EVALUATING SUITABILITY OF ESOCID HABITAT IN GEORGIAN BAY

MODELLING AND EVALUATING SUITABILITY OF ESOCID HABITAT IN RESPONSE TO CHANGES IN WATER LEVELS OF GEORGIAN BAY (LAKE HURON)

By

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A Thesis
Submitted to the School of Graduate Studies
in Partial Fulfillment of the Requirements
for the Degree
Doctor of Philosophy

McMaster University

Doctor of Philosophy (2018) McMaster University
(Biology) Hamilton, Ontario

TITLE: Modelling and evaluating suitability of esocid habitat in response to changes in water levels of Georgian Bay (Lake Huron)

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NUMBER OF PAGES: xix, 264

LAY ABSTRACT

This Ph.D. thesis describes how changes in water levels may affect habitats used by Muskellunge and Northern Pike, two important species of sport fish, in Georgian Bay (Lake Huron). Coastal wetlands were identified as critical habitats, especially for early-life stages, and are directly influenced by water levels of the Great Lakes. I developed several tools to assist in identification, evaluation, and management of coastal wetlands in Georgian Bay, a relatively undisturbed coastal region in Ontario. These tools use physical features of the landscape to predict how wetlands will respond to different lake-level conditions and influence habitat suitability for Muskellunge and Northern Pike, as well as Great Lakes fish communities in general. My thesis provides tools for environmental agencies to adaptively manage important fish habitat in a period of unpredictable water levels associated with global climate change.

GENERAL ABSTRACT

Muskellunge (*Esox masquinongy*) and Northern Pike (*E. lucius*) are ecologically and economically important fish species that rely on coastal habitats in Georgian Bay, especially coastal marshes. These habitats have adapted to the high natural water-level fluctuations of Lake Huron but are threatened by changing water-level conditions associated with global climate change. The overall goals of this thesis were to identify important esocid habitats and understand how their suitability will be affected by changing water levels.

First, I used tracking information from radio telemetry studies of esocid populations in spatially distinct regions of Georgian Bay to identify important habitats during breeding and non-breeding seasons. I documented the strong affinity of Muskellunge to re-use specific spawning grounds close to known nursery habitat in coastal marshes. Both Muskellunge and Northern Pike used coastal marshes during the non-breeding season, and physical habitat structure was a more important driver of habitat use in the summer months than water temperature.

Next, I created a GIS model using only hydrogeomorphic features (depth, slope, and wave exposure) to map the extent of coastal marshes throughout eastern and northern Georgian Bay to assess how habitat would shift under a range of possible lake elevations scenarios (175.5 – 177.5 m). The geomorphology at low lake levels favoured large areas of shallow (< 0.5 m) habitat at the expense of deeper habitats (0.5 – 1.5 m) that can support an aquatic vegetation community more suitable for young esocids. I used a similar approach to develop a Resilience Index to rank coastal marshes according to their resilience/vulnerability to stable low water levels, for use as a regional screening tool to identify critical esocid habitat. This research advances the understanding of the effects of water levels on coastal marshes and provides applicable tools to assist in conservation and management of these important recreational fisheries.

ACKNOWLEDGMENTS

First and foremost, I must express my gratitude to Dr. Pat Chow-Fraser for her mentorship and support over these many long years. Her relentless passion and enthusiasm for Georgian Bay has been inspiring and made my time in the lab an unforgettable experience.

I am grateful to Dr. Mike Waddington, Dr. Jon Stone, and Dr. Graham Scott for agreeing to serve as members on my supervisory committee, and whose guidance and input helped shape this thesis.

I am eternally grateful to have had Georgian Bay as my “laboratory”, which wouldn’t have been possible without the support of the Georgian Bay Great Lakes Foundation and the many Georgian Bay residents who provided support along the way. A special thanks to Roy and Diana Schatz, Harvey and Lorna Meirke, Bill and Freda Klassen, and David and Brenda Flowers who opened their homes to us and whose kindness and willingness to put up with our rag-tag crew of students made this work an absolute joy. And to Mary Muter whose fierce advocacy for Georgian Bay has made so much of this work possible.

The support of many groups and agencies has been instrumental to this work. I’d like to directly acknowledge the efforts of Arunas Liskauskas of the Ontario Ministry of Natural Resources and Forestry for invaluable logistical support towards our tagging work, as well as Muskies Canada Inc. and the Georgian Bay Musky Association.

Thank you to all the lab-friends. Thank you to Chris Biberhofer, Dallas Taylor, Chantel Markle, Julia Rutledge, Nick Luymes, Stuart Campbell, and Steve Savoie for your friendship and shared struggles in the field. A special thanks to James Marcaccio, arguably the kindest human being I have ever encountered, for your friendship through big waters, big, fish, and more crashed GIS programs than I can count. I'm sure I've missed some people, but not the jippopatamus. I can't thank JP Leblanc enough; besides the fact that his thesis laid the groundwork for so much of my own, his friendship and guidance during my earliest days in the lab are large part of why I have stuck around and tried to carry on the legacy of Musky Hunter, PhD.

I am deeply grateful for the unwavering support of my family, in spite of my frequent and sometimes lengthy absences, and the reassurance of knowing that they are always there if I need them.

Thank you to Theo for his ceaseless support during the writing process and making sure that I kept my priorities straight.

Finally, thank you Lindsey Boyd, for your love and support and patience. Simply put, I would not have made it here without you.

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LIST OF ABBREVIATIONS AND SYMBOLS

AICc	Akaike Information Criterion
AUC	Are Under the Curve
ASL	Above Sea Level
CHS	Canadian Hydrographic Service
°	Degrees (Directional Bearing)
°C	Degrees Celsius
DEM	Digital Elevation Model
DFO	Department of Fisheries and Oceans
$\bar{d}_{min}$	Average Nearest Neighbour Distance
ID	Identity (Radio Tagged Esocids)
GB-DEM	Georgian Bay DEM (Chapter 3)
GCC	Global Climate Change
GIS	Geographic Information Systems
GLM	Generalized Linear Model
HGM	Hydrogeomorphic
HSC	Habitat Suitability Curve
IGLD85	International Great Lakes Datum 1985

KUD	Kernel Utilization Distribution
LIDAR	Light Detection and Ranging
MCWI	McMaster Coastal Wetland Inventory
NGB	Northern Georgian Bay
NEGB	Northeastern Georgian Bay
OMNRF	Ontario Ministry of Natural Resources and Forestry
REI	Relative Exposure Index
RI	Resilience Index
ROC	Receiver Operating Characteristic
SMIN	Spring Muskellunge Index Netting
SAV	Submersed Aquatic Vegetation
SCOOP	South Central Ontario Orthophotography Project
SE	Standard Error
SEGB	Southeastern Georgian Bay
TAD	Tadenac Bay
TL	Total Length of Fish
VIn	Vulnerability Index

DECLARATION OF ACADEMIC ACHIEVEMENT

The following Ph.D. thesis includes five chapters prepared as manuscripts for submission in peer-reviewed journals. A General Introduction is included to place this research into context. *Chapter 1* has been published in the *Transactions of the American Fisheries Society*. *Chapter 3* and *Chapter 4* have been submitted for publication to *Wetlands Ecology and Management*; both been accepted pending revisions. *Chapter 5* has been submitted for publication to *Ecological Indicators* and is accepted pending revisions. *Chapter 2* is presented as a manuscript but has not yet been submitted for publication. Completed references for all chapters, regardless of status, are found below. As first author on all chapters, I analyzed the data and wrote the manuscripts under the supervision of Dr. Pat Chow-Fraser. For *Chapter 1*, John Paul Leblanc and Arunas Liskauskas were included as co-authors as they were instrumental in collecting the data used for this study. Similarly, for *Chapter 2*, Christopher Biberhofer, John Paul Leblanc, and Jonathan Midwood are included as co-authors as they collected significant portions of the field data used in this study. Collection of field data used throughout this thesis relied of the effort and support of many graduate and undergraduate students, local stakeholders, and partners who are more formally recognized in the acknowledgements section.

Weller JD, Leblanc JP, Liskauskas A, Chow-Fraser P (2016) Spawning season distribution in subpopulations of Muskellunge in Georgian Bay, Lake Huron. Transactions of the American Fisheries Society 145(4):795–809.

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Weller JD, Chow-Fraser P (2018/CH4) Simulated changes in extent of Georgian Bay low-marsh habitat under multiple lake levels. Submitted to Wetlands Ecology and Management, submission ID: WETL-D-18-00081 (Chapter 4).

Weller JD, Chow-Fraser P (2018/CH5) Development of a multi-scale wetland resilience index from Muskellunge nursery habitat in Georgian Bay, Lake Huron. Submitted to Ecological Indicators, submission ID: ECOLIND-12193 (Chapter 5).

GENERAL INTRODUCTION

Muskellunge (*Esox masquinongy*) is an ecologically and economically valuable species that support a high-quality recreational fishery in Georgian Bay (Lake Huron) that is naturally reproducing, self-sustaining (Kerr 2007; Kerr 2011) and capable of producing trophy-sized individuals (Casselman et al. 1999; Kerr 2007; Kerr 2011). Restrictive harvest regulations (Kerr 2011) and widespread adoption of catch-and-release practices among the Muskellunge angling community (Fayram 2003; Gaeta et al. 2013) have been effective at maintaining a trophy-caliber fishery and keeping large, reproductively valuable individuals in the population (Kerr 2007). The more pressing threat to Muskellunge fisheries is the loss of critical spawning and nursery habitat (e.g. Dombeck et al. 1986; Leblanc et al. 2014; Rust et al. 2002) that has long been identified and reaffirmed as a key management priority (Craig and Black 1986; Crane et al. 2015; Dombeck et al. 1986; Farrell et al. 2007).

Early-life habitat for Muskellunge is critical because they are at their most vulnerable during this period. Esocids are broadcast spawners that offer no parental care and their small size through the first year (age-0, < 12 inches; Scott and Crossman 1973) leaves them especially vulnerable to predators, and survival rates are very low (Farrell 2001). In the Great Lakes, coastal wetlands provide this early-life habitat (Jude and Pappas 1992; Wei et al. 2004). Coastal wetlands occur along the fringes of the Great Lakes shorelines, have persistently inundated areas, are heavily influenced by large-lake processes, and are dominated by submergent and floating aquatic vegetation (NWWG 1997). Spawning typically occurs in shallow areas but documented spawning habitat characteristics are incredibly variable, aside from features like sufficient dissolved oxygen at the substrate and limited depredation (Diana et al. 2017). Detailed characterizations of suitable Muskellunge nursery habitat from the St. Lawrence River (Crane and Kapuscinski 2017; Kapuscinski and Farrell 2014; Murry and Farrell 2007; Werner et al. 1996) are largely consistent with habitat descriptions from Georgian Bay (Craig and Black 1986; Leblanc 2015; Leblanc et al. 2014), despite occurring in remarkably different environments. Intermediate densities of aquatic vegetation that provide structure throughout the water column are ideal (Crane and Kapuscinski 2017; Leblanc 2015) and support fish communities with adequate forage species and few predators (Kapuscinski and Farrell 2014; Leblanc 2015). This type of habitat structure supports a high diversity of fish species (Dibble et al. 1997; Eadie and Keast 1984; Smokorowski and Pratt 2007).

Water levels play an important role in structuring aquatic vegetation communities and thereby producing the complex habitat structure required by age-0 Muskellunge. Wetland vegetation occurs along a depth gradient and fluctuating water levels act a disturbance which promotes greater diversity in the plant community (Keddy and Reznicek 1986; Wilcox and Meeker 1991; Wilcox and Nichols 2008). Great Lakes coastal wetlands have adapted to lake levels fluctuating on cycles ranging from days to decades (Lu and Nairn, in submission; Trebitz 2006), and the absence or dampening of such fluctuations has been associated with declines in wetland plant diversity (Farrell et al. 2010; Midwood and Chow-Fraser 2012; Wilcox and Meeker 1991) and fish diversity (Midwood and Chow-Fraser 2012; Wilcox and Meeker 1992).

Anthropogenic activities can have a negative impact on wetland habitat in the form of land use changes within a watershed (Jennings et al. 1999; Rust et al. 2002) or more directly in the form of shoreline modification and vegetation removal (Radomski and Goeman 2001; Radomski et al. 2010). Shoreline modification has been identified as a stressor in Georgian Bay (Craig and Black 1986, Leblanc et al. 2014) and incremental human development pressures persist, however water levels appear to be the more pressing threat. From 1999 – 2013, Georgian Bay experienced an unprecedented period of sustained low water levels (Sellinger et al. 2008) that was linked to declines in wetland fish and plant diversity in eastern Georgian Bay (Midwood and Chow-Fraser 2012) and the absence of age-0 muskellunge from historic habitat in southeastern Georgian Bay (Leblanc et al. 2014). In 2014, water levels in Georgian Bay rebounded to above-average conditions but a wide range of forecasts exist for future lake levels in the Great Lakes basin that include moderate to extreme lake level declines (Angel and Kunkel 2010; Lofgren and Rouhana 2016) and prolonged periods of stable lake levels (Lu and Nairn, in submission). These potential water level conditions could have adverse impacts on esocid habitat so a better understanding of suitable esocid habitat and its response to potential water-level scenarios is needed.

Habitat suitability indices provide a relatively simple and intuitive means to assess the overall condition of a habitat for a particular species. Indices of habitat suitability for esocids are not new (Cook and Solomon 1987; Inskip 1982), but were developed to evaluate whole lakes and considered habitat suitability across multiple life stages (i.e. spawning through adult). Leblanc and Chow-Fraser's (2017) Index of Nursery Habitat Suitability was based off improved characterizations of Muskellunge nursery habitat in Georgian Bay (Leblanc 2015) to evaluate specific nursery sites (i.e. wetlands). Similarly, early-life habitat suitability models developed for Muskellunge (Crane et al. 2014; Dombeck et al. 1986; Rust et al. 2002) have relied on site-level data. These are valuable management tools but their reliance on site-level field data (e.g. fish and plant community composition) limit their application to where appropriate field sampling has already been conducted. An *ex situ* habitat identification and evaluation method is needed to esocid management. Nohner and Diana (2015) developed a predictive spawning habitat model using Geographic Information Systems (GIS) that used landscape-level features (e.g. site morphometry) but also included field-surveys for vegetation data. A method using only landscape features could provide an initial assessment of habitat quality and act as a screening mechanism to target subsequent field studies.

Key aspects of esocid habitat, namely wetland vegetation communities, are directly affected by landscape-level features like substrate slope (Duarte and Kalff 1986; Duarte et al. 1986) and wave exposure (Fonseca et al. 2002; Keddy 1982, 1984a, 1984b). These are features that can be readily measured from elevation data sets (i.e. bathymetry and topography) using GIS. Coarse to medium resolution elevation datasets are widely available and usually maintained by government agencies (e.g. Ontario Ministry of Natural Resources and Forestry, Canadian Hydrographic Service), proving an ideal opportunity to use landscape-level habitat features and processes to identify and evaluate suitable habitat for esocids. Field surveys of aquatic habitats are resource intensive and therefore management agencies must allocate their efforts strategically; a landscape-level habitat assessment that can be performed remotely using geospatial tools and available elevation data would provide an efficient solution to this problem.

Thesis Objectives

The main goals of this thesis are to characterize esocid habitat in Georgian Bay and use landscape-level features and processes to predict how coastal aquatic habitats in Georgian Bay may respond to changing water levels. This work and the tools developed herein are ultimately intended as a resource to aid management agencies in designing conservation and management strategies in the face of uncertain water-level conditions associated with global climate change.

