed with the statement (28% ± 32). Similarly, property owners agreeing with the importance of neighbors' manicured shorelines reported significantly ($P < 0.0005$) lower coverages of aquatic plants (44% ± 26) than those that disagreed with the statement (58% ± 30). On average, property owners used their properties primarily for four activities on the land and six in the water, with the most common land activities being relaxation (86%), eating and cooking (62%), campfires (60%), children playing (59%), and gardening (57%), and the most common water activities being enjoying the view (93%), wildlife watching (86%), swimming (73%), fishing (70%), and operating non-motorized (72%) or motorized (61%) watercraft.

Table 3.1. Mean values (SD) for survey parameters reported by shoreline property owners in Michigan's Lower Peninsula.

Parameter	Mean (SD)
Distance from permanent address (km)	141.7 (367.1)
Ecological knowledge (very low = 1 to very high =5)	4.05 (0.81)
Education (years)	15.8 (2.5)
Invasive species (present = 1, absent=0, don't know = 0.5)	0.68 (0.36)
Lakeshore development (percent developed or agriculture)	29.3 (21.6)
Natural plants in riparian buffer (percent coverage)	56.2 (32.4)
Number of land uses (0-9)	3.99 (1.85)
Number of water uses (0-9)	4.96 (1.67)
Respondent's fishing trips (number / year)	10.6 (10.2)
Shoreline frontage (m)	40.6 (16.6)
Social pressure (low = 1 to high =5)	2.91 (1.26)
Time spent (person days / year)	97.7 (33.3)

Demographic influences on WTA

We developed two different logit models predicting the probability of a respondent agreeing to the littoral or the riparian easements to test whether respondents' personal and property characteristics were related to their probability of participating in these conservation programs. We created the logit model predicting probability of littoral easement enrollment using 12 parameters describing respondents and their properties in addition to parameters on the payment offer and intercept (Table 3.2). The parameter on ln(payment) was positive and significant ($P < 0.0005$) indicating that higher easement payments increased enrollment. Respondents were significantly less likely to agree to the littoral easement if they felt it was important to their neighbors that they maintain a manicured lawn (social pressure). They were more likely to agree to the littoral easement if they had more education, larger shoreline frontage, more natural plants in the riparian buffer, greater ecological knowledge, or if they lived on a lake with more developed or agricultural shoreline land cover. Because the scales of the variables were different, we compared the magnitude of the coefficients to the average values in the data to determine relative importance. The statistically significant variables predicting littoral easement enrollment, in decreasing order of importance were ecological knowledge, education, shoreline frontage, social pressure, natural plants in riparian buffer, and degree of lakeshore development. In candidate models where water uses, land uses, fishing trips, and social pressure were removed, the sign and significance of coefficients did not change for any variable except lakeshore development, which was no longer statistically significant, suggesting that the model was robust to potentially endogenous variables.

In the logit model predicting probability of riparian easement enrollment, the parameter on ln(payment) was positive and significant (*P* < 0.0005) indicating that higher easement payments would increase enrollment. Respondents were significantly less likely to agree to the riparian easement if they described social pressure for manicured lawns, but were more likely to agree to the easement if they had more education, more natural plants in their riparian buffer, or more shoreline frontage (Table 3.2). The statistically significant variables predicting riparian easement enrollment listed by decreasing order of importance were education, social pressure, natural plants in the riparian buffer, and shoreline frontage. In candidate models where water uses, land uses, fishing trips, and social pressure were removed, the sign and significance of coefficients were the same for all variables, suggesting that the model was robust to potentially endogenous variables. The only exception was ecological knowledge, which in the alternative specifications showed evidence for a statistically significant positive relationship with enrollment and thus may be correlated with an underlying, unmeasured variable.

Table 3.2. Model coefficients (SE) for the littoral easement and riparian easement logistic regression models predicting the probability of a respondent accepting the easement based upon characteristics of the respondent and their lakeshore property. Sample size was 439 for littoral and 426 for land easement models. Statistically significant differences from zero are denoted by * (P < 0.05), ** (P < 0.01), and *** (P < 0.0005).

Parameter	Water	Land
Intercept	-8.057 (1.338)***	-6.314 (1.383)***
ln(payment)	0.483 (0.076)***	0.335 (0.078)***
Distance from permanent address (km)	-1.01×10^{-4} (3.57×10^{-4})	-3.94×10^{-4} (4.17×10^{-4})
Ecological knowledge (very low = 1 to very high =5)	0.543 (0.149)***	0.239 (0.152)
Education (years)	0.096 (0.048)*	0.116 (0.052)*
Invasive species (present = 1, absent=0, don't know = 0.5)	-0.180 (0.315)	0.337 (0.347)
Lakeshore development (percent developed or agriculture)	0.014 (0.006)*	0.003 (0.006)
Natural plants in riparian buffer (percent coverage)	0.012 (0.004)**	0.02 (0.005)***
Number of land uses (0-9)	0.028 (0.077)	0.074 (0.08)
Number of water uses (0-9)	0.007 (0.086)	-0.082 (0.093)
Respondent's fishing trips (number / year)	0.013 (0.012)	0.004 (0.013)
Shoreline frontage (m)	0.026 (0.007)***	0.026 (0.008)**
Social pressure (low = 1 to high =5)	-0.321 (0.104)**	-0.433 (0.11)***
Time spent (person days / year)	-0.005 (0.004)	-0.006 (0.004)

Supply of shoreline conservation easements

We used the parameters of the logit models described above to predict the potential supply of shoreline property owners willing to enroll in conservation easements. We estimated supply of lakeshore property owners for littoral easements by plotting the proportion of "yes" responses at each payment amount as well as the proportion indicating that they would enroll with no payment (Figure 3.2). The proportion of "yes" responses generally increased monotonically, except for potentially between the $5,000 and $10,000 estimates, which did not differ significantly. Approximately 29.8% (SE = 2.2) of respondents indicated that they would enroll even without a payment, and 67.1% (5.2) would enroll with a $5,000 incentive. Many of these respondents cited fish and wildlife habitat, a desire for natural conditions, and the belief that their current property management was already in compliance with the proposed conservation easement. When easement incentives are low (< $1,000), the marginal gains in probability of enrollment from an increase in the incentive are very high, meaning additional investments to increase incentives are most efficient when incentives are low and become less influential at higher incentive levels. For example, increasing the incentive from $0 to $1,000 raises the probability of enrollment from 29.8% (SE = 2.2) to 44.7% (5.4). However, at incentives above $2,000, the marginal increases decline as the probability of enrollment begins to plateau around roughly 65%. The predicted probability of enrollment based upon the logit model at average parameter values shows concurrence between the model predictions and the proportion of "yes" responses in the data for each payment amount. The estimated mean WTA for the littoral easement was $1365.11.

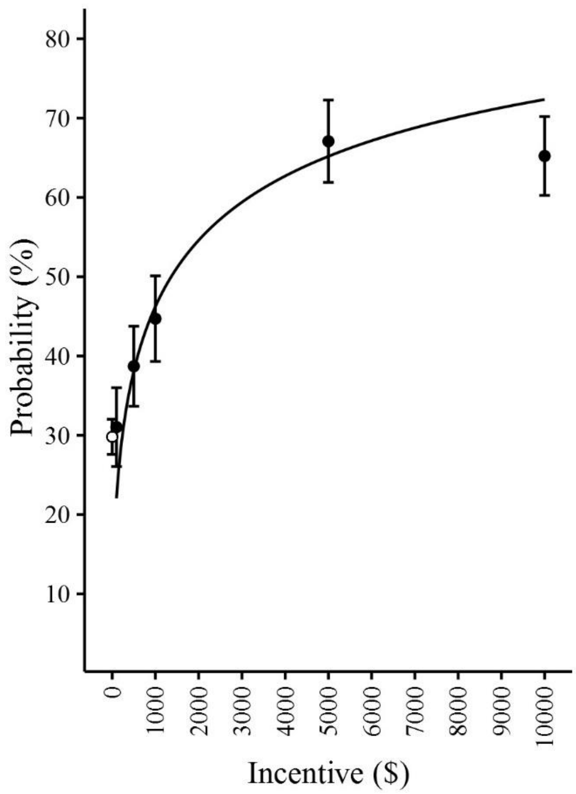

Figure 3.2. Estimated probabilities of a shoreline property owner accepting the littoral easement. The line indicates modeled probabilities based upon logistic regression results across the range of payments ($100 - $10,000) offered in the survey, solid black points indicate the proportion (± SE) of easement offers accepted in the survey at each payment level, and the hollow point indicates the proportion (± SE) of respondents indicating that they would voluntarily enter the easement without incentive.