In Chapter 1, I will use tracked adult Muskellunge in three regions of Georgian Bay to identify spawning habitats. I hypothesize that Muskellunge in Georgian Bay exhibited fidelity for specific spawning sites (Crossman 1990; Jennings et al. 2011; LaPan et al. 1996) and that spawning and nursery sites are closely linked (LaPan et al. 1996; Zorn et al. 1998), as has been documented in other areas in its range. This mechanism would explain the absence of age-0 muskellunge from historic nursery sites in Georgian Bay. Movements and locations of tracked Muskellunge will reveal important spawning habitat and the habitat characteristics that can be used to develop models for Muskellunge spawning habitat.

In Chapter 2, I will continue to use radio telemetry to investigate habitat use of Muskellunge and the congeneric Northern Pike (*Esox lucius*) after the spawning season (i.e. summer). I hypothesize that the different thermal preferences between the cool-water Northern Pike and warm-water Muskellunge contributes to spatial segregation that allows the two apex predators to exist in sympatry (Inskip 1986). This chapter will provide a description of post-spawn habitat use by Georgian Bay esocids and assess the risks of habitat loss due to effects of global climate change.

Coastal wetlands are important habitat for Georgian Bay Muskellunge (Craig and Black 1986; Leblanc 2015), and were confirmed as such for early-life habitat in Chapter 1 and adults in Chapter 2. In Chapter 3, I will use landscape-level features derived from spatial elevation data sets to develop a model to predict the extent and distribution of low marsh, the inundated area of coastal wetlands, in eastern and northern Georgian Bay. I will use the McMaster Coastal Wetland Inventory (Midwood et al. 2012), a comprehensive wetland habitat inventory, and several elevation data sets to train and validate the model. This will provide a useful management tool to predict how the availability of coastal wetland habitat will change under different lake level scenarios.

In Chapter 4, I will use the model developed in Chapter 3 to investigate how the availability of low marsh habitat in Georgian Bay may change under a range of possible lake level scenarios. I will evaluate changes in low marsh area and volume to infer how suitability for fish habitat changes with water levels.

The absence of age-0 muskellunge in southeastern Georgian Bay was attributed to habitat becoming unsuitable due to stable low lake levels (Leblanc et al. 2014), but suitable habitat persisted in northern Georgian Bay under the same stable lake level conditions (Leblanc 2015). I hypothesize that the resilience of the northern sites was due to hydrogeomorphic characteristics that affected the aquatic vegetation community. In Chapter 5, I will compare physical features of northern and southern nursery sites to identify characteristics of resilient sites. I will then develop an index to score the resilience of wetlands to stable lake levels, using features that can be derived from elevation data sets. This index will be applicable at multiple spatial scales, tailored to addressing particular wetland management activities.

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Chapter 1

SPAWNING SEASON DISTRIBUTION IN SUBPOPULATIONS OF MUSKELLUNGE IN GEORGIAN BAY

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Weller JD, Leblanc JP, Liskauskas A, Chow-Fraser P (2016) Spawning season distribution in subpopulations of Muskellunge in Georgian Bay, Lake Huron. Transactions of the American Fisheries Society 145(4):795–809.

doi.org/10.1080/00028487.2016.1152300

Abstract

Loss of spawning and nursery habitats has been implicated as a major factor in the widespread decline of Muskellunge *Esox masquinongy* populations in North America. Although there is limited evidence of spawning site fidelity in Great Lakes populations of Muskellunge, such behavior could result in recruitment failure if individuals return each year to spawning sites that have become degraded. We compared the spawning behaviors of individual Muskellunge across three subpopulations in Georgian Bay, Lake Huron, to address the hypothesis that the use of specific spawning sites and spawning site fidelity are independent of the habitat's suitability for successful recruitment. The study regions (southeastern, northeastern, and northern Georgian Bay) have experienced different impacts from human development and sustained low water levels. We radio-tagged 49 adult Muskellunge and tracked them for up to 3 years (between 2012 and 2015). Sufficient multiyear data were only acquired for 18 individuals in the southeastern region; among those fish, 16 showed fidelity to at least one activity center over 2–3 years. Male Muskellunge occupied significantly smaller activity centers and shallower depths than females during the spawning season. The locations of adult Muskellunge were in close proximity to current and historic nursery sites that had been identified in each region by other studies, supporting the close spatial linkage between spawning habitat and nursery habitat. This study is the first to confirm spawning site fidelity in Georgian Bay Muskellunge, and our results support the spatial association between spawning

and nursery habitats. The repeated use of degraded habitat by spawning adults, as appears to be the case in southeastern Georgian Bay, highlights the need to identify and protect spawning and nursery habitats.

Introduction

Georgian Bay in Lake Huron currently supports a self-sustaining Muskellunge *Esox masquinongy* population. Despite the apparent health of the population as a whole, a recent study in southeastern Georgian Bay failed to find age-0 Muskellunge at historic and suspected nursery sites (Leblanc et al. 2014), even though reproductively mature adults were still being captured in the area. Leblanc et al. (2014) proposed multiple stressors that could be responsible for reproductive failure in the southeastern subpopulation of Georgian Bay Muskellunge, including alteration of nursery habitat in coastal wetlands by sustained low water levels and increased human modification of the shoreline.

As with most Muskellunge populations, the Georgian Bay population is managed to support and sustain a recreational fishery. Common strategies for protecting Muskellunge populations have included restrictions on harvest size and possession limits (Wingate 1986; Casselman et al. 1999) and encouraging a strict catch-and-release ethic among dedicated anglers (Kerr 2007). Despite efforts that are intended to protect reproductively valuable adults, many Muskellunge populations have declined due to the loss or degradation of suitable spawning and nursery habitats (Dombeck et al. 1984; Dombeck 1986; Zorn et al. 1998; Rust et al. 2002; Farrell et al. 2007). Survival rates of Muskellunge from the egg stage through the first year are naturally very low (Scott and Crossman 1998; Farrell 2001), so additional stressors during that vulnerable time period could affect recruitment success. The over 10 years of sustained low water levels in Georgian Bay (Sellinger et al. 2008) have been linked to a loss of wetland area (Fracz and Chow-Fraser 2013) and a homogenization of the aquatic plant and fish communities (Midwood and Chow-Fraser 2012). Either type of alteration could adversely affect the quality of the coastal wetlands that Muskellunge use as spawning and nursery areas (Scott and Crossman 1998). Similarly, increased shoreline modification has also been linked to the loss and degradation of wetland habitat (Radomski and Goeman 2001; Radomski et al. 2010) and Muskellunge habitat in particular (Dombeck 1986; Rust et al. 2002).

In general, suitable spawning habitat is described as exceeding some minimum level of substrate dissolved oxygen required for spawning (Dombeck et al. 1984) but can occur over various types of substrate (Strand 1986; Zorn et al. 1998; Farrell 2001; Rust et al. 2002; Crane et al. 2014; Nohner and Diana 2015). By comparison, age-0 Muskellunge require (1) some structural complexity, usually provided by aquatic vegetation (Craig and Black 1986; Farrell and Werner 1999; Murry and Farrell 2007; Kapuscinski and Farrell 2014); and (2) the presence of suitable prey (Wahl and Stein 1988; Kapuscinski et al. 2012). It has been hypothesized that there is a close spatial linkage between Muskellunge spawning sites and nursery sites (LaPan et al. 1996; Zorn et al. 1998; Farrell et al.

2007). The underlying assumption is that after hatching, the vulnerable age-0 Muskellunge will not stray far from the safety of their wetland habitat, which should provide both suitable forage and refuge from predators (Crowder and Cooper 1982; Eadie and Keast 1984; Diehl and Eklov 1995). If so, then the degradation of nursery habitat can be a serious problem if Muskellunge cannot seek out suitable habitat when spawning or nursery habitats become degraded.

Spawning site fidelity in Muskellunge has been documented over a range of habitat types, including large lake chains (Crossman 1990), inland lakes (Jennings et al. 2011), and large rivers (LaPan et al. 1996; Younk et al. 1996; Farrell et al. 2007), and such fidelity is consistent with the genetic evidence for distinct populations of Muskellunge throughout the Great Lakes (Kapuscinski et al. 2013). Even though spawning site fidelity has not been documented in the Georgian Bay population, this could explain why age-0 Muskellunge can no longer be found in the relatively disturbed wetlands of southeastern Georgian Bay (Leblanc et al. 2014). Assuming that spawning habitat and nursery habitat are closely linked, then if nursery habitat has become degraded and adults are spawning in the same areas year after year, we would expect limited recruitment success.

The goal of this study was to use radio telemetry to identify the locations and distribution of adult Muskellunge in Georgian Bay during the spawning season. We investigated the specificity of spawning site use by individual fish and explored the hypothesis that Georgian Bay Muskellunge demonstrate spawning site fidelity. Our intent was to advance the understanding of Muskellunge spawning in Georgian Bay while providing a mechanism to explain the apparent absence of age-0 Muskellunge in southeastern Georgian Bay.

Methods

Study Area

The eastern and northern shores of Georgian Bay (Figure 1.1A) are relatively undisturbed areas that are underlain by the Precambrian Shield and consist of a complex array of sheltered embayments and protected wetlands (DeCatanzaro and Chow-Fraser 2011). This study was conducted in three regions of Georgian Bay (Figure 1.1A): southeastern (Severn Sound), northeastern (Pointe au Baril), and northern (Eager Bay and Plant Lake; lake names have been changed to satisfy local stakeholders). All three locations support recreational Muskellunge fisheries that produce adults in excess of the legal harvest size (137 cm TL). Severn Sound (Figure 1.1B) covers approximately 200 km^2 and is underlain by limestone to the south and the Precambrian Shield to the north. The northeast segment of the Severn Sound shoreline, where our work was focused, is characterized by shallow-sloping nearshore bathymetry, with complexes of small bays, wetlands, and islands. The majority of the Severn Sound shoreline has experienced some level of human development, mostly residential or recreational, and there is significant boat traffic during the summer months. The township of Severn (population = 12,000 people) and the town of Honey Harbour (population

= 2,500) are located along the northeast shoreline of Severn Sound, where most homes and cottages have road access.

The northeastern region of Georgian Bay (Figure 1.1C) primarily consists of Sturgeon Bay and the Pointe au Baril Channel (10 km^2). The area is underlain by the Precambrian Shield and generally has steeply sloping nearshore bathymetry. During the summer, the human population in this area consists of approximately 8,000 local and seasonal residents, and the eastern and northern shorelines are accessible by road. Similar to the southeastern region, much of the shoreline in the northeastern region has undergone some level of human modification, including docks, boathouses, and maintained lawns.

The northern region of Georgian Bay (Figure 1.1D) covers approximately 20 km^2 and consists of Eager Bay (15 km^2) and Plant Lake (4 km^2), which are connected by a 3-km inland channel. The mouth of Eager Bay opens directly into Georgian Bay, whereas Plant Lake is connected via the inland channel to Eager Bay in the east and Georgian Bay to the west. The area is characterized by steeply sloping nearshore bathymetry and small wetland complexes. The town of Killarney is approximately 50 km away, and the area is only accessible by boat. Human influence in the northern region is limited to less than 100 seasonal cottagers, fishermen, and recreational boaters.

We conducted the present study across these three regions to (1) account for potential differences in terms of shoreline modification and nearshore bathymetry and (2) evaluate differences in spawning season behavior among geographically distinct populations of Muskellunge.

Tagging and Tracking

Muskellunge tagging and tracking occurred during the spawning season (~April–May) in the spring of each year and began approximately 1–2 weeks after ice-off. The exception to this was in 2012, which had a very warm winter, with open water occurring on some areas of Georgian Bay by late March. The tagging and tracking effort encompassed approximately 2–3 weeks, and we attempted to be on the water each day when boating conditions were safe. Due to the size of the Severn Sound area, we had to split our efforts between the northern and southern reaches of the Severn Sound shoreline. Tagging was carried out in Severn Sound during spring 2012 (May 1–2), 2013 (April 24–May 9), and 2014 (May 7–15) and in Pointe au Baril during spring 2015 (May 15–20) in conjunction with the Ontario Ministry of Natural Resources and Forestry's (OMNRF) Spring Muskellunge Index Netting Program (A. Liskauskas, unpublished data). In northern Georgian Bay, tagging was conducted during spring 2012 (May 25 and 27) and 2013 (May 4–18) by researchers and field technicians (without assistance from OMNRF biologists).

Adult Muskellunge were caught with trap nets (40-mm mesh; 1.83- × 1.83-m crib) and hoop nets (40-mm mesh; 91-mmdiameter hoops) that were deployed in coastal wetlands for 24 h. Muskellunge that were suitable for tagging (>1,000 g) were isolated and transferred to a floating pen (1.0 × 1.5 m; 1.0 m deep) attached to the boat. We did not tag any fish that exhibited signs of injury or stress while in the floating pen; those individuals were monitored in the pen and were released when they appeared to have recovered. Research-quality clove oil (Xenex Laboratories, Inc., Coquitlam, British Columbia, Canada) was used to anaesthetize the fish during surgery. A single dose (60 mg/L) was added to the anesthetic bath (60–100 L of water obtained from the capture site), and a maintenance dose of 30 mg/L was pumped across the gills during surgery. Clove oil was dissolved with ethanol in water temperatures below 15°C (Anderson et al. 1997). Each fish was placed individually into the anesthetic bath and was monitored for up to 10 min until equilibrium was lost and the opercular rate slowed. The fish was placed in a supine position on a foam surgery platform. The maintenance dose of clove oil was supplied through a plastic tube that was inserted into the mouth and positioned to permit the flow of anesthetic across the gills. Muskellunge were tagged with MCFT2-3A radio tags (Lotek, Newmarket, Ontario; 16-mm diameter, 46-mm length, and 16-g weight). Although a subset of tags transmitted pressure and temperature information, only locational data from the tags were examined for this study. A 2–3-cm incision was made midventral and anterior to the pelvic girdle, and the radio tag was inserted. The tag was anchored to the body cavity by feeding the trailing whip antenna through a hollow, 16-gauge needle that was inserted adjacent to the incision. The incision was closed with two or three interrupted sutures (3-0 monofilament). Total surgery time was 5–10 min, after which the Muskellunge was transferred to a cradle secured in the floating pen and was allowed to recover. Individuals took up to 1 h to regain equilibrium and become responsive to external stimuli, at which point they were released.

Fish were not actively tracked until 2 weeks after surgery. Tagged Muskellunge were tracked from an open boat with a Lotek SRX600 receiver and three-piece Yagi antenna. Where possible, the boat was positioned over the tracked fish, and geographic coordinates were acquired with a handheld GPS (3–5-m accuracy; Garmin, Olathe, Kansas). When conditions precluded approaching the tagged fish (e.g., areas that were too shallow or with high wave action), we approximated the fish's location by taking the strongest signal bearing and estimating the distance from the boat based on the signal strength.

Since Severn Sound was the most intensively studied of our Georgian Bay regions (three consecutive years of tagging and tracking compared to 2 years in the northern region and 1 year in the northeastern region), our data analysis focused primarily on Severn Sound. We present our results separately for two distinct sections (south and north) of Severn Sound because (1) greater effort was expended in south Severn Sound in terms of capture and tracking, and (2) no tagged Muskellunge were found outside of the section in which they were originally tagged. Where possible, we used data from the northern and northeastern regions of Georgian Bay to compare against the results from Severn Sound, which allowed us to evaluate the transferability of results across different regions of the bay.