To estimate the quantity of littoral zone supplied from properties of different sizes, we used probabilities of enrollment from the logistic regression at average values across all parameters except shoreline frontage; shoreline frontage values were set to each of the four possible responses in the survey. These predictions were then scaled up to a hypothetical 1,000-property owner sample to illustrate the difference in strategies targeting property owners of each frontage size class (Figure 3.3). Property owners with shoreline frontages greater than 30 m produced much higher enrollment than for properties with less than 30 m of frontage. This difference was driven by increased frontage enrolled for each property owner that agrees to the easement as well as by the increased probability that owners of properties with large shoreline frontages were more likely to agree. Quantity enrolled increased most rapidly at low costs per meter of shoreline enrolled. Multiplying the quantity enrolled by the cost per meter in Figure 3.3 produces the expected total program costs for any expected quantity and size class. If a manager were attempting to maximize enrollment with a theoretical $100,000 budget for each shoreline frontage size class, this would occur at a cost of $1,249.34 m^{-1} (expected enrollment = 80 m), $99.53 m^{-1} (1001 m), $25.90 m^{-1} (3826 m), and $19.69 m^{-1} (4990 m) for properties with 0 – 15 m, 15 – 30 m, 30 – 60 m, and > 60 m of frontage, respectively. This amounts to more than a 60-fold increase in enrollment in littoral easement frontage when targeting properties with large (>60 m) over those with small (< 15 m) frontages at the same total program cost.

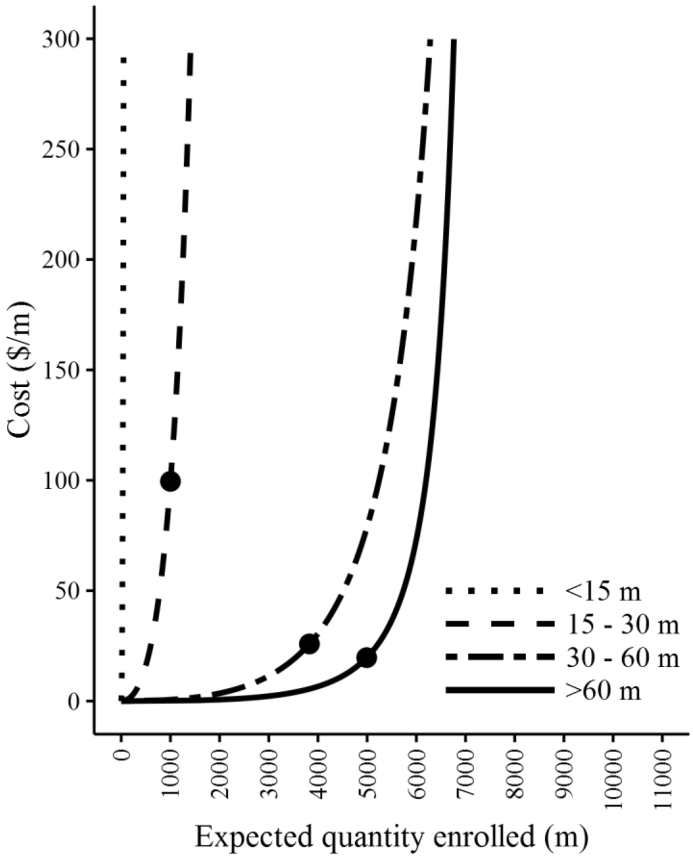

Figure 3.3. Estimated quantity of shoreline enrolled in a hypothetical littoral easement based upon coefficients from a logit model predicting probability of easement acceptance at the average value for all parameters and shoreline frontages of < 15 m, 15 – 30 m, 30 – 60 m, and > 60 m. Estimates are scaled based upon an easement offered to a hypothetical population of 1,000 property owners with differing shoreline frontages. Points represent the predicted quantity of shoreline enrolled when total cost is $100,000.

Probability of enrollment was lower in the riparian easement program (Figure 3.4) than it was in the littoral easement at most payment levels (range of differences = 5.4 – 20%) except at a payment of $500, where enrollment in the riparian easement was negligibly (1.9%) more likely. A plot of the probability of enrollment at each payment level and when no payment would be offered shows general agreement between survey data and logit model estimates at mean parameter values (Figure 3.4), indicating general correspondence between the model and the data. About 24.4% (SE = 2.1) of respondents indicated that they would enroll with no incentive;

many of these respondents cited wildlife habitat, water quality, a desire for natural conditions, and the belief that their current property management was already in compliance with the proposed conservation easement. About 55.2% (5.3) indicated they would enroll with a $10,000 incentive. The proportion of respondents agreeing to the program increased monotonically with increasing incentive payments except for between $100 (32.9% ± 5.1) and $500 (31.1% ± 4.9) payments, which did not differ significantly. The slight decline in mean acceptance between $100 and $500 is likely due to the size of the statistical error relative to the small difference in payment amounts. The greatest increases in enrollment were modeled to occur at relatively low incentive levels (e.g., from $100 to $1000). However, the proportion of respondents indicating that they would enroll at $100 and $1000 incentive levels only increased from 32.9% (5.1) to 33.3% (5.1), which were not significantly different. This small increase was consistent with the much lower marginal increases in modeled enrollment at low incentive levels for the riparian easement than for those modeled for the littoral easement. Similar to the littoral easement, the slope of riparian easement enrollment probability increased much less at high ($5,000 - $10,000) incentive levels. Estimated mean WTA for the riparian easement was $6956.11.

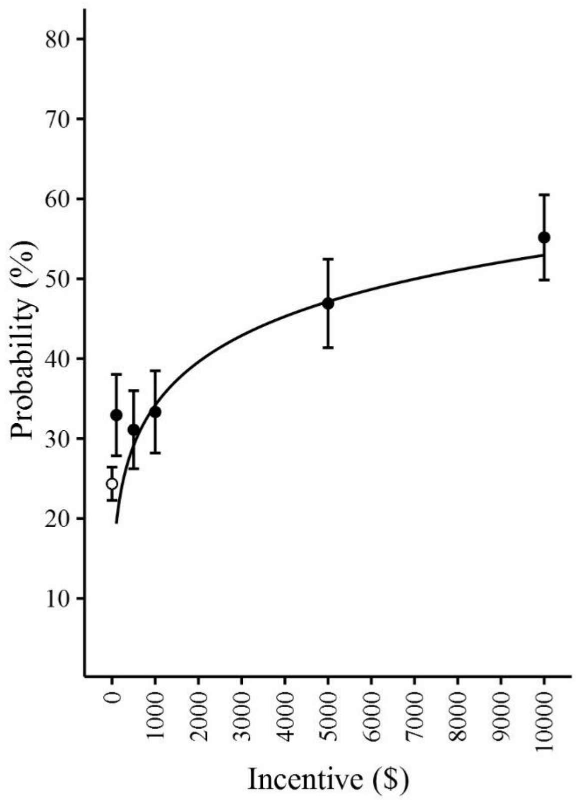

Figure 3.4. Estimated probabilities of a respondent accepting the riparian easement. The line indicates modeled probabilities based upon logistic regression results across the range of payments ($100 - $10,000) offered in the survey, solid black points indicate the proportion (± SE) of easement offers accepted in the survey at each payment level, and the hollow point indicates the proportion (± SE) of respondents indicating that they would voluntarily enter the easement without incentive.

The predicted quantity of shoreline in riparian easement supplied through an offer to 1,000 hypothetical property owners was plotted for easements targeting the shoreline frontage categories used in the survey (Figure 3.5). The greatest increase in quantity occurred at low costs (0 – 50 $/m), and the increase in length of shoreline enrolled decreased as cost increased. For a total budget of $100,000, we predicted that easements targeting properties with 0 – 15 m, 15 – 30 m, 30 – 60 m, and > 60 m of frontage would enroll 52 m, 648 m, 3,007 m, and 4,821 m of shoreline in their riparian easement programs at $1,937.01 m^{-1}, $153.25 m^{-1}, $32.92 m^{-1}, and

$20.67 m^{-1}$, respectively. This amounts to more than a 90-fold increase in enrollment in riparian easements when targeting land owners whose properties were large (>60 m) compared to those with small (< 15 m) frontages at the same total program cost.

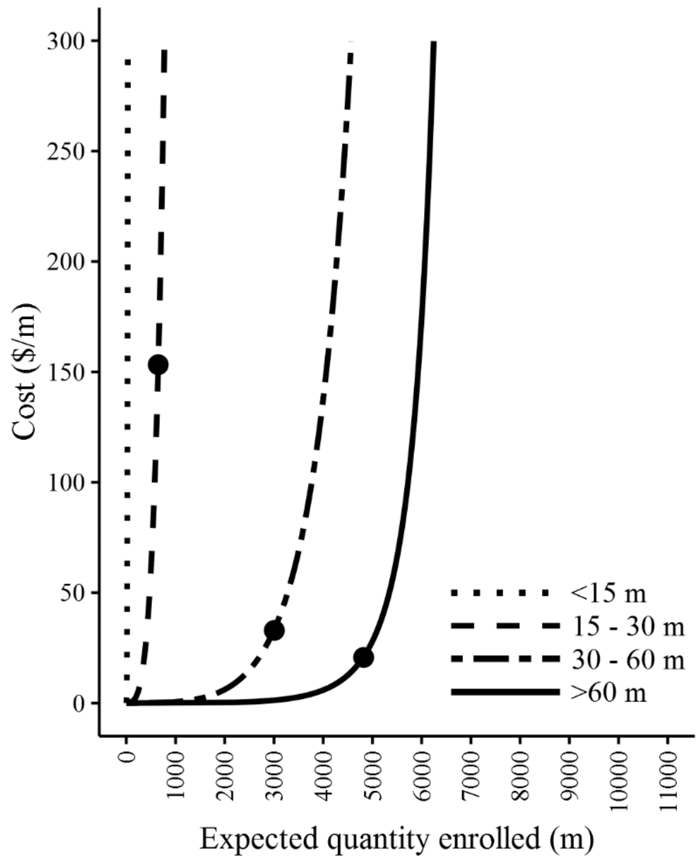

Figure 3.5. Estimated quantity of shoreline enrolled in a hypothetical riparian easement based upon coefficients from a logit model predicting probability of easement acceptance at the average value for all parameters and shoreline frontages of < 15 m, 15 – 30 m, 30 – 60 m, and > 60 m. Estimates are scaled based upon an easement offered to a hypothetical population of 1,000 property owners with differing shoreline frontages. Points represent the predicted quantity of shoreline enrolled when total cost is $100,000.

Discussion

We surveyed inland lake shoreline property owners in Michigan's Lower Peninsula in the broadest geographic assessment of shoreline conservation practices of this demographic to date.

Our survey assessed the potential supply of conservation easements in the riparian and littoral zones of inland Michigan lakes and identified characteristics of properties and property owners that influence the probability of conservation easement enrollment.

Shoreline property owners with larger frontages were more likely to accept both the littoral and riparian easements. As shoreline frontage increased, the number of activities on the land and water did not increase; therefore, increased easement acceptance on larger properties was likely due to the ability to conduct desired activities on the portion of the property not affected by the easement. The increased probability of acceptance and the increased shoreline frontage that large (> 60 m frontage) properties would commit to the program combined to improve the cost-effectiveness at least 60-fold, which should result in greater environmental benefits from targeting large-property owners for conservation easements. Unlike some characteristics of property owners, shoreline frontage can be readily determined through observation or existing records held by governments, allowing managers to target properties with larger frontages first to maximize cost-effectiveness and ecological benefits from conserving more shoreline.

Owners of properties with more riparian plants were also more likely to agree to the easement, which is consistent with Jorgensen and Stedman's (2006) finding that property owners were more favorable toward retaining native vegetation if they reported lower development on their properties. The decision of whether to enroll in conservation easements, especially the riparian easement requiring plants, is potentially caused by underlying, unmeasured variables that influenced past decisions to conserve riparian plants. However, inclusion of this variable has important consequences for protection of riparian buffers. Protecting existing vegetation does not require soil disturbance and may be able to take advantage of deeper, established root systems providing better soil erosion mitigation in the short term when new plantings would not yet be established, thus providing greater benefits to water quality through mitigated erosion. Programs can achieve cost-efficiency by targeting properties with existing riparian plants, increasing the likelihood of acceptance. One caveat to this argument is that if properties with more riparian plants are targeted, there may be little benefit to enrolling them in a conservation easement that requires property owners to do what they already are doing (i.e., some properties might offer little additionality); however, the rapid development and changes to land cover on lake shorelines (Peterson et al. 2003; Stedman and Hammer 2006; Baker et al. 2008) implies that many of these properties with riparian vegetation at present may lose such riparian vegetation in the future. To determine whether properties with riparian vegetation are likely to remove riparian vegetation in the future and are thus worth investment through conservation easements, future research should address the potential for riparian vegetation management to change due to new ownership, changing preferences, or other reasons.

We found that shoreline property owners that agreed their neighbors should maintain a manicured lawn had lawns with more mowed grass, littoral zones with fewer aquatic plants, and were less likely to agree to the easement in the survey, despite accounting for the lack of natural vegetation on respondents' lawns. Shaw et al. (2011) identified subjective norms such as social pressure to be important factors in determining whether participants utilized conservation measures (rain barrels) to benefit water quality in a Wisconsin watershed. Our results extend this pattern of social pressure influencing conservation decisions to riparian and littoral easements, and suggest that a strategy for increased conservation easement acceptance could be to address the social norm that property owners expect and perceive a need for a manicured lawn. For example, the Michigan Natural Shoreline Partnership's Shoreland Stewards Program acknowledges shoreline property owners for applying conservation practices such as vegetated buffers or allowing fallen trees to remain in the water and provides notice to neighbors through yard signs. The yard signs provide recognition and encourage neighbors to apply these practices to benefit water quality and fish and wildlife habitat.