Spatial and Statistical Analysis

All spatial analyses were completed in ArcMap version 10.2 (ESRI, Inc., Redlands, California); statistical analyses were performed with PASSaGE 2 software (Rosenberg and Anderson 2011) and JMP version 12.0.1 (SAS Institute, Inc., Cary, North Carolina). All geographic coordinates corresponding to sites where Muskellunge had been captured or tracked during this study were imported into the GIS environment. Capture locations were pooled with the tracking locations because the location of capture and the time of tagging were considered to constitute a spatially (±50 m) and temporally (within 24 h) accurate representation of a location that was used by the fish during the spawning season. Since the purpose of this study was to investigate the distribution of adult Muskellunge during the spawning season, we only included locations that were deemed representative of the spawning period. This included all locations that were recorded between late April and May, the typical spawning season for Georgian Bay Muskellunge, with the exception of locations acquired late in the season that were consistent with post-spawning behavior. A Muskellunge was considered to have finished spawning if locations were obtained late in the expected spawning season (i.e., mid- to late May) and if the individual was detected as using offshore areas away from potential spawning locations (i.e., coastal wetlands). Hereafter, we use the term “locations” in reference to the observed locations of Muskellunge during this study, which include the capture locations and all tracked locations that were representative of spawning season behavior. When locations for an individual were collected across multiple years, all data were pooled. We follow Crossman's (1990) usage of "spawning sites" to represent specific areas where Muskellunge are thought to be spawning, and we consider the term "spawning grounds" to represent general habitat that is used during the spawning season. We limit our presentation and discussion of results to "spawning ground use" and "spawning ground fidelity" since we could not confirm that spawning had taken place (e.g., we did not conduct visual observations or collect eggs). We also imported the locations of historic (Craig and Black 1986) and current (J. P. Leblanc, unpublished data; J. D. Weller, unpublished data) Muskellunge nursery sites from each region to provide spatial context for the spawning season locations we acquired relative to known nursery habitats.

Distribution during the Spawning Season

We limited our formal analysis of spawning season distribution to individuals with at least five locations. To characterize the distribution of a Muskellunge's locations during the spawning season, we calculated the average nearest-neighbor distance ($\bar{d}_{min}$) for each individual as a relative measure of clustering or dispersion in the observed locations (O'Sullivan and Unwin 2010). Ripley's K-function (Ripley 1976, cited by O'Sullivan and Unwin 2010) was used as a means to further group individuals based on the extent and type of clustering observed. Ripley's K compares the observed number of neighboring points to the number of neighbors that would be expected within a given radius around each point; this is repeated for multiple values of the radius to evaluate how the clustering or dispersion in the point pattern changes over a range of distances. We performed this analysis in ArcMap at 100 different distances in 40-m increments to a maximum distance of 4,000 m (the maximum distance moved by a Muskellunge over a 1-d period during the present study). The maximum boundary was set to encompass the areas to which an individual could have moved during our study. Confidence limits were established from 999 permutations. Individuals were classified based on the significance of clustering over the majority of the distances evaluated. Clustering was defined as tightly clustered (significant clustering over the majority of distance bands), loosely clustered (nonsignificant clustering over the majority of distance bands), or dispersed (dispersion of points over the majority of distance bands). No category was created for significantly dispersed points, as that would represent a uniform pattern, which would not be expected to occur naturally. This analysis was used only as a means to further classify the degree of clustering observed rather than to examine the spatial scale of clustering.

We also used activity centers to approximate areas in which an individual Muskellunge spent the majority of its time during the spawning period in each year. The kernel density function in ArcGIS was used to estimate a kernel utilization distribution (KUD)—a technique that is widely used in animal movement and home range analysis (e.g., Worton 1989; Laver and Kelly 2008). The KUD is a probability surface based on known locations (i.e., observed

Muskellunge locations) and predicts the likelihood that an individual will be found at a particular location. High-use areas as determined by the investigator are bounded by isolines that contain a set percentage of the distribution. For example, 95% of the KUD is a typical boundary for home range analysis (Worton 1989). Since we were interested in "core" use areas, we bounded the Muskellunge activity centers with 10, 25, and 50% isolines (Afonso et al. 2008). A kernel density surface was determined for each individual in ArcMap (cell size = 10 m; bandwidth from Silverman's rule; Silverman 1986), and we used a custom-built tool in ArcMap to delineate the activity centers. The total area within each activity center (excluding land) was calculated, and areas for all activity centers were pooled under each KUD boundary condition. Spawning ground fidelity was assessed based on the repeated use of the same activity center over multiple years. Activity centers were also calculated for the subpopulation by pooling the locations from all individuals to identify any regionally important spawning grounds.

To assess differences in the size of activity centers and the depths of areas used by male and female Muskellunge, we used a partial Mantel test, which examines for correlations between two distance matrices while controlling for the effects of a third distance matrix (Legendre and Legendre 1998). We tested whether male and female Muskellunge were using different depths (sex = matrix 1; maximum depth at spawning season locations = matrix 2) or different-sized activity centers (sex = matrix 1; KUD area = matrix 2). Matrix 3 included the weight at capture, which was held constant to account for size differences between males and females. Available topographic and bathymetric data (OMNR 2006; NOAA 1996) were compiled to create a digital elevation model for estimating the maximum depth at each location. The depth comparison refers to the maximum water depth corresponding to the observed location rather than the depth at which the fish were found within the water column. Results were tested for significance by permutation (999 times at $\alpha = 0.05$).

Results

Tagging and Tracking

Overall, 49 Muskellunge were tagged and tracked from 2012 to 2015 across all three study regions of Georgian Bay (Figure 1.2). We tagged 24 adult Muskellunge in the southeastern region (Severn Sound) during 2012–2014 (Table 1.1). Capture and tracking efforts in this region were focused primarily along the northeast segment of the Severn Sound shoreline. In total, 298 locations were acquired over the 3 years of tagging and tracking in Severn Sound (245 in south Severn Sound, 53 in north Severn Sound; Figure 1.3A, B). Of the 24 tagged adults, 22 were confirmed as being active at the end of May in 2014. The signal from tag identification number (ID) 15 was found in the same location for the duration of 2013 tracking and again in 2014, so we presumed that the fish died prior to the 2013 season. One individual, ID 32, had been tagged in 2013 but was not located again in 2014. In the northeastern region, we tagged and tracked 13

Muskellunge during the spawning season in 2015 and acquired a total of 86 locations for those fish (Figure 1.4A; Table 1.2). In the northern region, 12 Muskellunge were tagged and tracked, with a total of 30 locations (Figure 1.4B; Table 1.2). Due to the early spring in 2012, our capture and tracking effort in the northern region missed the majority of the spawning season, so no tracking data were acquired during that year.

Distribution during the Spawning Season

Among the 24 adult Muskellunge that were tagged in Severn Sound, 18 had at least five locations. Of those, 17 were tracked for more than one season; ID 48 had one season of locations available. Twelve of these Muskellunge were from south Severn Sound. The $\bar{d}_{min}$ for these individuals ranged from 53 ± 29 m (ID 19) to 600 ± 213 m (ID 28), with a median value of 162 m (Table 1.3). Of the nine females, seven had $\bar{d}_{min}$ values greater than the median; IDs 18 and 31 were the exceptions. The majority of males (7 of 9) had $\bar{d}_{min}$ values that were less than the median; the exceptions were IDs 35 and 40. The $\bar{d}_{min}$ values were consistent with the groupings based on Ripley's K-function (Table 1.3). Of the 18 individuals evaluated, 10 were classified as exhibiting tight clustering, 7 were classified as having loose clustering, and 1 was classified as showing a dispersed pattern. The individuals with tight clustering were mostly males (8 of 10) except for IDs 18 and 31. The individuals with loose clustering were mostly females (6 of 7), with the exception of ID 40. The only individual that demonstrated dispersion was a female (ID 28).

The 18 fish were localized to between one and five activity centers, depending on the KUD boundary condition (Table 1.4). Due to the number and distribution of locations for some individuals, some of the delineated activity centers only contained one location, and those activity centers were eliminated from further consideration. There was a large range in the total area of activity centers for each Muskellunge both within and between KUD boundaries (e.g., 0.7–209.9 ha at 10% KUD; 2.0–866.2 ha at 50% KUD). The number of activity centers delineated was variable, but several patterns of use were evident. The most common example was the use of one main activity center. This included individuals that only had one identifiable activity center (e.g., IDs 18, 20, and 29; Figure 1.5) and individuals that had several activity centers but one obvious "primary" activity center, which accounted for the majority of the total activity center area (e.g., IDs 11, 16, and 39; Figure 1.5). The "secondary" activity centers were generally areas in which an individual was found only two or three times over the course of the study. The other major pattern of use was a relatively even split between two main activity centers. Locations for ID 19 were split between two activity centers at the western and central areas of the Green Island channel (Figure 1.6); locations for ID 22 were split between two activity centers north of Waubaushene (Figure 1.6). The only individual that was classified as dispersed, ID 28, was found across nearly all of south Severn Sound (Figure 1.5) during this study but was located on five occasions in or adjacent to Oak Bay, which is a large wetland area and possible spawning ground. When individuals had more than one activity center, they were never separated by a distance greater than 1 km (Table 1.4). Two individuals, IDs 37 and 19, had the most spatially distinct activity centers, as the centers were separated by 854 and 827 m, respectively (10% KUD boundary).

Some level of spawning ground fidelity was observed in all but one fish that were tracked in Severn Sound for 2 or more years (17 individuals; Table 1.4). Since we measured fidelity as the use of the same activity center over multiple years, the KUD boundary condition affected the degree of fidelity observed. Moving from the more conservative estimate of core use areas (10% KUD) to the more generous estimate (50% KUD), the activity centers expanded and encompassed more locations, which led to higher incidences of repeat use with the larger KUD boundaries. As such, under the 50% KUD boundaries, ID 41 was the only individual that did not show fidelity to at least one activity center between years. Under the 10% KUD, three individuals displayed no sign of fidelity (IDs 18, 40, and 41). Multiple-year use was observed in individuals from the tightly clustered, loosely clustered, and dispersed groups and in both sexes. The most common occurrence was fidelity to one primary activity center from a tightly clustered individual (Figure 1.6; IDs 16 and 20) or a loosely clustered individual (Figure 1.6; IDs 29 and 39). Muskellunge were found to use mainly these activity centers over multiple years, although multiyear use of other, smaller activity centers was also observed (IDs 16 and 39). Fish IDs 19 and 22 showed fidelity to each of their two main activity centers (Figure 1.6); however, ID 22 appeared to use both activity centers in both 2013 and 2014, whereas ID 19 heavily favored one activity center in each of those years.

The activity centers for pooled locations from the south and north areas of Severn Sound revealed several major spawning grounds. In south Severn Sound (Figure 1.3A), the channel on the north side of Green Island was a hot spot for spawning activity in the area, as was the eastern portion of the shoreline to the north of Waubaushene. Notable spawning grounds in north Severn Sound included the areas to the immediate east and south of Tonch Point and the eastern shore of Robert’s Island (Figure 1.4B).

Male and female Muskellunge in Severn Sound exhibited different patterns in their spawning season distributions. Males had significantly smaller activity center areas than did females under each KUD boundary condition (Table 1.5). For example, under the 10% KUD condition, the average total activity center area was 7.2 ha (SE = 2.1; n = 9) for males compared with 67.1 ha (SE = 22.5; n = 9) for females (partial Mantel test: P = 0.001). The magnitude of the difference in activity center areas between males and females was consistent at the 25% KUD and 50% KUD boundary conditions. Fish IDs 18 and 31 were both females with total activity center areas of 1.9 and 14.9 ha, respectively (10% KUD), closer to the male average; in contrast, the remaining females had activity center areas in excess of 20 ha. Similarly, one male (ID 40) had an activity center area of 21.2 ha (10% KUD) that was larger than that of other males (<12 ha; 10% KUD). Females were also found in significantly deeper areas than were males (females: 2.6 ± 0.3

m; males: 1.9 ± 0.2 m; partial Mantel test: $P = 0.042$; Table 1.5). In general, males occupied smaller areas and were found in shallower waters than females.

Tracking data from the northern and northeastern regions appeared consistent with our observations from Severn Sound. Of the northeastern Muskellunge that were tagged and tracked in Sturgeon Bay and Pointe au Baril (11 individuals), six showed obvious clustering at specific sites and three showed possible evidence of clustering. The sizes of the areas used by these individuals appeared to be consistent with those of the tightly clustering and loosely clustering groups identified in the Severn Sound analysis (~10 ha for males). Tracking data from the northern region were sparse during the spawning season and were primarily obtained in 2013. One male, ID 8, appeared to use a specific area towards the northeast shore of Eager Bay, which was also where that individual was captured in 2012. Besides ID 8, there were insufficient multiyear data to provide further support for spawning ground fidelity in the northern region.

Discussion

The apparent absence of age-0 Muskellunge in southeastern Georgian Bay (Leblanc et al. 2014) is puzzling. Even though the quality of some coastal wetlands in that region is lower than the quality of those in the rest of eastern and northern Georgian Bay, they are still in excellent condition relative to the remainder of the Great Lakes (Cvetkovic and Chow-Fraser 2011). The extent of shoreline modification within Muskellunge nursery sites in Severn Sound has increased in recent years (Leblanc et al. 2014) but is limited primarily to residential development (e.g., docks and boathouses), whereas strong populations of Muskellunge (adults and age 0) appear to be persisting in areas that have experienced much more significant modifications to the shoreline, such as the Niagara River (Kapuscinski et al. 2014) and the Fox River (Kapuscinski et al. 2007). Concurrent with our study, age-0 Muskellunge were observed in our northern and northeastern regions despite the fact that those regions have also experienced the same sustained low water levels as the southeastern region. It is therefore possible that other factors related to or independent of shoreline modifications or water levels (e.g., changes to fish community, habitat structure, or climate) could be affecting the recruitment success of age-0 Muskellunge in Severn Sound. Nevertheless, Muskellunge in Georgian Bay should theoretically be able to seek out other suitable breeding habitat since they are capable of moving great distances (e.g., Crossman 1977; LaPan et al. 1996), and the shorelines of eastern and northern Georgian Bay provide continuous access to thousands (Midwood et al. 2012) of high-quality coastal wetlands (Cvetkovic and Chow-Fraser 2011) that should be capable of supporting Muskellunge spawning and nursery activities. However, what is possible in theory has not proven to be the case in reality, and our findings support our main hypothesis of spawning site fidelity as a potential mechanism for the absence of age-0 Muskellunge in Severn Sound.

Movement to specific areas during the spawning season has been well documented in many Muskellunge populations (Miller and Menzel 1986; Strand 1986; Crossman 1990; LaPan et al. 1996; Younk et al. 1996; Farrell et al. 2007; Diana et al. 2015). Muskellunge in each of our study regions exhibited an affinity for particular areas during spawning, consistent with previous observations. Similarly, spawning site fidelity has also been documented in Muskellunge populations within multiple waterbodies throughout the species' range (Crossman 1990; LaPan et al. 1996; Younk et al. 1996; Farrell et al. 2007; Jennings et al. 2011), but this is the first study to document such behavior in Georgian Bay Muskellunge. Of the individuals that were successfully tracked for two or more years, only one (ID 41) did not use the same activity center across multiple years. The most conclusive evidence for spawning site fidelity came from the individuals that were tagged in south Severn Sound during 2012. Those fish were tagged relatively late in the spawning season but were tracked for the entirety of the subsequent two seasons. A full season of tracking was needed before preferential site use was obvious, and an additional season was required to confidently claim that the fish were displaying spawning site fidelity. Several multiyear telemetry studies (LaPan et al. 1996; Younk et al. 1996) have also observed strong spawning site fidelity in individual fish, whereas studies using mark–recapture techniques have reported weaker fidelity (Crossman 1990; Jennings et al. 2011). This may be a result of behavioral differences between populations or, alternatively, a product of net avoidance. During the present study, we rarely recaptured tagged individuals despite the fact that they were frequently located in the immediate vicinity of deployed nets. Spawning site fidelity among Muskellunge also provides a mechanism for the genetically distinct populations (Koppelman and Philipp 1986; Kapuscinski et al. 2013) that are found throughout the Muskellunge's range. In Georgian Bay, Kapuscinski et al. (2013) identified three genetically unique populations along a 100-km reach of shoreline that extended from our southeastern region (Severn Sound) to our northeastern region (Pointe au Baril), where each population was separated by approximately 50 km. Bosworth and Farrell (2006) and Miller et al. (2001) documented similar genetic population structuring in the congeneric Northern Pike *Esox lucius*.

The literature indicates that male Muskellunge tend to arrive earlier to spawning grounds than females and then stay longer, whereas females are more often found staging offshore of the spawning grounds (Minnesota: Strand 1986; Mississippi River: Younk et al. 1996). Differences between sexes have been documented for Muskellunge during the spawning period. This is consistent with our observations of finding females in significantly deeper water, whereas males were usually found in shallower waters (<2 m), where spawning typically takes place (e.g., Farrell et al. 1996; Scott and Crossman 1998; Zorn et al. 1998). The fact that the smaller, shallower activity centers of male Muskellunge in Severn Sound were all in coastal wetland areas near probable spawning sites suggests that those males were staging at or near a spawning site. Female Muskellunge also showed spawning ground fidelity, but they staged in deeper waters over generally larger areas that were adjacent to multiple candidate spawning habitats. This appears to present the opportunity for females to spawn over a greater range of potential areas and to spawn multiple times during a given season (Lebeau 1991). Although we were unable to confirm that spawning had actually occurred, we did capture females that either (1) were full of eggs or (2) had no eggs but showed signs that they had recently spawned. Coupled with the observed degree of spawning ground fidelity, especially among males, we are confident that spawning did take place within the activity centers we determined for individuals and subpopulations. We propose that the site specificity and fidelity observed in male Muskellunge are driving the repeated use of potentially degraded breeding habitat, as females are spawning in locations near the staging males.

The results of this study were consistent with our hypothesis regarding spawning site fidelity as a mechanism for the absence of age-0 Muskellunge in Severn Sound; however, we did not directly address the presumed spatial association between spawning and nursery habitats. Since surveys of nursery habitat were conducted concurrently with this study, we are able to offer strong support for the spatial linkage of spawning and nursery habitats within each study region. Age-0 Muskellunge were found by seining in both northeastern Georgian Bay (during 2015; J. D.Weller, unpublished data; Figure 1.4A) and northern Georgian Bay (during 2012 and 2013; J. P. Leblanc, unpublished data; Figure 1.4B). One age-0 Muskellunge was found in the northeastern region west of Bigwood Island, within 300 m of a cluster comprising six locations that belonged mostly to one male (ID 58; Figure 1.4A). In the northern region, 17 nursery sites were identified. In particular, those towards the northwest end of Eager Bay and the western side of Plant Lake were in close proximity to the locations of adult Muskellunge during the spawning season (Figure 1.4B). Indeed, the nursery locations identified in 2012 were used to successfully guide the placement of nets during the 2013 tagging effort in the northern region. LaPan et al. (1996) similarly identified nursery sites in the St. Lawrence River that were in close proximity to capture sites or tracked locations of adults during spawning. Age-0 Muskellunge were not found in Severn Sound with this study (Leblanc et al. 2014), so we cannot evaluate the association between concurrent spawning season locations and nursery sites in the region. However, historic nursery sites (Craig and Black 1986) were close to the activity centers documented here (Figure 1.3). It is notable that the activity centers for south Severn Sound Muskellunge bordered six of the eight historic nursery sites in the region and were within 500 m of the remaining two nursery sites (Figure 1.3A). Furthermore, a previous Muskellunge telemetry study in Severn Sound (Black 1981, cited by Liskauskas 1996) found a Muskellunge using that same activity center. The continued use of this area by adult Muskellunge during the spawning season suggests that the multiple-year affinity we observed may in fact span decades.

Muskellunge in each of our Georgian Bay study regions showed an affinity for particular spawning grounds, and we have conclusive evidence of spawning ground fidelity in the southeastern region. Muskellunge may be unable to adapt to changing conditions if spawning habitat becomes degraded, as appeared to be the case in Severn Sound (Leblanc et al. 2014). Our findings highlight the importance of identifying and protecting Muskellunge habitat, which has long been a goal of managers (Craig and Black 1986; Farrell et al. 2007; Crane et al. 2015; Midwood et al. 2015). Shoreline modifications and anthropogenic impacts continue to be major stressors on spawning and nursery habitats (Dombeck 1986; Rust et al. 2002; Leblanc et al. 2014) and have been identified as critical issues for Lake Huron, including Georgian Bay (Liskauskas et al. 2007). Wetland mitigation strategies—notably habitat compensation or no-net-loss policies (e.g., Policy for the Management of Fish Habitats; DFO 1986)—are unlikely to be effective in offsetting lost or degraded Muskellunge habitat. The high affinity that adult Muskellunge display for specific spawning sites appears to be driven not by the suitability of that habitat but rather by the location of the habitat. Without a greater understanding of the mechanisms that drive spawning site fidelity (e.g., natal homing), the protection and restoration of identified breeding habitat should be of top priority if the overall management goal is to maintain a self-sustaining population of Muskellunge in Georgian Bay.

Acknowledgements

We thank the members of the Chow-Fraser laboratory and field technicians for their assistance with data collection, and we thank the OMNRF for logistical support. We are grateful to our many hosts, who provided us with accommodations and support: David and Brenda Flower, Glen Willis, Harvey and Lorna Meirke, Jerry Burke, Roy and Diana Schatz, Pitfields General Store, and Queen's Cove Marina. This project was funded in part by scholarships to J.P.L. (Ontario Graduate Scholarship; and Muskies Canada, Inc.) and to J.D.W. (Natural Science and Engineering Research Council [NSERC] Undergraduate Student Research Assistantship; NSERC Canada Graduate Scholarships–Master's; and Ontario Graduate Scholarship); a research grant from the Sierra Club Canada Foundation, including the Great Lakes Basin Conservancy (Grant 5-21077); the OMNRF through the Canada– Ontario Agreement (Grant 5-21092); and in partnership with the Georgian Bay Musky Association. We appreciate the comments of two anonymous reviewers, whose input contributed to improving the quality of the manuscript.

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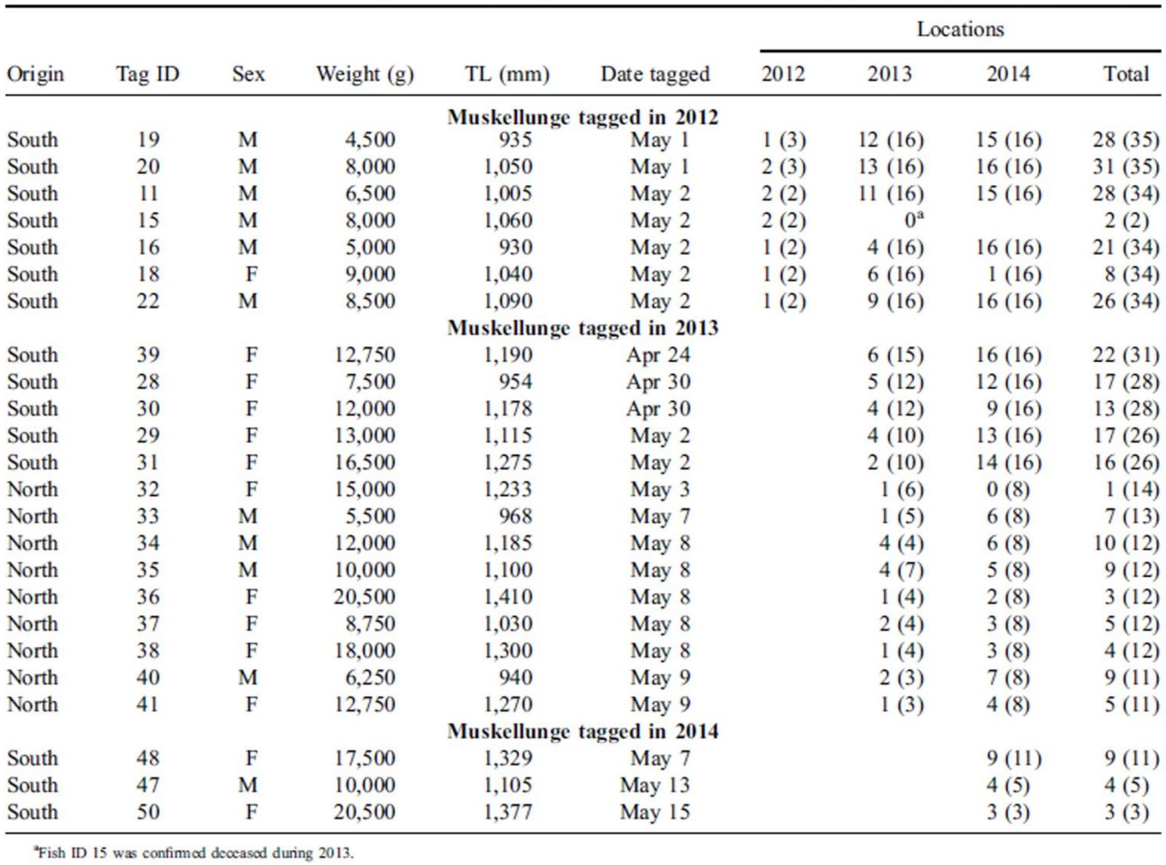
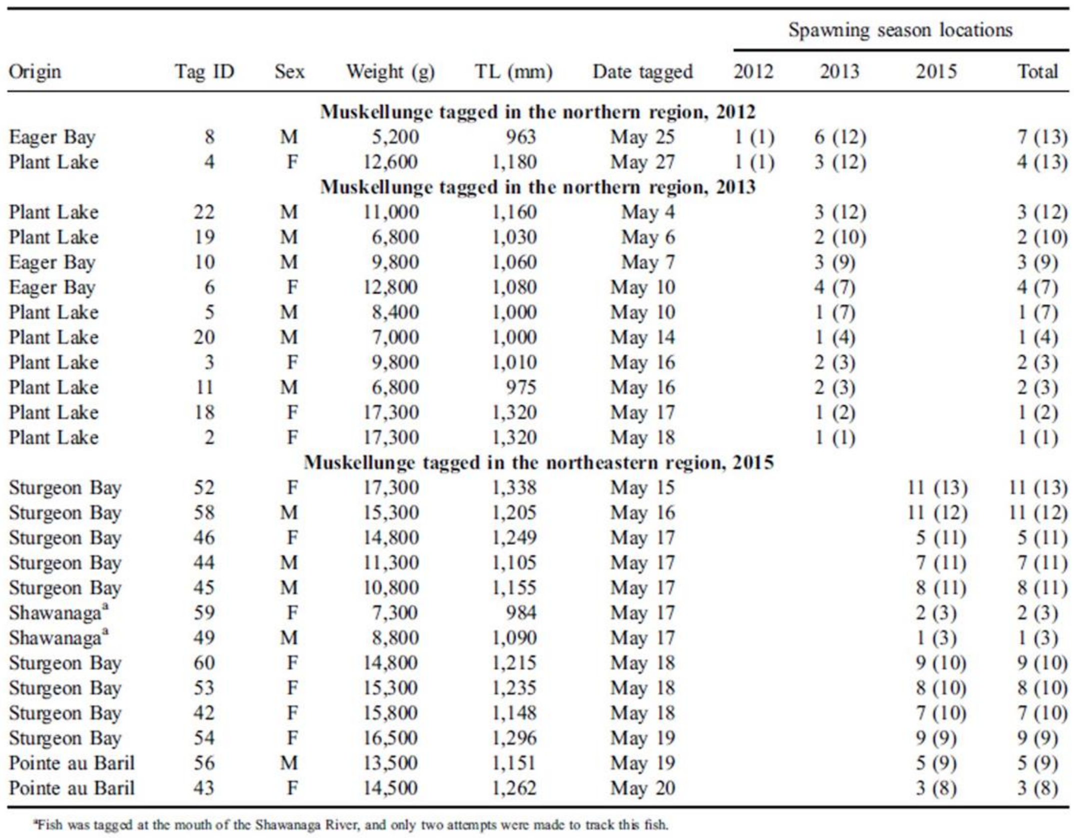
Table 1.1: Biological information and telemetry data from each Muskellunge captured and tracked in the southeastern region. Size measurements and sex of the fish were taken prior to implanting the radio tag. The number of locations acquired in each year are presented relative to the number of days spent tracking the fish (in parentheses).



						Locations			
Origin	Tag ID	Sex	Weight (g)	TL (mm)	Date tagged	2012	2013	2014	Total
				Muskellunge tagged in 2012					
South	19	M	4,500	935	May 1	1 (3)	12 (16)	15 (16)	28 (35)
South	20	M	8,000	1,050	May 1	2 (3)	13 (16)	16 (16)	31 (35)
South	11	M	6,500	1,005	May 2	2 (2)	11 (16)	15 (16)	28 (34)
South	15	M	8,000	1,060	May 2	2 (2)	0[a]		2 (2)
South	16	M	5,000	930	May 2	1 (2)	4 (16)	16 (16)	21 (34)
South	18	F	9,000	1,040	May 2	1 (2)	6 (16)	1 (16)	8 (34)
South	22	M	8,500	1,090	May 2	1 (2)	9 (16)	16 (16)	26 (34)
				Muskellunge tagged in 2013					
South	39	F	12,750	1,190	Apr 24		6 (15)	16 (16)	22 (31)
South	28	F	7,500	954	Apr 30		5 (12)	12 (16)	17 (28)
South	30	F	12,000	1,178	Apr 30		4 (12)	9 (16)	13 (28)
South	29	F	13,000	1,115	May 2		4 (10)	13 (16)	17 (26)
South	31	F	16,500	1,275	May 2		2 (10)	14 (16)	16 (26)
North	32	F	15,000	1,233	May 3		1 (6)	0 (8)	1 (14)
North	33	M	5,500	968	May 7		1 (5)	6 (8)	7 (13)
North	34	M	12,000	1,185	May 8		4 (4)	6 (8)	10 (12)
North	35	M	10,000	1,100	May 8		4 (7)	5 (8)	9 (12)
North	36	F	20,500	1,410	May 8		1 (4)	2 (8)	3 (12)
North	37	F	8,750	1,030	May 8		2 (4)	3 (8)	5 (12)
North	38	F	18,000	1,300	May 8		1 (4)	3 (8)	4 (12)
North	40	M	6,250	940	May 9		2 (3)	7 (8)	9 (11)
North	41	F	12,750	1,270	May 9		1 (3)	4 (8)	5 (11)
				Muskellunge tagged in 2014					
South	48	F	17,500	1,329	May 7			9 (11)	9 (11)
South	47	M	10,000	1,105	May 13			4 (5)	4 (5)
South	50	F	20,500	1,377	May 15			3 (3)	3 (3)

[a] Fish ID 15 was confirmed deceased during 2013.