Similarly, after controlling for other factors, we found that property owners with higher levels of formal education were more likely to agree to both littoral and riparian easements, while those with greater ecological knowledge were more likely to agree with the littoral easement. Previous research has shown a similar increased value of water quality corresponding to formal education level (Jordan and Enlnagheeb 1993). Shaw et al. (2011) and Stern (2002) found that knowledge of an environmental problem may lead to conservation actions as stakeholders are aware of potential ecological problems, whereas others (McKenzie-Mohr 2000) argue that knowledge alone may not be enough, since stakeholders must also care about an ecological problem and there may be financial, logistical, or other barriers to them acting to address the problem. Our findings support a relationship between formal and environmental education and conservation action, but do not directly demonstrate that increases to knowledge and understanding cause increases in conservation actions such as allowing native vegetation to grow naturally or allowing fallen trees to remain in the lake. The discrepancy between knowledge of a conservation problem and taking corresponding action to mitigate the problem is well-studied, but linkages between the two are indirect and complex (Kollmuss and Agyeman 2002) with some researchers hypothesizing that information will only produce a change if the lack of information is the only impediment to action (Stern 2002). The tragedy of the commons, whereby benefits from an individual’s actions are shared with the public but the costs are borne by the individual (Hardin 1968), generally applies to inland lakes and provides a potential barrier to action, although strategies to combat tragedies of the commons have been developed (Dietz et al. 2003). Given these concerns about the complex relationship between increased knowledge and conservation actions, future research should test the causality of increased ecological knowledge influencing acceptance of conservation easement programs in varying circumstances to determine whether outreach programs increasing ecological knowledge would be effective in achieving conservation goals.

Finally, shoreline property owners that lived on lakes with more overall developed or agricultural land cover were more likely to agree to the littoral easement. This pattern could be due to an increased perception of the lake’s unnatural state in such settings, in which case the knowledge of ecological degradation may spur the desire to participate in conservation programs (Shaw et al. 2011). However, it should be noted that this result was not robust across trial models and may be a result of a different, unmeasured variable such as income or socioeconomic status that could correlated with characteristics of the lake, property, or owner that are the actual underlying reason for willingness to enroll in a littoral easement.

We did not detect relationships between acceptance of conservation easements and the predictor variables representing number of land or water uses, fishing trips, or time spent at the property. Jorgensen and Stedman (2006) also found that time spent on a lake property and the number of activities that owners participated in were not related to perceptions of native flora or existing development on the property due to complex interactions with other factors affecting the property, the owner's attitudes, and their sense of place.

Conservation easement programs with limited resources should target more willing property owners to increase cost efficiency for enrollment, assuming properties are similar ecologically. By targeting this demographic, incentive levels can be decreased such that more enrollments are gained for the same total cost. We demonstrated the efficacy of this targeting strategy for properties with the easily observable characteristic of large shoreline frontages, but if possible we also recommend targeting property owners with more ecological knowledge and formal education, those with riparian vegetation already in place, those on lakes with relatively more urban or agricultural shoreline development, and those that do not place importance on social norms for manicured lawns. This strategy will increase the likelihood of enrollment at any given cost.

There is currently no market for littoral easements on Michigan lakes. However, Burnett County, Wisconsin operates a tax incentive program whereby an initial $250 tax incentive is provided in the first year with $50 tax incentives in each following year in exchange for a permanent covenant that property owners will maintain a 9.14 m (30 foot) riparian vegetation buffer on their properties. While Burnett County does not monitor the program's impact to water quality or fish and wildlife populations, the county considers the program successful in the context of the known negative effects of riparian and littoral habitat degradation to water quality (Nürnberg and LaZerte 2004), fish (Helmus and Sass 2008), birds (Lindsay et al. 2002; Newbrey et al. 2005), and amphibians that rely on the habitat throughout their lives (Woodford and Meyer 2003;

Henning and Rembsburg 2009). Of the approximately 80% of eligible property owners that are estimated to be aware of Burnett County's program, the participation rate was estimated at 15% (D. Ferris, personal communication). This participation rate provides a strong external validation of our results in a real market, because it is almost exactly the rate we would expect if we extrapolate our modeled riparian easement to an annual incentive level of $50, which would predict an overall average participation rate of 16% for lake owners in the Lower Peninsula of Michigan.

Since no real market exists for shoreline easements in Michigan, this study used a contingent valuation approach to estimate WTA and test characteristics of properties and property owners that influence WTA. This approach can lead to WTA estimates that are overestimates of the actual value; in a meta-analysis Murphy et al. (2005) found that hypothetical bias increased values by a factor of about 1.35, with greater effects for WTA than for willingness to pay (WTP) studies. However, our use of a consequentiality statement may mitigate such bias if property owners thought there was even a very small probability that the survey would be used to inform decisions regarding potential future easement programs (Herriges et al. 2010). Vossler and Evans (2009) provided empirical evidence for this theory when they could not detect elicitation bias for consequential referenda but could detect such bias for purely hypothetical referenda. We were confident that some respondents did believe the survey results would be used to inform policy and thus was consequential, because we received follow-up phone calls from survey recipients expressing interest in the potential program being started in their area.

This study demonstrates the feasibility of no-cost or low-cost easements for protecting riparian and littoral habitats in Lower Peninsula Michigan lakes. If offered to lakefront property owners, our estimates show that more than one quarter of property owners would be willing to enroll in such programs at no cost to enhance water quality and fish and wildlife habitat. With relatively small incentives of $100 to $500 dollars per property owner, an additional 10% of owners are predicted to enroll in the program, improving water quality and fish and wildlife habitat. The easements in this study applied to 50% of each property's shorelines; programs meeting the Michigan Department of Natural Resources' goal of conserving 75% of the shoreline (O'Neal and Soulliere 2006) would likely be more expensive or have lower enrollment. Decisions on whether littoral easements, riparian easements, or some combination thereof would be more beneficial depend upon the management objectives and the ecological context of the properties, lakes, and watersheds in question. For example, the Minnesota Department of Natural Resources focuses its shoreline conservation to protect fish habitat on lakes that have watersheds with undeveloped land cover (Jacobson et al. 2016). In order to protect water quality and habitat, we recommend that state and local governments as well as non-profit organizations consider implementing conservation easements, potentially through expansion of existing shoreland conservation programs that do not currently provide financial incentives or through creation of tax incentives or direct payments in exchange for conservation easements.

APPENDICES

APPENDIX A

Survey invitation to lakefront property owners

Figure A.1. Survey invitation to lakefront property owners, page 1.

MICHIGAN STATE
UNIVERSITY

August 7, 2015

$To
$Street Address
$City, $State $Zip

Dear $To:

We need your help with a survey of lakeshore property owners that is very important for shoreline and lake management in Michigan.

Please take a few minutes to share your thoughts and opinions; it is critical that our study includes you! The results of this study will be used by non-profit organizations and resource managers working to maintain healthy lake ecosystems and meet the diverse needs of lakeshore stakeholders.

The survey is being conducted on the internet. To access the survey, please type the following web address into the address bar of your web browser:

Web address: $Website

If you have any questions about this study, please contact us at 115 Manly Miles Building, 1405 S. Harrison Rd., East Lansing, MI 48823; jnohner@msu.edu; or 517-432-5238.

Thank you for your assistance!

Sincerely,

Joel Nohner
Ph.D Candidate
Department of Fisheries and Wildlife
Michigan State University

William W. Taylor
Distinguished Professor
Department of Fisheries and Wildlife
Michigan State University

Department of Fisheries and Wildlife

Michigan Lakefront Property Owner Survey

Joel Nohner
Ph.D. Candidate
115 Manly Miles Building
1405 S. Harrison Rd.
East Lansing, MI 48823

517-432-5238
jnohner@msu.edu

Figure A.2. Survey invitation to lakefront property owners, page 2.

Frequently Asked Questions

How was I selected?
Your property was randomly selected by a computer program from a list of lakeshore properties in Michigan. You are part of a small group selected to participate in this survey about lakeshore properties.

Why does this survey matter?
Non-profit organizations and managers need more information about the opinions of lakeshore property owners. They will use this information to develop strategies to protect Michigan's lakes and better meet the goals of stakeholders.