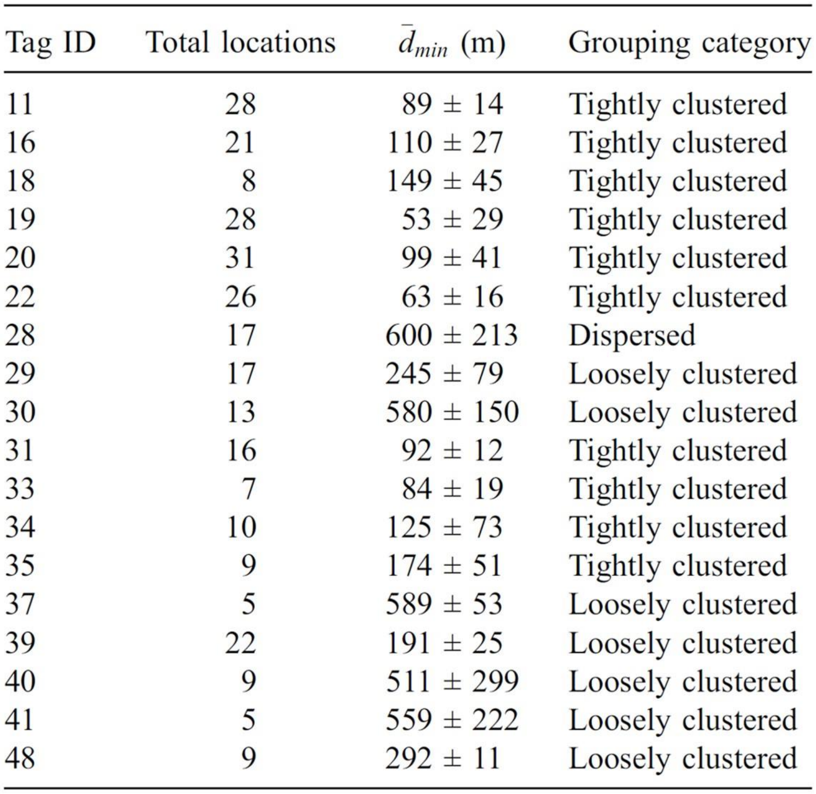
Table 1.2: Biological information and telemetry data from each Muskellunge captured and tracked in the northeastern region (2015) and northern region (2012 and 2013). Size measurements and sex of the fish were taken prior to implanting the radio tag. The number of locations acquired in each year are presented relative to the number of days spent tracking the fish (in parentheses).



						Spawning season locations			
Origin	Tag ID	Sex	Weight (g)	TL (mm)	Date tagged	2012	2013	2015	Total
Muskellunge tagged in the northern region, 2012									
Eager Bay	8	M	5,200	963	May 25	1 (1)	6 (12)		7 (13)
Plant Lake	4	F	12,600	1,180	May 27	1 (1)	3 (12)		4 (13)
Muskellunge tagged in the northern region, 2013									
Plant Lake	22	M	11,000	1,160	May 4		3 (12)		3 (12)
Plant Lake	19	M	6,800	1,030	May 6		2 (10)		2 (10)
Eager Bay	10	M	9,800	1,060	May 7		3 (9)		3 (9)
Eager Bay	6	F	12,800	1,080	May 10		4 (7)		4 (7)
Plant Lake	5	M	8,400	1,000	May 10		1 (7)		1 (7)
Plant Lake	20	M	7,000	1,000	May 14		1 (4)		1 (4)
Plant Lake	3	F	9,800	1,010	May 16		2 (3)		2 (3)
Plant Lake	11	M	6,800	975	May 16		2 (3)		2 (3)
Plant Lake	18	F	17,300	1,320	May 17		1 (2)		1 (2)
Plant Lake	2	F	17,300	1,320	May 18		1 (1)		1 (1)
Muskellunge tagged in the northeastern region, 2015									
Sturgeon Bay	52	F	17,300	1,338	May 15			11 (13)	11 (13)
Sturgeon Bay	58	M	15,300	1,205	May 16			11 (12)	11 (12)
Sturgeon Bay	46	F	14,800	1,249	May 17			5 (11)	5 (11)
Sturgeon Bay	44	M	11,300	1,105	May 17			7 (11)	7 (11)
Sturgeon Bay	45	M	10,800	1,155	May 17			8 (11)	8 (11)
Shawanaga[a]	59	F	7,300	984	May 17			2 (3)	2 (3)
Shawanaga[a]	49	M	8,800	1,090	May 17			1 (3)	1 (3)
Sturgeon Bay	60	F	14,800	1,215	May 18			9 (10)	9 (10)
Sturgeon Bay	53	F	15,300	1,235	May 18			8 (10)	8 (10)
Sturgeon Bay	42	F	15,800	1,148	May 18			7 (10)	7 (10)
Sturgeon Bay	54	F	16,500	1,296	May 19			9 (9)	9 (9)
Pointe au Baril	56	M	13,500	1,151	May 19			5 (9)	5 (9)
Pointe au Baril	43	F	14,500	1,262	May 20			3 (8)	3 (8)

[a] Fish was tagged at the mouth of the Shawanaga River, and only two attempts were made to track this fish.

Table 1.3: Relative measure of clustering in fish from southeastern region with more than five locations. Average nearest neighbour distances ($\bar{d}_{min}$ ± SE) and categorized grouping based off Ripley's K function analysis



Tag ID	Total locations	$\bar{d}_{min}$ (m)	Grouping category
11	28	89 ± 14	Tightly clustered
16	21	110 ± 27	Tightly clustered
18	8	149 ± 45	Tightly clustered
19	28	53 ± 29	Tightly clustered
20	31	99 ± 41	Tightly clustered
22	26	63 ± 16	Tightly clustered
28	17	600 ± 213	Dispersed
29	17	245 ± 79	Loosely clustered
30	13	580 ± 150	Loosely clustered
31	16	92 ± 12	Tightly clustered
33	7	84 ± 19	Tightly clustered
34	10	125 ± 73	Tightly clustered
35	9	174 ± 51	Tightly clustered
37	5	589 ± 53	Loosely clustered
39	22	191 ± 25	Loosely clustered
40	9	511 ± 299	Loosely clustered
41	5	559 ± 222	Loosely clustered
48	9	292 ± 11	Loosely clustered

Table 1.4: Activity center analysis of fish from southeastern study region from Kernel Utilization Distribution (KUD) indicating the number locations for each individual (Total), the number of activity centers delineated (#), the total activity centers area (Area; ha), the average nearest neighbour distance between activity centers (Near) the number of locations within the activity centers (Core), and the percent of activity centers that were used over multiple years (MYU).

		10% KUD					25% KUD					50% KUD				
Tag ID	Total	#	Area	Near	Core	MYU	#	Area	Near	Core	MYU	#	Area	Near	Core	MYU
11	28	2	9.1	117	16	100	1	17.4	--	19	100	5	43.6	207	27	100
16	21	1	5.6	--	12	100	2	10.2	591	15	100	2	18.9	522	17	100
18	8	1	1.9	--	3	0	1	3.5	--	4	0	1	8.7	--	6	100
19	28	2	12.0	827	24	50	2	20.9	730	27	100	2	32.0	613	27	100
20	31	2	3.8	56	19	100	1	6.9	--	26	100	1	10.5	--	28	100
22	26	2	6.3	428	16	50	2	11.2	332	19	50	2	24.8	87	24	100
28	20	3	133.0	498	13	100	1	249.2	--	13	100	1	343.8	--	13	100
29	17	1	22.0	--	10	100	1	41.1	--	13	100	1	63.4	--	14	100
30	13	3	202.9	633	8	33	2	443.5	647	9	50	2	866.2	--	12	50
31	16	2	14.9	718	13	50	2	26.1	638	15	50	2	42.9	415	16	100
33	7	1	3.4	--	4	100	1	5.8	--	5	100	2	14.6	373	7	50
34	10	2	0.7	55	7	50	2	1.3	37	8	50	2	2.0	19	8	50
35	9	1	3.1	--	3	100	1	8.7	--	6	100	1	15.8	--	7	100
37	6	2	121.7	854	5	50	2	187.1	669	5	50	2	267.5	523	5	50
39	22	1	36.0	--	11	100	3	81.6	499	19	100	3	145.5	314	20	100
40	9	1	21.2	--	5	0	2	53.1	299	7	50	1	93.3	--	7	100
41	5	1	30.1	--	2	0	1	49.3	--	3	0	1	104.1	--	4	0
48	9	3	87.1	223	9	--	2	142.1	351	9	--	2	206.0	90	9	--

Table 1.5: Sex-based differences in spawning season habitat use from 18 tagged Muskellunge in Severn Sound (Partial Mantel Test; significance set at $P < 0.05$ based on 999 permutations). Habitat Use Metrics are presented for each gender as the mean ± standard error. Distance matrices for each habitat metric were respectively correlated with gender while weight at capture was held constant.

Habitat Use Metric	Male	Female	Mantel correlation	*P* value
Max Depth	1.8 m ± 0.1	2.4 m ± 0.1	0.19055	0.023
10% KUD	9.5 ha ± 2.9	77.4 ha ± 25.1	0.28522	0.002
25% KUD	18.5 ha ± 5.7	146.8 ha ± 51.9	0.25586	0.003
50% KUD	36.0 ha ± 11.1	243.0 ha ± 97.9	0.19925	0.004

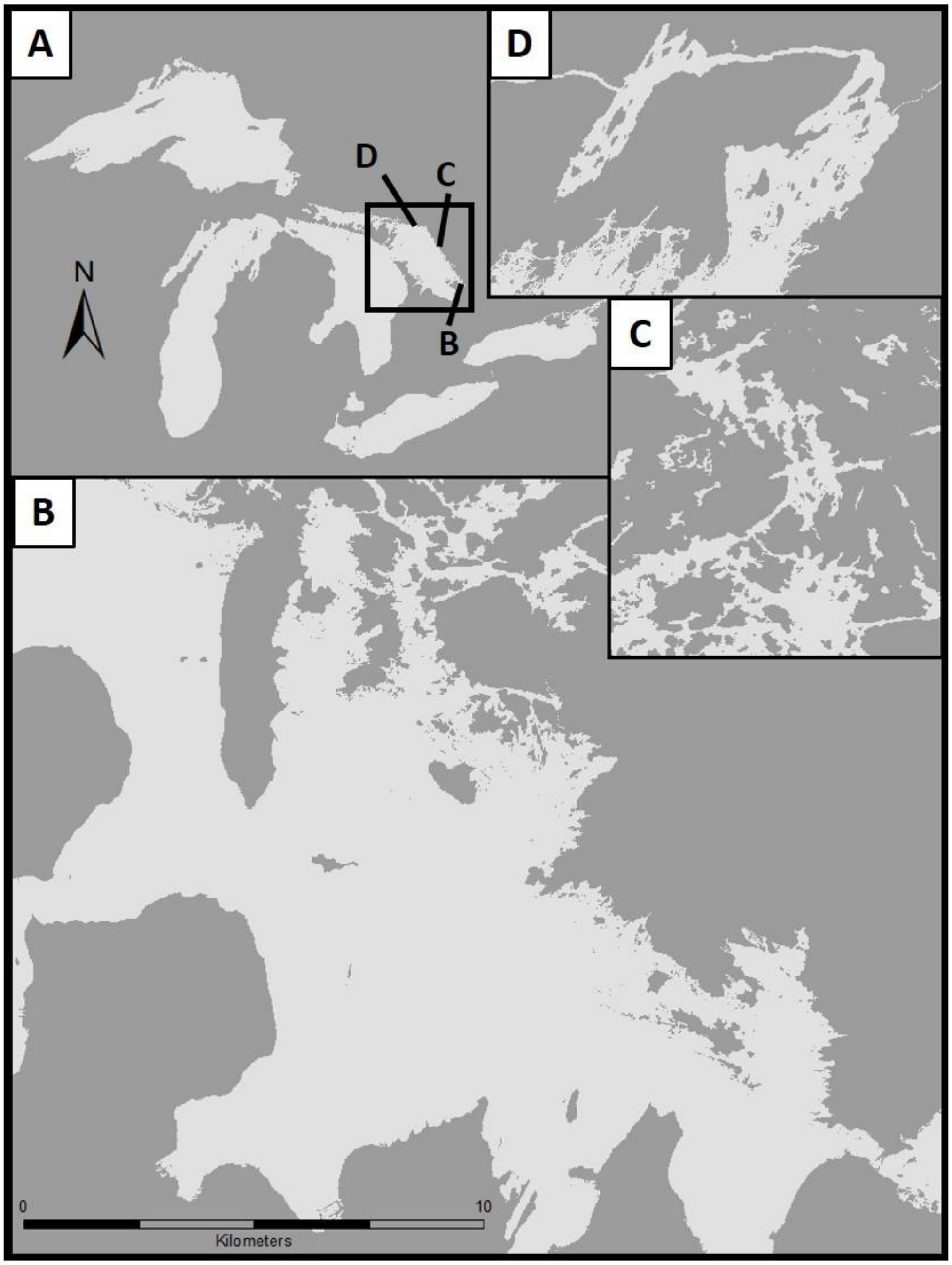


Figure 1.1: Georgian Bay, Lake Huron (A) and our study areas in southeastern (B), northeastern (C), and northern Georgian Bay (D). Insets B, C, and D are all drawn to the same scale.

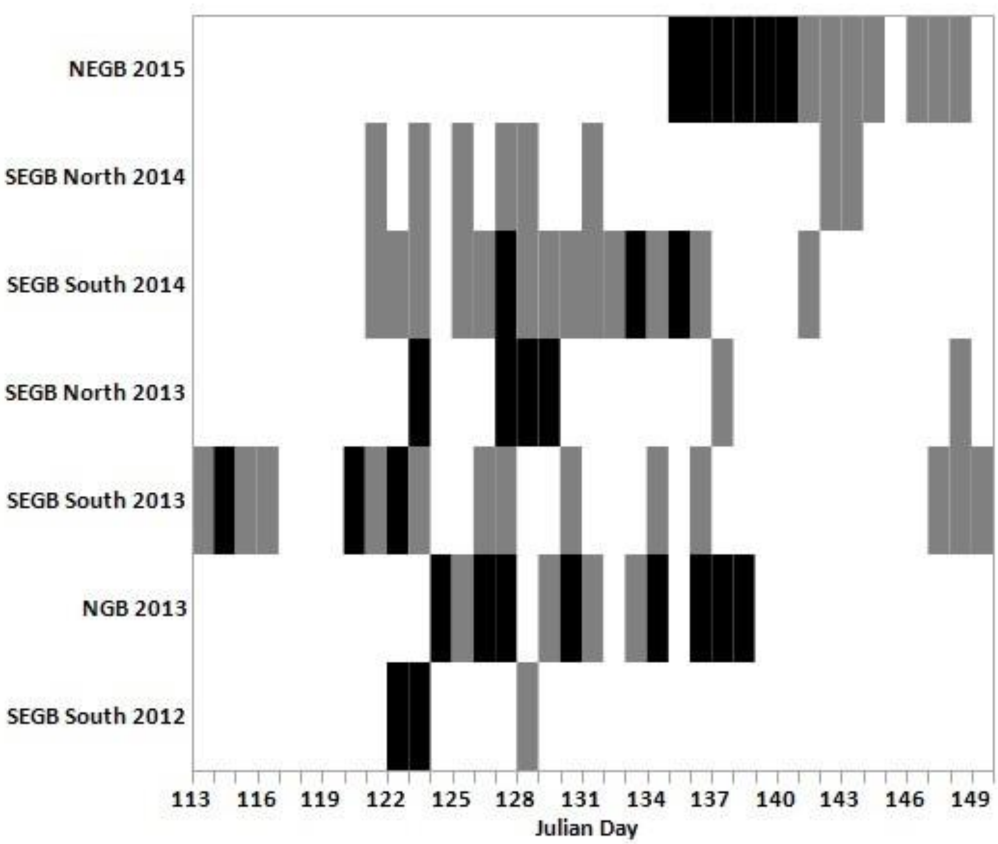


Figure 1.2: Tracking effort from each study region each year. Each filled box indicates that tracking occurred on that day and a black box indicates that a fish was also tagged. Site codes are SEGB = southeastern, NEGB = northeastern, and NGB = northern. Tracking Effort in NGB 2012 was omitted because only two fish were tagged and no tracking occurred during the spawning season.

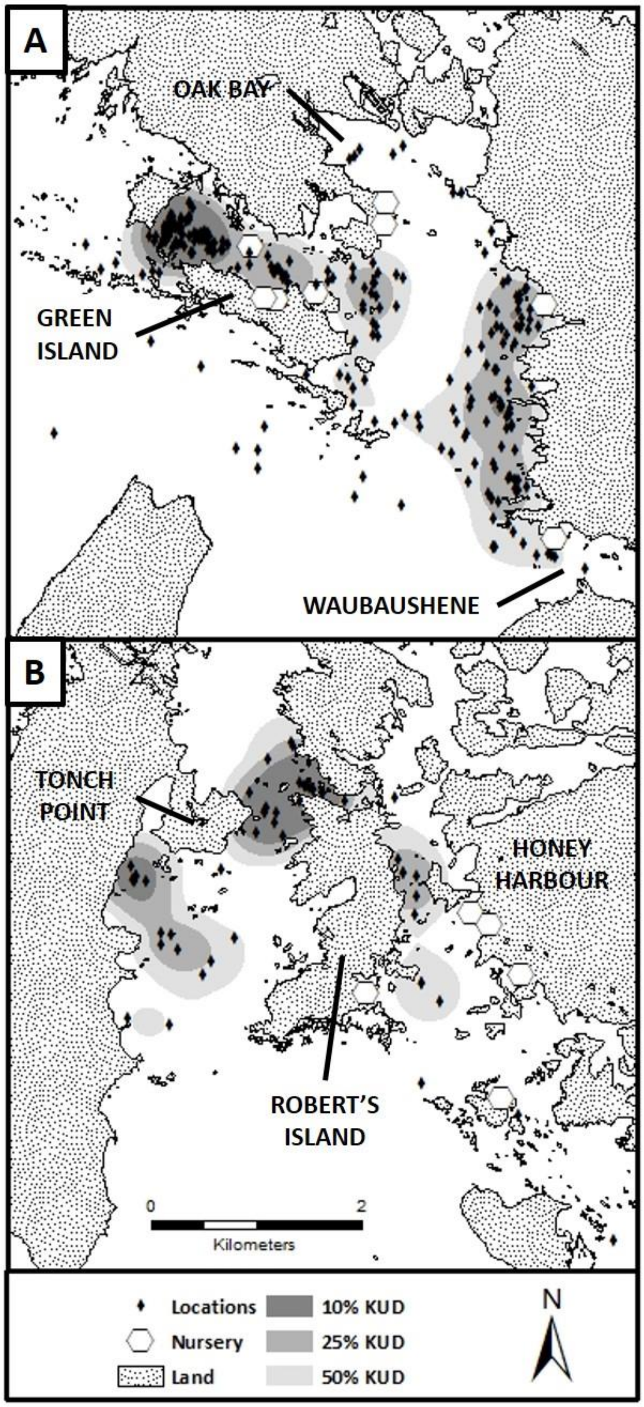


Figure 1.3: Locations of tracked Muskellunge from the southeastern region, partitioned into South Severn Sound (A) and North Severn Sound (B). Activity centers for each group indicate major spawning grounds in the respective sections. Nursery sites were identified in 1981 (Craig and Black 1986).

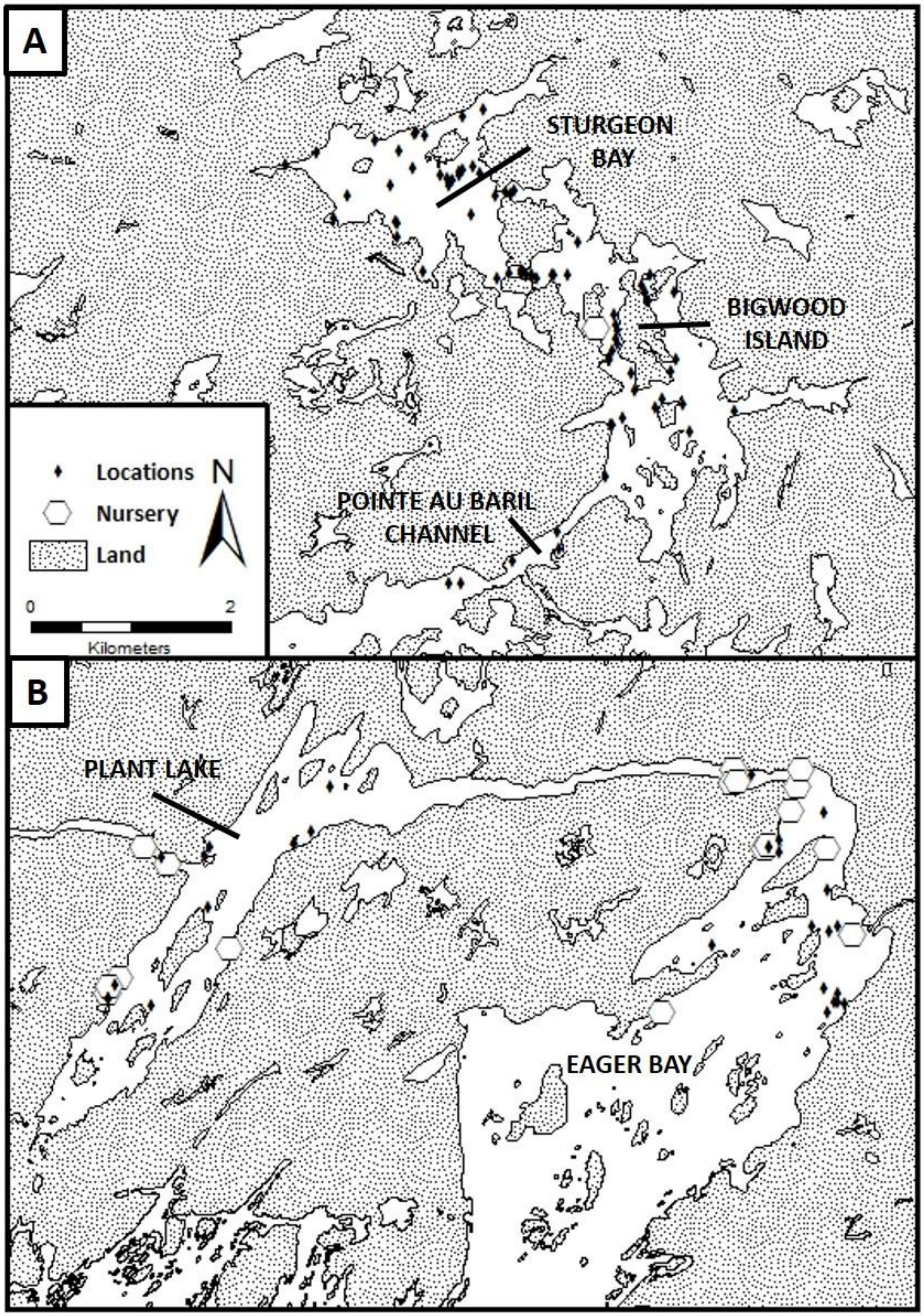


Figure 1.4: Locations of tracked Muskellunge from the northeastern (A) and northern (B) regions. Nursery sites were identified concurrent with this study.

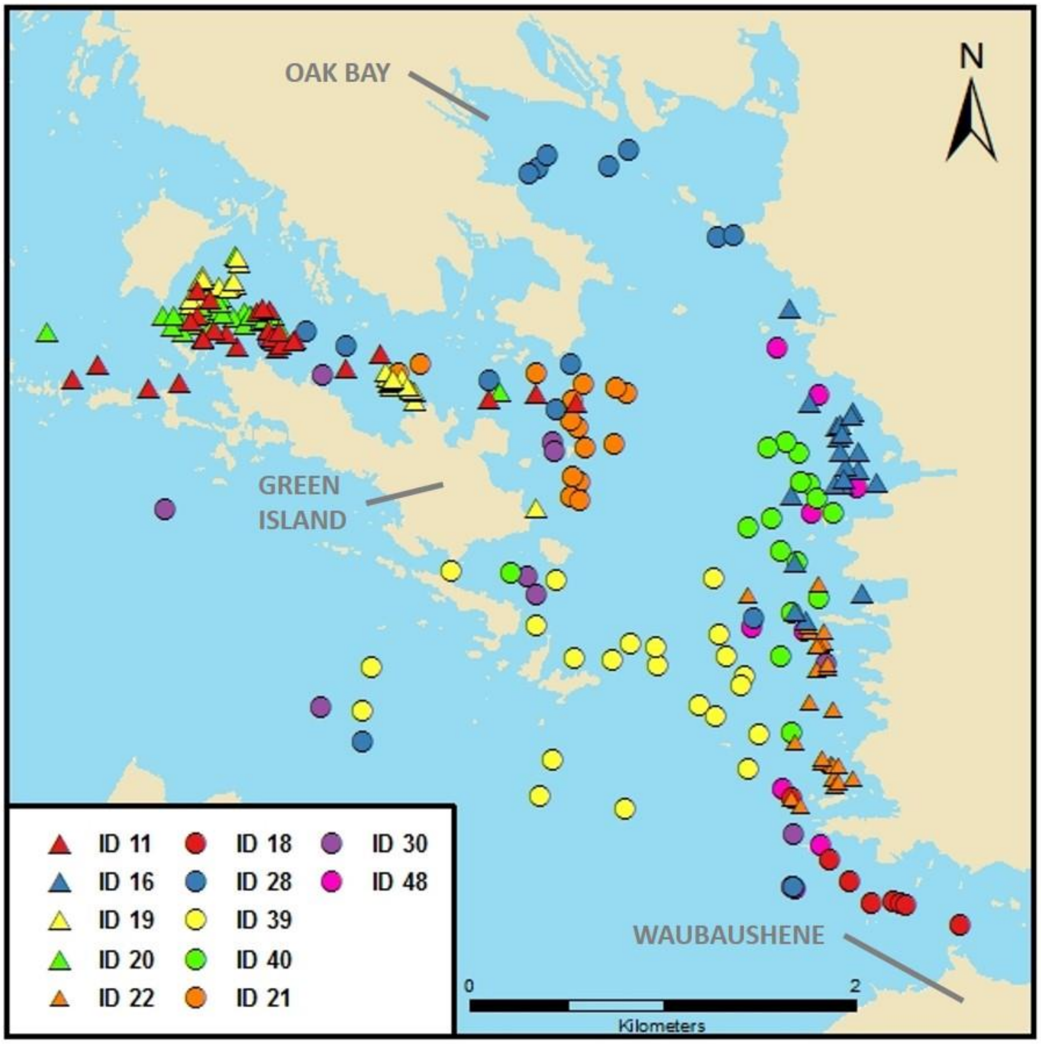


Figure 1.5: Locations of Muskellunge in South Severn Sound with ≥5 locations acquired from 2012-2014. Differences in clustering and distribution are presented between males (triangles) and females (circles).

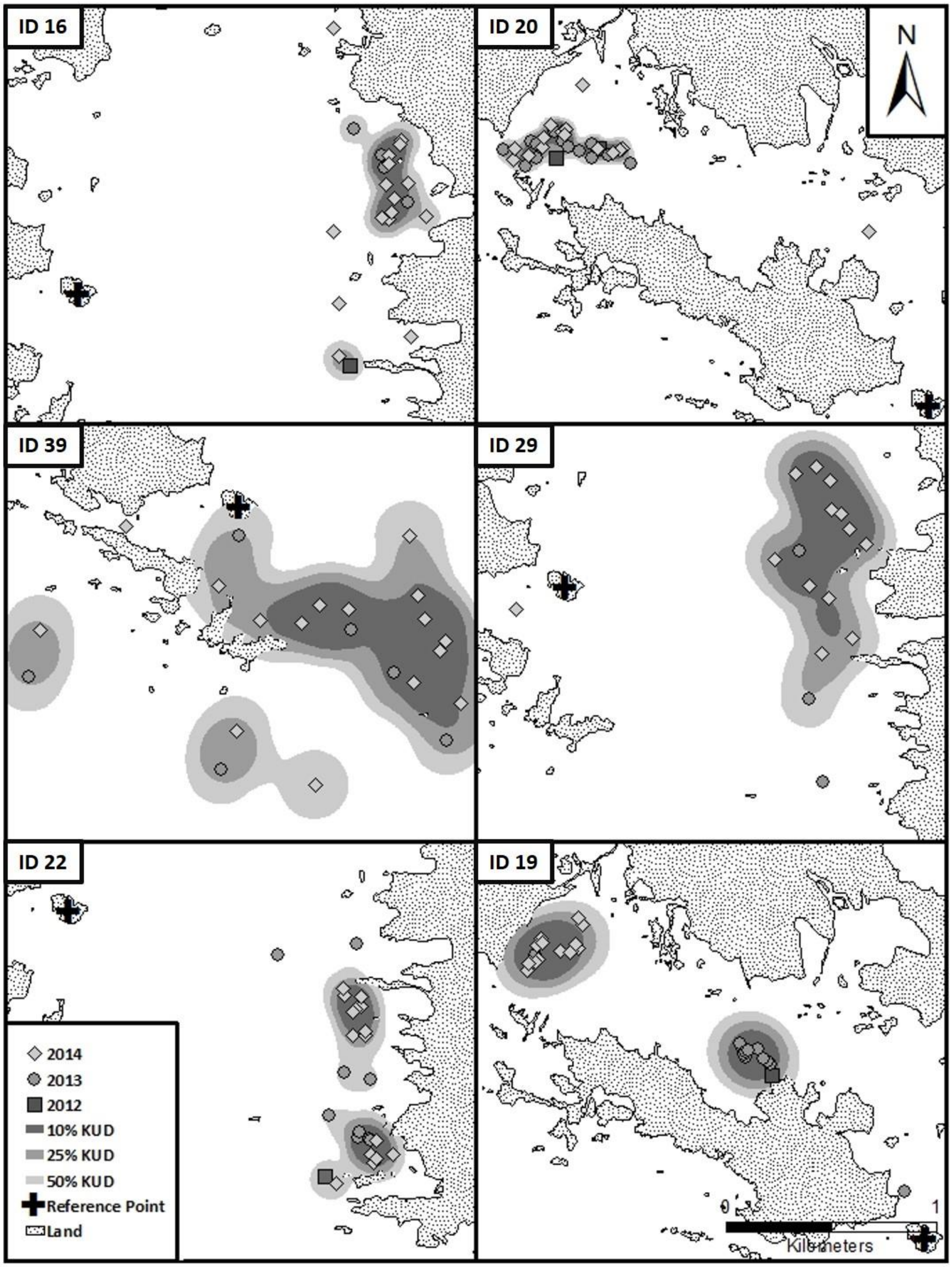


Figure 1.6: Yearly breakdown of locations from fish tracked in South Severn Sound from 2012-2014 and respective activity centers. Illustrative examples of: tightly clustered with one primary activity center (ID 16, ID 20), loosely clustered with one primary activity center (ID 39, ID 29), and tightly clustered with split activity centers (ID 22, ID 19).