Why do you want me to do this survey?
We need your help because you are part of a small, scientifically selected sample designed to be representative of Michigan lakeshore property owners.

Who sees my answers?
Your responses are saved directly into a secure database that does not contain your name. Your answers will remain anonymous. Only a small team of researchers working on this project will have access to your answers.

How is my privacy protected?
Our mailing list and data are stored on password-protected computers in locked offices. Everyone who works on the survey has completed training and signed an oath saying that they will not share any private information they see while working on the survey.

I have entered the web address, but it does not take me to the survey web page.
Please make sure that you type the web address into the address bar of your internet browser and not the search bar. The address bar is typically located on the top, left side of the screen.

How do I get help with web survey access or other problems?
If you have trouble accessing the web survey or if you have other technical issues, you should contact our research team by email (jnohner@msu.edu) or phone (517-432-5238).

How can I see the results?
Contact our research team by email (jnohner@msu.edu) or phone (517-432-5238) to request a copy of the results, which should be available in six to twelve months.

APPENDIX B

Follow-up survey invitation postcard

Figure B.1. Follow-up survey invitation postcard, front.

Michigan Lakefront Property Owner Survey

Joel Nohner
115 Manly Miles Building
1405 S. Harrison Rd.
East Lansing, MI 48823

We need your help!

Please complete the Michigan Lakefront Property Owner Survey

$To
$Street Address
$City, $State $Zip

MICHIGAN STATE UNIVERSITY
Founded 1855

Figure B.2. Follow-up survey invitation postcard, back.

Michigan Lakefront Property Owner Survey
We need your help!

We recently contacted you about a web survey of lakeshore property owners.

If you have not filled out the survey, we still need your help. You are part of a small, scientific sample, and your answers help represent Michigan lakeshore property owners.

To complete the survey, please type the web address below into the address bar of your web browser.

Web address: $Website

NOTE: Enter the web address into the address bar of your web browser. It will not work if you type it in the search bar. If you need help, please contact us.

If you have any questions about this study, please contact us at jnohner@msu.edu; or 517-432-5238.

Thank you for your help with this important study!

Sincerely,

Joel Nohner
Ph.D Candidate

William W. Taylor
Distinguished Professor

MICHIGAN STATE UNIVERSITY
Founded 1855

APPENDIX C

Second follow-up survey invitation

Figure C.1. Second follow-up survey invitation, page 1.

MICHIGAN STATE UNIVERSITY

August 7, 2015

$To
$Street Address
$City, $State $Zip

Dear $To:

We have recently contacted you about a web survey of lakeshore property owners that is very important for shoreline and lake management in Michigan. Although we have received completed surveys from many people, to the best of our knowledge, we have not received a completed survey from you.

We are writing to you one last time because your input is vital! You are part of a small sample that represents all Michigan lakefront property owners.

The results of this study will be used by non-profit organizations and resource managers working to maintain healthy lake ecosystems and meet the diverse needs of lakeshore stakeholders.

Please complete your survey by visiting the website below OR returning your completed survey in the postage-paid return envelope.

Web address: $Website

If you have any questions about this study, please contact us at 115 Manly Miles Building, 1405 S. Harrison Rd., East Lansing, MI 48823; jnohner@msu.edu; or 517-432-5238.

Thank you for your assistance!

Sincerely,

Joel Nohner
Ph.D Candidate
Department of Fisheries and Wildlife
Michigan State University

William W. Taylor
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Michigan Lakefront Property Owner Survey

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Figure C.2. Second follow-up survey invitation, page 2.

Frequently Asked Questions

I have entered the web address, but it does not take me to the survey web page.
Please ensure that you enter the web address into the web address bar, not the search bar, of your browser. The web address bar often is found on the top left side of your browser and may contain text such as ".com" or "http" while the search bar (Google, Bing, Yahoo!, etc.) is often lower or on the right.

How was I selected?
Your property was randomly selected by a computer program from a list of lakeshore properties in Michigan. You are part of a small group selected to participate in this survey about lakeshore properties.

Why does this survey matter?
Non-profit organizations and managers need more information about the opinions of lakeshore property owners. They will use this information to develop strategies to protect Michigan's lakes and better meet the goals of stakeholders.

Why do you want me to do this survey?
We need your help because you are part of a small, scientifically selected sample designed to be representative of Michigan lakeshore property owners.

Who sees my answers?
Your responses are saved directly into a secure database that does not contain your name. Your answers will remain anonymous. Only a small team of researchers working on this project will have access to your answers.

How is my privacy protected?
Our mailing list and data are stored on password-protected computers in locked offices. Everyone who works on the survey has completed training and signed an oath saying that they will not share any private information they see while working on the survey.

How do I get help with web survey access or other problems?
If you have trouble accessing the web survey or if you have other technical issues, you should contact our research team by email (jnohner@msu.edu) or phone (517-432-5238).

How can I see the results?
Contact our research team by email (jnohner@msu.edu) or phone (517-432-5238) to request a copy of the results, which should be available in six to twelve months.

APPENDIX D

Michigan Lakefront Property Owner Survey

Figure D.1. Michigan Lakefront Property Owner Survey, cover page.

Michigan Lakefront Property Owner Survey

We need your help!

Please complete this survey and return it in the enclosed, postage-paid envelope.

Michigan State University
Department of Fisheries & Wildlife

Figure D.2. Michigan Lakefront Property Owner Survey, page 1.

This survey is intended for an adult member of a household that owns or leases shoreline property on a lake in Michigan. This includes properties with shorelines on canals that connect to lakes. If you own or lease multiple lakeshore properties, please respond to all questions in reference to the lakeshore property that you most frequently use.

1. Do you own or lease a lakeshore property?

- ☐ Own
- ☐ Long-term lease (contract duration greater than five years)
- ☐ None of the above. (*If you do not own or lease, please stop here. Please return the survey using the enclosed, prepaid and preaddressed envelope!*)

2. Is the property you own or lease on a canal, channel, or other waterway connecting it to the lake?

- ☐ Yes
- ☐ No

3. How does your household use the <u>water and shoreline</u> directly out from your lakefront property? (*Please check all that apply*):

- ☐ Boat storage or access (e.g. parking boats on the shore, docking boats, etc.)
- ☐ Boating or motorized watersports (water skiing, jet skiing, etc.)
- ☐ Fishing
- ☐ Hunting
- ☐ Non-motorized water activities (e.g. kayaking, paddleboarding, etc.)
- ☐ Swimming
- ☐ View of the lake
- ☐ Wildlife viewing (e.g. ducks, frogs, turtles, etc.)
- ☐ None of the above
- ☐ Other, please describe ______________________________

4. What activities does your household participate in on your <u>land within 50 feet of the shoreline</u>? *Note: 50 feet is the width of a basketball court.* (*Please check all that apply*):

- ☐ Bird or wildlife watching
- ☐ Campfire
- ☐ Eating or cooking outdoors
- ☐ Hunting
- ☐ Landscaping or gardening
- ☐ Recreational equipment storage
- ☐ Relaxation
- ☐ Yard games/children playing
- ☐ None of the above
- ☐ Other, please describe ______________________________

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Figure D.3. Michigan Lakefront Property Owner Survey, page 2.

5. Which of the following best describes the amount of time you spent at your lakefront property in 2014? Each trip counts as at least one day, even if it was a shorter trip. Do not include other members of your household.