Chapter 2

THERMAL HABITAT USE OF EMBAYMENT-RESIDENT ESOCIDS IN GEORGIAN BAY: IMPLICATIONS OF GLOBAL CLIMATE CHANGE

For submission: Weller JD, Biberhofer CR, Leblanc JP, Midwood JD, Chow-Fraser P (2018/CH2) Thermal Habitat Use of Embayment-Resident Esocids in Georgian Bay: Implications of Global Climate Change (Chapter 2)

Abstract

Anticipated impacts of global climate change (GCC) include warmer temperatures and lower water levels that may limit hydrological connectivity between open-waters and nearshore areas of Georgian Bay (Lake Huron) that are important habitat for two apex predators, Muskellunge (*Esox masquinongy*) and Northern Pike (*E. lucius*). We used telemetry data acquired in three embayments during the summers (June to August) from 2011 to 2016 to determine habitat use by these congeners in allopatry (Northern Pike only) and in sympatry. We found that Northern Pike in all three embayments occupied shallower water (2.5 m ± 0.1; $\bar{x}$ ± SE) than Muskellunge (7.3 m ± 0.4) throughout the summer. Although esocids were found in water up to 25 m deep, estimates of their position in the water column based on a subset of pressure-sensitive radio tags indicated they primarily used the epilimnion; Muskellunge generally used the upper 10 m, while Northern Pike used the top 2 m. For both species, the average temperature of habitat used through the summer months reflected seasonal changes in epilimnetic temperatures. Availability of suitable thermal habitat did not limit the spatial distribution of esocids in these regions, but proximity to the thermocline appeared to be an important criterion of habitat suitability for Muskellunge. Instead, the primary factor appeared to be physical habitat structure (e.g. wetland vegetation, shoals, ledges, or docks) with which fish associated, and this is consistent with the ambush style of foraging typical of esocids. Expansion of hypoxic or anoxic

conditions in the water column due to increased cottage development and nutrient enrichment is an immediate management concern.

Introduction

Recreational fisheries in Ontario are valued at more than $2 billion (OMNRF 2015), which include the Great Lakes populations of Muskellunge (*Esox masquiningy*) and Northern Pike (*E. lucius*). In Georgian Bay (Lake Huron), both esocids support naturally-reproducing recreational fisheries and Muskellunge are known for their trophy potential (Kerr 2011). Although the two congeners are apex predators and tend to compete directly for the same resources (Inskip 1986), sympatric populations are known to occur within the Great Lakes basin (Scott and Crossman 1973). One possible mechanism for their coexistence is spatial and temporal segregation in the nearshore (Inskip 1986), where they have spawning and nursery habitat (Farrell 2001; Leblanc 2015; Pankhurst et al. 2016) and spatial segregation in deeper waters (Scott and Crossman 1973) where they employ a similar ambush-style foraging strategy (Inskip 1986).

Muskellunge are considered warm-water fish while Northern Pike are cool-water fish; distinction between warm-water and cool-water species is typically based on optimal or preferred temperature above or below 25°C (Coker et al. 2001; Casselman 2002). Optimal growth temperatures for Northern Pike have been measured at 19 – 21°C (Casselman 1978) and estimated for

Muskellunge at 24.0 – 26.6°C (Jobling 1981, based on measurements by Jackson and Price 1949 in Ferguson 1958). Since these measurements are usually conducted in a laboratory setting, smaller-sized individuals (e.g. juveniles or sub-adults) are used, and these results may not necessarily apply to wild populations, with larger adults. Adult Northern Pike have been known to preferentially occupy water temperatures between 16 – 21°C (Pierce et al. 2013) in north temperate lakes, 8 – 18°C in a glacial lake (Neumann et al. 1994), and avoid temperatures above 25°C in impoundments (Headrick and Carline 1993), with larger individuals favouring cooler, deeper waters (Chapman and Mackay 1984; Jacobson 1992). By comparison, adult Muskellunge in a Tennessee reservoir used warmer average water temperatures of 22.1°C (Cole and Bettoli 2014), and lakes with summer surface temperatures between 23°C and 25°C (Miller and Menzel 1986), although water temperature has not been identified as a decisive driver of summer habitat use (Strand 1986; Younk et al. 1996). Only a few field studies have described habitat use of Muskellunge and Northern Pike in sympatry (Inskip 1986) and none of these have included thermal characteristics (Pankhurst et al. 2016) or focused on adult fish (Farrell et al. 2014; Gallagher et al. 2016). It is also notable that no such study has yet been conducted in Georgian Bay for either Muskellunge or Northern Pike during the non-breeding season.

Global climate change is expected to have wide-ranging implications for Great Lakes fisheries, including altered hydrological conditions (e.g. precipitation and lake levels), warmer and more variable water temperatures, and interactions with existing stressors like invasive species and anthropogenic impacts (as reviewed in Collingsworth et al. 2017). Changes to thermal habitat are among the most direct effects on fish, as they rely on surrounding water temperatures to regulate their metabolism. Projected increases in water temperatures (Lofgren 2014; Trumpickas et al. 2015) and changing thermal stratification characteristics (Kling et al. 2003; Lehman 2002; McCormick and Fahnenstiel 1999; Trumpickas et al. 2009) could alter the availability of suitable thermal habitat, particularly during the summer when warming is expected to be greatest (Kling et al. 2003). Effects of global climate change on Great Lakes water levels (Angel and Kunkel 2010) could also exacerbate warming water temperatures through smaller lake volumes and shallower water depths (Trumpickas et al. 2009; Trumpickas et al. 2015), and may be worsened still in embayments protected from the main lake (Bolgrien and Brooks 1992; Murphy et al. 2011). Although warming may be potentially beneficial to certain warm-water species by producing a longer growing season or expanding existing home ranges, there may also be negative impacts to cool-water species by reducing their body size and reducing availability of suitable habitat (Graham and Harrod 2009; Meisner et al. 1987; Jeppesen et al. 2010).

Muskellunge and Northern Pike are ambush predators, and they require protective cover from which to strike out at their prey (Scott and Crossman 1973). Such cover is commonly provided by aquatic vegetation (Casselman and Lewis 1996; Miller and Menzel 1986; Murry and Farrell 2007), which is also likely to be affected by global climate change. An ontogenetic shift to use of deeper submersed aquatic vegetation (SAV) is apparent in both species (Casselman and Lewis 1996; Strand 1986). Water depth and cyclical fluctuations in water levels play an important role in structuring aquatic vegetation communities in coastal marshes, where esocids tend to aggregate (Keddy and Reznicek 1986; Wilcox and Meeker 1991). Recent studies have shown how stable low water levels in Georgian Bay negatively impacted the nearshore SAV community (< 2 m depth; Midwood and Chow-Fraser 2012) that had obvious implications for habitat quality of early life stages of Muskellunge (Leblanc et al. 2014; Smith et al. 2007); however, the interactions between lake levels and bottom morphology that may affect the availability of deeper SAV communities (>2 m) has so far been understudied, and may have implications for how large adult esocids use this habitat during the non-breeding season.

Throughout their range in N. America, protection of spawning and nursery habitat has been identified as management priorities for both species (Casselman and Lewis 1996; Craig and Black 1986; Crane et al. 2015; Farrell et al. 2007), because population declines for both Muskellunge (Dombeck 1986; Kapuscinski et al. 2007; Leblanc et al. 2014; Rust et al. 2002) and Northern Pike (Casselman and Lewis 1996; Cooper et al. 2008; Farrell et al. 2006) have been linked to loss and degradation of these habitats, often due to anthropogenic activities. Since holistic consideration of the effects of climate change on all life stages of esocids is key (Crane et al. 2015), more research is needed to understand aspects of habitat use by adult esocids in the nearshore zone of Georgian Bay.

This paper contributes to the dearth of information on use of thermal habitat by wild populations of Muskellunge and Northern Pike in Georgian Bay. We assembled radio telemetry data collected in three geographically disparate regions of Georgian Bay from 2011 to 2016 to identify and characterize habitat use by adult Muskellunge and Northern Pike during the non-breeding season. We compiled data from two previously published studies carried out in 2011 (Midwood and Chow-Fraser 2015) and in 2012 to 2015 (Weller et al. 2016/CH1) and then added data from an unpublished study completed in 2016. This is the first basin-wide study focused on thermal habitat use by adult esocids in Georgian Bay, and will allow us the rare opportunity to compare their habitat use with laboratory-derived thermal preferenda and maxima. We will focus on thermal habitat use and location of these fish relative to physical structure such as wetland vegetation, shoals, ledges, or docks, and estimate the vulnerability of key habitat features to potential global climate change scenarios, thereby providing important data to help maintain the self-sustaining status of these esocid populations.

Methods

Study Area

We used data collected in three spatially distinct regions along the eastern and northern shoreline of Georgian Bay, Lake Huron, where viable populations of Muskellunge and/or Northern Pike reside (Figure 2.1). This stretch of Georgian Bay shoreline is underlain by Canadian Shield (Weiler 1988) and is characterized by a configuration of small islands and protected embayments that support thousands of high-quality coastal wetlands (Cvetkovic and Chow-Fraser 2011; Midwood et al. 2012). In each region, a telemetry study was carried out in a protected embayment with one or more distinct basins, and that had a permanent hydrologic connection to Georgian Bay proper through a main channel. Each embayment supported at least one basin that was sufficiently deep to thermally stratify during the summer.

The three embayments are located in Tadenac Bay (TAD; Midwood and Chow-Fraser 2015), northern Georgian Bay (NGB; Weller et al. 2016/CH1) and northeastern Georgian Bay (NEGB; Weller et al. 2016/CH1). TAD covers an area ~ 3.5 km^2, is privately owned and managed, and has a minimal human footprint (i.e. two buildings). The club conservatively regulates the Northern Pike fishery, which is open only to a limited number of members at any time. There is a deep northern basin (~ 30 m maximum depth) fringed by coastal wetlands and a shallower southern basin (< 5 m maximum depth) that supports abundant coastal wetlands and submersed aquatic vegetation (Figure 2.1A). NGB (~16.5 km^2)

consists of eastern (~20 m maximum depth) and western basins (~25 m maximum depth) connected by a narrow channel, both basins having a direct connection to Georgian Bay proper (Figure 2.1B). This is a remote area accessible only by boat, and the human footprint is limited to a low number of seasonal cottagers and recreational use. The most human-impacted site is NEGB (6.5 km^2; Figure 2.1C), which has a north (~14 m maximum depth) and a south basin (~10 m maximum depth). The region has a cottage population of 8,000 in the summer months, and has road access along the eastern shoreline. Homes and cottages cover much of the shoreline of which has been associated with eutrophic conditions (Sturgeon Bay; Campbell and Chow-Fraser 2018).

Tagging and Tracking

Although telemetry data have been assembled from two published and one unpublished studies, the same field and tracking protocols were employed. During April and May in 2011 to 2016, we captured esocids using trap-nets and hoop-nets that were deployed overnight in coastal wetlands suspected of being used for spawning. Netting in NGB was supplemented with individuals caught by angling and an additional round of tagging in late September 2012. Only fish weighing more than 1,000 g were considered for tagging, and fish were not tagged if they appeared injured or stressed from the capture event. Using surgical protocols described by Cooke et al. (2003) and Koed et al. (2006), we anesthetized individuals in a bath of 60 ppm clove oil (Xenex Laboratories Inc., Coquitlam, BC, Canada) and surgically implanted transmitters into their body cavities. All fish were implanted with a variant of the Lotek MCFT2 series radio transmitter (Lotek, Newmarket, Canada; 16mm diameter, 46mm length, 16g weight). Tags were programmed to transmit every 5 seconds and had a lifespan of up to 3 years. We deployed identity-only (ID) tags, temperature-sensitive tags (ID/T; 0.6°C intervals), and tags with temperature and pressure sensors (ID/T/P; 1 PSI intervals). After tagging, esocids were held and monitored in a floating pen, and then released them once they fully recovered from the anesthetic.

At least monthly, fish were tracked by boat over a 4 to 10 day period (referred to as the "tracking window"). A SRX600 receiver (Lotek, Newmarket, Canada) equipped with a three-piece Yagi antennae was used in all cases. When a fish was detected, we attempted to maneuver the boat as close to the fish as possible and recorded the coordinates of the tracked location using a handheld GPS device (Garmin Ltd., 3-5m accuracy). Tracking windows in TAD and NEGB typically lasted 5 days while those in NGB lasted 10 days. We tracked along a set path to search the entire embayment to determine which individuals were present. One tracking run was performed each day in NEGB and NGB. In NGB, the eastern and western basins were typically tracked on alternate days due to the size of the study site and travel constraints, but the longer tracking window ultimately yielded similar tracking coverage (i.e. equivalent to 4 to 5 runs for each deep basin in each tracking window). Although a more intensive regime (3 times daily) had been employed in TAD, in this study, we only considered one randomly selected location for each individual per day to keep the effort consistent with the NEGB and NGB data. A full account with details of the fish tracking can be found in Midwood and Chow-Fraser (2015) and Weller et al. (2016/CH1) for TAD and NGB/NEGB, respectively.

Habitat Use

We used two methods to measure water temperature at each esocid location. For the subset of esocids with temperature-sensitive tags, we recorded the temperature measurement directly from the receiver when the location was acquired. Hereafter, we refer to this as "tag temperature". While this is actually a measurement of the internal temperature of the fish, we assumed it to be representative of the surrounding water temperature. For all tracked locations, regardless of tag type, we calculated the mean temperature of the vertical profile at that location. Hereafter, we refer to this as "water column temperature". We used different methods to collect profile measurements in each region. In NGB and NEGB, a temperature and dissolved oxygen profile was collected at or near each tracked location with a multi-parameter sonde (YSI DO200 or 600OMS; Yellow Springs, OH) at meter intervals. The NGB profiles were measured to a maximum depth of 10 m; therefore, we cut off all profiles at a maximum depth of 10 m. In TAD, water temperature data loggers (HOBO Tidbit v2) were deployed at 1 – 2 m depth intervals on buoys placed strategically throughout the embayment. Loggers were deployed throughout the season, encompassing all three tracking windows, and logged at 6-h intervals. The closest water temperature profile, both spatially and temporally, was assigned to each tracked location. Assigned profiles were restricted to the maximum depth of the tracked location, and to a maximum depth of 10 m for consistency with NEGB and NGB. Since profiles did not extend beyond 10 m, mean temperatures of the water column were typically representative of thermal conditions in the well-mixed epilimnia of all three embayments.

For fish equipped with pressure-sensitive tags, we estimated the position of the esocid in the water column by converting the pressure measurement (in pounds per square inch) to water depth (meters below surface). Maximum depth was estimated at each tracked location from a digital elevation model (DEM) of each region. DEMs were constructed in ArcGIS Pro v2.1 (ESRI, Redlands, California) with bathymetric data from the Canadian Hydrographic Service navigational charts and topographic data from the Ontario Contour (OMNR 2009a) and Spot (OMNR 2009b) elevation datasets (Weller and Chow-Fraser 2018/CH5). We collected additional bathymetry data using boat-mounted sonar (Lowrance, Tulsa, Oklahoma) to resolve coverage gaps in TAD and NEGB. The Topo to Raster tool in ArcGIS Pro (based on the ANUDEM program; Hutchinson 1989) was used to build the DEM for each region with a 5-m resolution. We determined water depths relative to the mean summer lake level during the tracking year (i.e. mean of June - August monthly lake levels). DEM depths were not necessarily indicative of the actual position of the fish in the water column at each location, but we inferred that an esocid used or had access to cooler water based on its presence over water deep enough to stratify.