- ☐ 0 days
- ☐ 1 - 10 days
- ☐ 11 - 30 days
- ☐ 31 - 90 days
- ☐ 91+ days

6. How often did any of the following people use your lakefront property in 2014? (*Please mark each row)*

	Never (or not applicable) *0 days*	Rarely *1-5 days*	Occasionally *6-30 days*	Commonly *31+ days*
You	☐	☐	☐	☐
Spouse or partner	☐	☐	☐	☐
Other immediate family	☐	☐	☐	☐
Other relatives	☐	☐	☐	☐
Friends	☐	☐	☐	☐
Renters	☐	☐	☐	☐
Children under 18	☐	☐	☐	☐

7. Before you turned 18, how much time did you spend at ANY lake in a typical year? Each trip counts as at least one day, even if it was a shorter trip. Do not include other members of your household.

- ☐ None
- ☐ Little (a week or less)
- ☐ Some (between a week and a month)
- ☐ Many or all (more than a month)

8. How many times did you fish in your lake in 2014? Do not include other members of your household.

- ☐ 0 times
- ☐ 1 – 5 times
- ☐ 6 – 30 times
- ☐ 31+ times

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Figure D.4. Michigan Lakefront Property Owner Survey, page 3.

9. Approximately how much shoreline and/or canal frontage does your property have?

☐ 1 - 49 feet of shoreline
☐ 50 - 99 feet of shoreline
☐ 100 - 199 feet of shoreline
☐ 200+ feet of shoreline

10. Do you have a hardened, man-made structure at the water's edge on your lakefront property? Hardened structures include man-made rock walls, sea walls, boulders, or rip rap that were placed by people between the land and the water.

☐ No
☐ Yes, on part of my shoreline
☐ Yes, on all of my shoreline

11. Do you have or maintain a man-made sand beach at your lakefront property?

☐ Yes, for more than 50% of my shoreline
☐ Yes, for less than 50% of my shoreline
☐ No

12. Did you have a dock on your shoreline in 2014?

☐ Yes
☐ No

13. Invasive plants are plants that are not naturally in your lake and which have negative effects on the lake (e.g. Eurasian watermilfoil, starry stonewort, phragmites, purple loosestrife, etc.). Are there currently any invasive aquatic plants in your lake?

☐ Yes
☐ No
☐ Do not know

14. In 2014, were any of the following methods or devices used to remove living aquatic plants from the water in front of your lakefront property? (*Please check all that apply*)

☐ Rake, hand tools, or hand-pulling
☐ Automated device (e.g. Weed Roller)
☐ Chemical treatment
☐ Biological control (e.g. addition of plant-eating insects)
☐ Screen or mat blocking plant growth (e.g. Benthic Barrier)
☐ Professional aquatic plant harvester
☐ Other, please describe: _______________
☐ None

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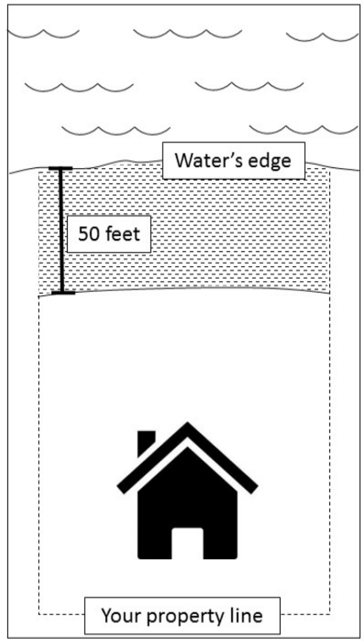
Figure D.5. Michigan Lakefront Property Owner Survey, page 4.

For the following questions, please consider "land" to be dry land and "water" to include any wetlands, cattails, marshes, etc. that contain standing or open lake water.

15. Think about the plants on the land near the water's edge on your property as if you were looking at them from above. What proportion of the land within 50 feet of the water's edge (shaded area in figure) is covered by the plant categories below? Your answers may add up to more than 100%, since multiple plant types may be present in an area. (*For each row, please check the appropriate percentage)*

Plant type	0%	25%	50%	75%	100%
Trees (including branches etc.)					
Shrubs					
Uncut or natural grass					
Mowed grass					
Wetlands plants on the land (e.g. cattails)					
No plants (e.g. bare ground, concrete, sand)					



16. Now, think about the shallow water from the shoreline out 50 feet into the lake in front of your property. If you were looking at it from above during the summer in 2014, what percentage of this area had aquatic plants? Aquatic plants are plants in the lake or on the water's edge. Your answer should reflect the actual conditions; do not include any plants that you removed or areas that are too deep to see the bottom in your answer.

- 0%
- 25%
- 50%
- 75%
- 100%

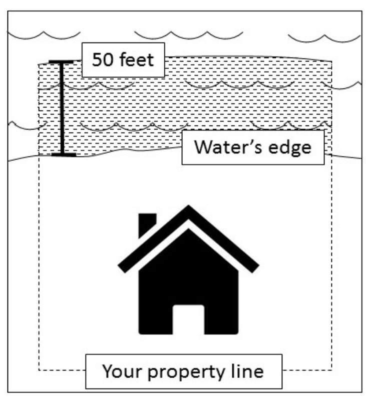


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Figure D.6. Michigan Lakefront Property Owner Survey, page 5.

17. From what sources do you obtain information on maintaining the plants, land, and water on your shoreline property? (*Please check all that apply*)

- ☐ None
- ☐ Neighbor
- ☐ Friends or family members
- ☐ Lake or property association
- ☐ Local government (e.g. county or township)
- ☐ State government or resource agency (e.g. Department of Natural Resources or Department of Environmental Quality)
- ☐ Other non-profit organizations (e.g. Michigan Lake and Stream Association)
- ☐ Internet sources (not including those listed above)
- ☐ Other, please describe:____

18. Place a mark on each row to indicate whether you agree or disagree with the following statements.

Statement	Strongly Agree	Agree	Neutral	Disagree	Strongly Disagree
How I maintain my shoreline property affects how much wildlife is around the lake.	☐	☐	☐	☐	☐
How I maintain my shoreline property affects the number of fish in the lake.	☐	☐	☐	☐	☐
How I maintain my shoreline property affects water quality in the lake.	☐	☐	☐	☐	☐
Plants near the lakeshore help prevent soil erosion.	☐	☐	☐	☐	☐
It is important to me that my neighbors maintain a manicured lawn and shoreline.	☐	☐	☐	☐	☐

19. If a tree or branch fell into the water in front of your lakefront property, would you (or someone acting on your behalf) remove it?

- ☐ Yes
- ☐ Yes, but only if it blocked swimming, boating, or other access.
- ☐ No
- ☐ Do not know

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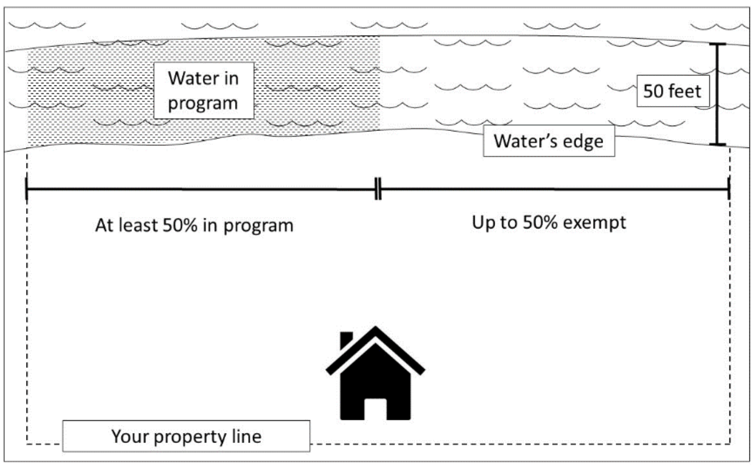
Figure D.7. Michigan Lakefront Property Owner Survey, page 6.

In the following questions, two different programs for shoreline properties are described. One program focuses on the ***WATER*** *and the other program focuses on the* ***LAND****. Please consider this difference as you answer the questions.*

Easement agreements are a common, voluntary way that non-profit organizations encourage property owners or lessees to improve habitat for fish and wildlife.

Think about these example easement terms in relation to the **WATER** out from your property:

- Allow any existing native plants **IN THE WATER** to grow naturally (without dredging, trimming, treatment, or other manipulation) from the water's edge out to a distance of 50 feet into the lake (see figure below). You or your lake association would be allowed to treat for invasive plants.
- Allow any branches that fall in the lake to remain in the lake.
- Conditions apply along 50% of a property's shoreline; owners or lessees are allowed to select one section of up to 50% of their shoreline to be exempt from the conditions for boating, swimming, and other uses. This exempt section can be on one side, as shown below, or anywhere in between the property lines (e.g. from left to right, 30% exempt, 50% in the program, and 20% exempt).



20. Place a mark on each row to indicate whether you agree or disagree with the following statements.

Statement	Strongly Agree	Agree	Neutral	Disagree	Strongly Disagree
My property already meets the terms described in the program above.	☐	☐	☐	☐	☐
I am aware that agreements similar to the one above are available for properties at some lakes in Michigan.	☐	☐	☐	☐	☐

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Figure D.8. Michigan Lakefront Property Owner Survey, page 7.

Think about the following voluntary program that could be implemented by a conservation organization, which offers to pay you $<XXX> per year to enroll your property in a conservation easement for the **WATER** at your lakefront property with these terms:

- The purpose is to improve habitat and increase the numbers of fish and aquatic wildlife.
- Allow all native plants IN THE WATER to grow naturally out 50 feet into the lake (can treat invasive plants).
- Allow any branches that fall in the lake to remain in the lake.
- Conditions apply along 50% of your shoreline; you would be allowed to select one section of up to 50% of your shoreline to be exempt.
- All properties on all lakes would qualify for the agreement regardless of current conditions.

We are asking whether you would be prepared to sign the legally binding agreement described above for a 5-year period. The $<XXX> would be paid to you every year. You would be able to cancel the program if you sell the property.

Note: The results of this study will be made available to policymakers and other organizations as a guide for future decisions about incentive programs such as this one.

21. Would you accept this voluntary offer of $<XXX> per year to allow aquatic plants and fallen tree branches in the water along 50% of your shoreline?

☐ Yes
☐ No

22. What were your reasons for answering Question 21 this way? (Please list below)

____

____

____

____

____

23. Would you be willing to enroll in a program such as the one described in Question 21 above, even if there were no payment?

☐ Yes
☐ No

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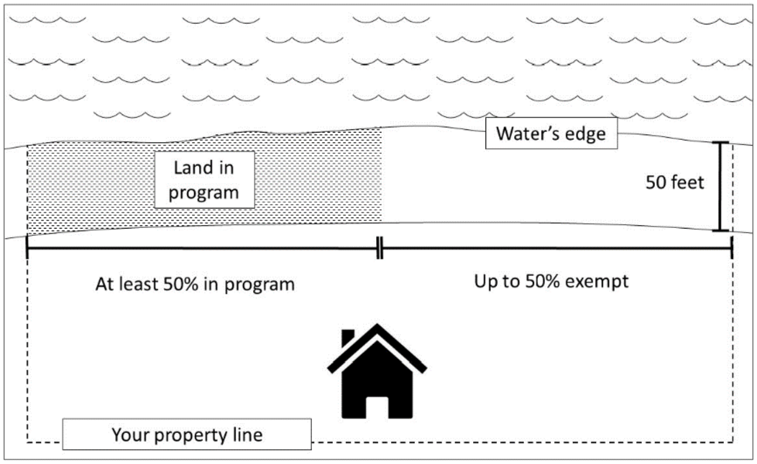
Figure D.9. Michigan Lakefront Property Owner Survey, page 8.

Now, think about the terms of a different voluntary easement program in relation to the **LAND** on your lakeshore property:

- Allow all native plants **ON THE LAND** within 50 feet of the shoreline to grow naturally (without mowing).
- Allowed to trim branches above a height of four feet to improve visibility to the lake.
- Conditions apply along 50% of a property's shoreline; owners or lessees are allowed to select one section of up to 50% of their shoreline to be exempt from the conditions for other uses (see figure below). This exempt section can be on one side, as shown below, or anywhere in between the property lines (e.g. from left to right, 30% exempt, 50% in the program, and 20% exempt).



24. Place a mark on each row to indicate whether you agree or disagree with the following statements.

Statement	Strongly Agree	Agree	Neutral	Disagree	Strongly Disagree
My property already meets the terms described in the program above.	☐	☐	☐	☐	☐
I am aware that agreements similar to the one above are available for properties at some lakes in Michigan.	☐	☐	☐	☐	☐

25. Do you have a house, cabin, or other dwelling within 50 feet of your shoreline? Do not include sheds etc.
Note: The area within 10 feet of a dwelling is typically exempt from such programs

☐ Yes
☐ No

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Figure D.10. Michigan Lakefront Property Owner Survey, page 9.

Think about a different, voluntary program that could be implemented by a conservation organization to pay you an annual incentive of $<XXX> to enroll your property in a conservation easement for the **LAND** on your lakefront property with these terms:

- The purpose is to improve habitat for fish and wildlife to benefit their populations, stabilize your shoreline, and improve water clarity in the lake.
- Allow all native plants **ON THE LAND** within 50 feet of the shoreline to grow naturally.
- You would be provided with native grass and shrub seeds as well as tree saplings that a naturalist might grow on your property, and would have the choice to plant them.
- Allowed to trim branches above a height of four feet to improve visibility to the lake.
- Conditions apply along 50% of your shoreline; you would be allowed to select one section of up to 50% of your shoreline to be exempt.
- All properties on all lakes would qualify for the agreement regardless of current conditions.

We are asking whether you would be prepared to sign the legally binding agreement described above for a 5-year period. The $<XXX> would be paid to you every year. You would be able to cancel the program if you sell the property.

Note: The results of this study will be made available to policymakers and other organizations as a guide for future decisions about incentive programs such as this one.

26. Would you accept this voluntary offer of $<XXX> per year to allow native plants to grow naturally on the land along 50% of your shoreline?

☐ Yes
☐ No

27. What were your reasons for answering Question 26 this way? (Please list below)

____

____

____

____

____

28. Would you be willing to enroll in a program such as the one described in Question 26 above, even if there were no payment?

☐ Yes
☐ No

Go to next page ➡

Figure D.11. Michigan Lakefront Property Owner Survey, back cover.

The information below is important for our study, because it may affect your answers to previous questions. All responses are confidential and anonymous.

29. What was the total income for your household in 2014 before taxes?

- ☐ Under $5,000
- ☐ $5,000 - $24,999
- ☐ $25,000 - $49,999
- ☐ $50,000 - $74,999
- ☐ $75,000 - $99,999
- ☐ $100,000 - $149,999
- ☐ $150,000 - $199,999
- ☐ $200,000 - $499,999
- ☐ $500,000 or above

30. What is the highest level of education you have attained to date?

- ☐ Some high school
- ☐ High school graduate or equivalent
- ☐ Technical or Associate's degree
- ☐ Bachelor's degree
- ☐ Master's degree
- ☐ Ph.D., law, medical, or other degree beyond a Master's degree

31. Which of the following best describes you?

- ☐ Female
- ☐ Male

32. Which of the following best describes you?

- ☐ One of the heads of the household (includes males and females)
- ☐ Head of the household's child
- ☐ Head of the household's relative (other than child)
- ☐ Head of the household's friend
- ☐ Other (please describe)____

33. What is your age? ______ years old

34. How many adults are in your household? ______ adults

35. How many children are in your household? ______ children

36. Permanent Residence Information (Primary address)

City________________________State__________ Zip code___________

Thank you for completing this survey! Please place this survey in the prepaid envelope, and mail it to Joel Nohner, 115 Manly Miles Building,1405 S. Harrison Rd., East Lansing, MI 48823.

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REFERENCES

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SYNTHESIS

Lake shoreline development will likely continue in the Upper Midwest, because shoreline properties are desirable and human populations will continue to increase. While lake shoreline development is correlated with loss of aquatic vegetation and LWD in the Upper Midwest United States (Christensen et al. 1996; Radomski and Goeman 2001; Jennings et al. 2003; Francis and Schindler 2006; Marburg et al. 2006; Wehrly et al. 2012; Czarnecka 2016), shoreline property owners, local and state governments, and nonprofit organizations can choose to decouple this correlation by stimulating property owners to apply best management practices through education and outreach campaigns, programs incentivizing natural shorelines, and regulations. Allowing native aquatic vegetation to grow undisturbed, planting and allowing riparian trees to grow and eventually fall into the lake, and leaving fallen trees and branches in the lake are best practices that would curb the loss of structural habitats to benefit Largemouth Bass in inland lakes. Restoration of aquatic vegetation and LWD in lakes where it has been lost could benefit fishes in those lakes if structural habitat is a limiting factor to fish populations. However, application of these conservation practices is hindered by a lack of understanding of lake fish-habitat relationships and the factors that influence willingness of shoreline property owners to participate in conservation. This dissertation answers critical questions for understanding the benefits of and influencing shoreline property owners to participate in shoreline conservation, specifically: 1) Is there a causal linkage between aquatic vegetation and fish (age-0 Largemouth Bass)? 2) Do relationships identified at small scales in microhabitat selection and mesocosm experiments scale up to cumulatively affect Largemouth Bass recruitment at the population level at a whole lake scale? and 3) Can we create and use assessments of shoreline properties and property owners to increase implementation of natural shoreline conservation.

I found that aquatic vegetation affects consumption and growth of Largemouth Bass during the critical summer and fall of the first year of their lives when mortality rates are highest, so aquatic vegetation is therefore likely to benefit recruitment (Ludsin and DeVries 1997). I used open-bottomed mesocosm enclosures with net walls in a glacial Michigan lake to conduct an experiment with three vegetation treatments (low coverage, edge, and high coverage). I found that age-0 Largemouth Bass consumed more fish prey and more prey overall (zooplankton, macroinvertebrate, and fish) in mesocosms with vegetation edge or high vegetation coverage than those with low vegetation coverage, and these increases in consumption led to increases in growth of age-0 Largemouth Bass. I concluded that this causal linkage between increased consumption and aquatic vegetation was due to the availability of more zooplankton, invertebrate, and small fishes in aquatic vegetation based on my field studies and the literature (Wiley et al. 1984; Beckett et al. 1992). This causal linkage provides the basis for predicting and interpreting patterns in recruitment at the whole-lake scale observed in the second chapter of this dissertation.

Second, I modeled relationships between age-0 Largemouth Bass and their microhabitats in 16 inland Michigan lakes and assessed whether these fish-habitat relationships affected recruitment (ratio of age-0 to adult Largemouth Bass in the fall; R:S). Specifically, I determined the influence of aquatic vegetation, large woody debris (LWD), and lake trophic status on Largemouth Bass catch and density. I conducted nighttime electrofishing surveys in the fall to assess age-0 and adult Largemouth Bass catch and found evidence that catches were higher at intermediate–to–high vegetation volumes (40 – 100%), near vegetation edges, near LWD, and in higher coverages of submersed aquatic vegetation. I developed maps of aquatic vegetation and

LWD and applied independently derived habitat-specific catchability rates for a boat electrofisher to estimate average littoral age-0 and adult Largemouth Bass density at the lake level. I found evidence that Largemouth Bass recruitment (R:S) increased across the range of lake trophic states (34 – 54) and mean submersed aquatic vegetation coverages (5 – 61%) observed in our study.

Together, the ecological conclusions from this dissertation should inform efforts to manage aquatic vegetation and LWD to improve Largemouth Bass recruitment. The common application of herbicides to reduce aquatic plants in inland lakes may harm Largemouth Bass populations, because our results show that littoral SAV coverages below 61% have detrimental effects to Largemouth Bass recruitment. If managers' or stakeholders' goal is to maximize Largemouth Bass recruitment, then SAV should not be removed below 61% overall littoral coverage; we did not have data for the effects of SAV on recruitment above 61% overall littoral coverage to determine the effects of SAV in this range. Furthermore, my findings that both age-0 and adult Largemouth Bass aggregate in microhabitats with moderate to high vegetation volumes (including emergent vegetation), near aquatic vegetation edges, and near LWD reinforce the need to conserve these habitats if conserving high-density habitats for age-0 Largemouth Bass is a priority for management. In addition to habitat conservation, natural resource managers can use the information from this study to assist in assessment of recruitment, diagnosis of potential recruitment threats, and potentially adjust fishery regulations (Allen and Pine 2000) in the context of anticipated recruitment for Largemouth Bass in north temperate lakes.

Third, for managers and stakeholders to apply the conservation recommendations above, it was critical to assess shoreline property and property owner characteristics to develop recommendations for more cost-efficient and effective conservation strategy implementation. I conducted a survey of Michigan's Lower Peninsula lakefront property owners to identify challenges to participation in shoreline conservation and more efficient strategies for addressing aquatic vegetation removal, LWD removal, and other lake ecosystem threats. I did this using a survey that asked respondents whether they would participate in two different types of conservation easements (littoral or riparian). Respondents were significantly less likely to enroll in littoral area easements to protect fish habitat and water quality if they felt more social pressure for manicured lawns. However, I found that more riparian owners were likely to enroll in littoral easements if they had more years of formal education, greater shoreline frontage, more naturally occurring riparian plants, more ecological knowledge, or if the lake had a more developed shoreline. Enrollment in riparian easements was significantly less likely if property owners felt more social pressure for manicured lawns, but was more likely if they had more years of formal education, more naturally occurring riparian plants, or greater shoreline frontage. These factors can be used to identify shoreline property owners that are more likely to enroll in littoral and conservation easements and more likely to enroll at lower costs. The average annual costs that it would take for a property owner to agree to my hypothetical littoral (\$1365) and riparian (\$6956) conservation easements were large, but some respondents would enroll in littoral (29.8 % ± 2.2; mean ± SE) and riparian (24.4 % ± 2.1) easements even without payment due to the benefits of the easements from the ecosystem services provided. Small increases to conservation payments at low payment levels (e.g. \$100-\$500/year) resulted in relatively large gains in enrollment.

The success of easement programs operated by land trusts, which often target relatively large properties at high costs, were consistent with my findings. Furthermore, the success of tax incentive programs such as the program operated by Burnett County, WI, are also consistent with the strategies identified through the survey of Michigan lakefront property owners, because Burnett County casts a wide net to all residential owners in the county with a low-cost tax incentive. State and local governments, lake property owner associations, and nonprofit organizations seeking to benefit fish, wildlife, and water quality should consider voluntary or incentivized programs to encourage littoral and riparian shoreline conservation. Such voluntary or incentivized conservation programs should be considered in addition to other components that have been successful in achieving shoreline conservation outcomes, such as creation and enforcement of regulations limiting aquatic and riparian vegetation removal and education and outreach campaigns that enable and inspire shoreline property owners to conserve their shorelines. Together, these approaches will be critical for ensuring that lake shoreline development occurs in a way that minimizes disturbance to wildlife and fish populations, such as Largemouth Bass, and preserves water quality in order to continue providing the ecosystems services that draw people to the lake in the first place.

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