As an alternative measure of access to cooler waters, we estimated the distance that an esocid would have to swim to reach waters deep enough to stratify (i.e. distance to metalimnion). Based on the thermal profile obtained at the deepest point in each embayment during July, we determined the lower boundary of the epilimnion for each region. The Least Cost Path tool in ArcGIS Pro was used to determine the shortest two-dimensional distance from each esocid location to a depth at or below the epilimnion.

Habitat Vulnerability

Based on our observations of habitat use, we estimated the response of key habitat features under a range of possible lake level and warming scenarios to determine which scenarios may result in compression of habitat below the epilimnion, which we will refer to as "thermal refuge", measured both in terms of volume and area below the epilimnion in each embayment. We assumed that this zone of cooler waters will provide esocids an opportunity to regulate their body temperature and metabolism should the epilimnetic temperatures become too warm for them. Assuming relatively stable stratification characteristics year-to-year (i.e. similar depth of thermal strata), the lower boundary of the epilimnion will vary according to surface elevations. Since a warming climate may cause the thermocline to deepen, we simulated how an expansion of the epilimnion might move the lower boundary of the epilimnion from 174.0 m (IGLD85) to 164.0 m, representing an extremely high-water scenario (lake level = 178.0 m) with a relatively thin epilimnion (4 m) and an extremely low-water scenario (174.0 m) with a thick epilimnetic layer of 10 m. We calculated the relative change in volume and surface area of the thermal refuge in each region during the July tracking window (i.e. considering unique lake level and epilimnetic thickness).

We also estimated potential changes in availability of physical habitat structure. Since both Muskellunge and Northern Pike are ambush predators, they often rely on physical habitat structure such as SAV, which in Georgian Bay can grow to depths up to 5 m (Midwood 2012). We considered the surface 5 m of each embayment as potential SAV habitat, and measured the amount (volume and surface area) of this habitat corresponding to lake elevations from 174.0 m to 178.0 m at meter intervals.

Results

Tagging and Tracking

There were 37 tagged esocids with sufficient tracked locations during the summer months to be included in this study (Table 2.1). They consisted of 6 Northern Pike in TAD, 19 esocids in NGB (12 Muskellunge, 7 Northern Pike), and 12 esocids in NEGB (9 Muskellunge, 3 Northern Pike). All individuals were tagged during the tracking year or the previous year. A total of 358 esocid locations were collected during the summer months. Tagged Muskellunge were on average larger (total length: $\bar{x}$ ± SE; 1,136 mm ± 25) than Northern Pike (735 mm ± 36) across the entire study population and within each region where both species were tagged (Figure 2.2). We excluded one Northern Pike (NGB_9_P) from subsequent analyses because its use of water depths were determined statistically to be outliers relative to the other Northern Pike included in this study (i.e. 4 of 7 locations were outliers).

Habitat Use

Maximum water depths at tracked locations showed that Muskellunge were found in significantly deeper water ($\bar{x}$ ± SE; 7.3 m ± 0.4) than Northern Pike (2.5 m ± 0.1) across all regions and in all months (Figure 2.3), and Muskellunge were found in a much greater range of maximum water depths (0.5 – 25.4 m) than Northern Pike (0.4 – 6.1 m). Both species were found in the deepest water in July, except for Northern Pike in NEGB that were in slightly deeper water in August (3.4 m ± 0.5 vs 3.0 m ± 0.4). Maximum water depth at Northern Pike locations corresponded with the typical lakeward edge of coastal wetlands that supported SAV (i.e. < 5m), whereas Muskellunge were typically found in or near water deep enough to stratify (i.e. > 10 m).

Even though tracking in each region occurred in different years, the general trends in thermal conditions were consistent across all three study regions. Surface water temperatures warmed rapidly through June, before peaking in July, and then began to cool in August (Table 2.2). The warmest conditions occurred in TAD during 2011, while conditions in NGB and NEGB were 1-2°C cooler during 2013 and 2016, respectively. Thermal strata developed throughout June and were well-established by the July tracking window. In NEGB and TAD, the epilimnion occupied the top 6 m of the water column during July. Hypoxic conditions (i.e. [dissolved oxygen] < 4 mg/L) developed in the hypolimnion in NEGB by mid-June and persisted throughout the summer. The epilimetic depth in NGB differed between the western and eastern basins (4 m and 6 m, respectively). Water column temperatures at tracked locations followed the same trends observed in the surface water temperatures, and were typically representative of thermal conditions in the epilimnion in each region during the tracking window (Figure 2.4). From these measurements we found little evidence of esocids using habitat below the epilimnion, but Muskellunge were found to be using cooler waters than Northern Pike.

Primary use of habitat in the epilimnion was evident in measurements from temperature- and pressure-sensitive tags. Water column positions confirmed that both species of esocid were almost exclusively using habitats above the thermocline (Figure 2.5); only a subset of esocids tagged in NGB had pressure-sensitive tags. Northern Pike were primarily found in the surface 2 m whereas Muskellunge averaged 3.3 m (± 0.4) and 4.7 m (± 0.6) in June and August, respectively. These water column positions roughly aligned with the bottom of the epilimnion in the respective tracking windows. The deepest estimate of a Muskellunge position in the water column was 12.0 m in the western basin of NGB in July, with a corresponding tag-temperature of 18.0°C. The metalimnion in that basin was very thick in July (4 – 20 m) with the thermocline estimated at 10 m. This was the deepest position of a Muskellunge in the water column indicated by the pressure-sensitive tags; however, NGB_9_P, which had been excluded from this study, was found on three occasions at this depth or in deeper water. Tag temperatures confirmed that esocids were using habitat primarily in the epilimnion and that Muskellunge were using cooler waters than Northern Pike (Figure 2.6).

Spatial analyses of the tracked locations clearly showed that the Northern Pike in all three regions were almost exclusively using coastal wetlands or adjacent areas that were shallow enough to support stands of SAV (i.e. < 5 m). In contrast, Muskellunge appeared to be clustering around the deeper areas in each basin. This is most evident in NGB, where Muskellunge locations in both the western and eastern basin essentially followed the perimeter of the deepest point in each basin, whereas Northern Pike locations, which are mostly in the western basin are in or near coastal wetlands and set back from the deeper areas occupied the Muskellunge. Habitat use by Northern Pike appeared to be driven primarily by the presence of SAV; in contrast, Muskellunge appeared to use habitat with relatively easy access to cooler waters. Muskellunge locations were on average 54 m (± 8) from the metalimnion compared to 551 m (± 51) for Northern Pike (Figure 2.7). Some Northern Pike locations were quite close to deeper waters, but these were shallow areas supporting SAV near the perimeter of the deeper areas.

Majority of Muskellunge locations have clear associations with physical structures that could provide cover while they are foraging. In NGB these were generally the lakeward edges of stands of SAV, similar to observed habitat use by

Northern Pike, and ledges or steeply-sloping sides of basins. In NEGB we observed similar use of SAV and steep slopes, in addition to underwater mounds, as well as frequent use of docks.

Habitat Vulnerability

Each embayment contained some thermal refuge during the tracking study (Figure 2.8). In TAD, the entire southern basin was less than 6 m deep, and therefore only the main basin supported thermal refuge ($8.52 \cdot 10^5$ m^2, $8.34 \cdot 10^6$ m^3) during the tracking year (2011). Under the most extreme scenario (i.e. thickest epilimnion), thermal refuge persisted in the main basin but declined in area (38.50%) and volume (49.58%). Similarly, the thermal refuge persisted in NGB in both the eastern and western basins, although the most extreme scenario would result in a much greater percentage loss of thermal refuge area (74.65%) and volume (73.16%) relative to the tracking year (2013). This loss, however, may not be a serious limitation because the thermal refuge in this region is much larger in area ($5.75 \cdot 10^5$ m^2) and in volume ($2.91 \cdot 10^7$ m^3). NEGB would experience the most dramatic losses in thermal refuge relative to the tracking year (2016; $2.06 \cdot 10^6$ m^2 in area; $5.30 \cdot 10^6$ m^3 in volume). Extending the bottom boundary of the epilimnion by 2 m would result in losses of over 50% of area and volume in thermal refuge, and nearly all of it would be lost under the most extreme scenario considered. During the summer season in the tracking year, the hypolimnion was hypoxic or anoxic, and we would expect these conditions to persist. Under the most extreme scenario, only a narrow band in the metalimnion would essentially be available as thermal refuge.

Lake level declines in all three regions were predicted to result in losses of potential SAV habitat (Figure 2.9). Declines were most dramatic in TAD, where losses of over 50% of the habitat, by area and volume, was expected under a lake level of 174.0 m. This was primarily attributed to the shallow southern basin in TAD which was considered completely SAV habitat during the tracking year. Declines in SAV habitat were predicted in NGB and NEGB but were less dramatic, with reductions of only approximately 30% by area and volume, due to the steeply sloping nature of the nearshore zone.

Discussion

Our observations of thermal habitat use by esocids did not indicate any clear selection or preferences based on water temperatures; both Muskellunge and Northern Pike almost exclusively used habitat within the epilimnion in all three embayments. Even during the warmest summer conditions, water temperatures ranging from 15 to 25°C were readily available in each region. NEGB could be distinguished from the other two because of the hypoxic or anoxic hypolimnion throughout the summer; however sufficiently well-oxygenated water was available in the metalimnion (between approximately 6 to 9 m depth) that was several degrees cooler than temperatures in the epilimnion (e.g. 20°C vs 23°C).

Surface temperatures in all regions peaked near 25°C; however, in TAD, temperatures approached 27.5°C during a 2 week period, although fish continued to use these warm habitats.

The upper incipient lethal limits for Muskellunge and Northern Pike have been measured at 32.2°C and 29.4°C, respectively (Scott and Crossman 1973). Northern Pike have shown avoidance of temperatures as high as 23°C (Casselman 1978, cited in Wismer and Christie 1987) and 25°C (Headrick and Carline 1993), and Muskellunge have been documented in water at least 27°C (Cole and Bettoli 2014; Dombeck 1979). The range of water temperatures used by esocids in this study, particularly during July and August (Muskellunge: 20.4 – 24.8°C, Northern Pike: 21.5 – 27.5°C) are consistent with field observations in similar studies (e.g. Cole and Bettoli 2014; Miller and Menzel 1986; Pierce et al. 2013; Headrick and Carline 1993; Strand 1986). Northern Pike have lower thermal tolerances than Muskellunge and a more northerly distribution so we would expect to find Pike using cooler waters than Muskellunge. However, we found Muskellunge using cooler water than Northern Pike, appearing to use or maintain close proximity to deeper water (Figure 2.7), yet we have little evidence indicating that habitats in the metalimnion or hypolimnion were being used based on water column positions (Figure 2.6). Most of our tagged Muskellunge were large individuals (> 950 mm), so the use of slightly cooler, deeper water is consistent with the expected ontogenetic shift in habitat use, similar to that observed in large Northern Pike (Pierce et al. 2013). However, these large Muskellunge typically had obvious associations with physical structure (e.g. SAV, shoals) so it unclear if thermal conditions are considered in this habitat use or simply associated with suitable physical habitat features.

We found physical habitat structure to be the primary driver of esocid habitat use, with nearly all of the tracked locations clearly associated with some form of physical structure. Northern Pike in all regions were in water depths and locations known to support SAV or other aquatic vegetation, even in water temperatures above 25°C. The use of aquatic vegetation by adult Northern Pike has been incredibly well-established (e.g. Scott and Crossman 1973; Casselman and Lewis 1996; Craig 2008) so this result was expected. We found similarly strong associations with physical structure from Muskellunge, but they were found exploiting a greater variety of structural types. As with Northern Pike, we saw Muskellunge associated with SAV, although further offshore in deeper water. Deep stands of SAV and macrophyte-open water interfaces are commonly used Muskellunge habitat (Miller and Menzel 1986; Scott and Crossman; Strand 1986), as are morphological features on the basin floor like sharp changes in bottom contours (Miller and Menzel 1986; Strand 1986). This was most evident in NGB where Muskellunge appeared to use the steeply-sloping basin contours around the deep area in each basin; they appeared to essentially be ringing the perimeter of the deep areas. In contrast, the deep area in the north basin of NEGB was surrounded by more gradually sloping basin morphology and the association with its perimeter was less obvious, and we observed frequent use of nearby man-made structures, namely docks.

We did see clear differentiation in habitat use between species in regions where both were tagged and tracked. Muskellunge used cooler (Figures 2.4, 2.6) and deeper waters than Northern Pike (Figures 2.3, 2.5). Despite the Muskellunge's higher thermal preferences (Scott and Crossman 1973; Jobling 1981), these differences were attributed to the size differences between the tagged esocids. Tagged Muskellunge were significantly larger than Northern Pike included in this study (Figure 2.2), and the different habitat use is consistent with ontogenetic shifts expected in esocids (e.g. Casselman and Lewis 1996; Chapman and Mackay 1984). We did not assume this to be necessarily indicative of a species-dependent difference in habitat use based on available movement and habitat use data from several esocids that we tagged but were not resident in our embayments during the summer. For example, a large Northern Pike (total length = 990 mm) tagged in NEGB left the embayment by early summer and was harvested by an angler 30 km away, in roughly 4 m of water. The use of deeper, cooler habitats by the larger Muskellunge relative to the smaller Northern Pike produced a clear spatial segregation between species with little overlap in habitat use. It is unclear if the lack of large, resident Northern Pike in the embayment during the summer, could be a result of competition with large Muskellunge. Multiple adult muskellunge occupy overlapping summer home ranges that encompass the habitat types considered suitable for large individuals of either species. While we did not see any interspecific competition between Muskellunge and Northern Pike, we did note what appeared to be competition between Muskellunge for a specific habitat feature. In NEGB, a mound rising out of deep water (> 10 m) with a stand of SAV vegetation (3 - 4 m deep) was a commonly used spot by multiple Muskellunge. We found three different Muskellunge using that exact spot over three consecutive days in July, with a progressively larger fish there each day, possibly displacing the smaller individual there previously.

One the goals of this study was to assess the vulnerability of adult esocid habitat to potential impacts of global climate change. Thermal conditions in our study embayments do not currently appear to be limiting, and fall within the range of water temperatures used by esocids elsewhere (e.g. Cole and Bettoli 2014; Pierce et al. 2013; Strand 1986). However, the summer lake surface temperatures peaked at approximately 25°C and water temperatures at some shallow esocid locations approached 28°C. Trumpickas et al. (2009) have predicted surface temperature increases in Lake Huron of up to 3.6°C by the end of the century, depending on the emission scenario considered. Under these conditions, shallow water habitats used primarily by Northern Pike would be approaching dangerous temperatures (e.g. upper incipient lethal limit = 29.4°C). Muskellunge may be less affected such warming since they were observed using cooler, deeper waters in this study and are a warmer-water species than Northern Pike. Muskellunge can be highly mobile and (e.g. Crossman 1977; Lapan et al. 1996; Strand 1986), as can Northern Pike (30 km + movements; Chow-Fraser unpub.), so the capability to seek out more appropriate thermal habitat exists if conditions become too warm. However, some level of summer home range fidelity has been documented in esocids (Kobler et al. 2008) so it remains to be seen if these individuals would abandon their embayments.

Some water level projections in the Great Lakes have called for extreme declines (e.g. Angel and Kunkel 2010; Lofgren et al. 2002), however more recent modelling efforts have suggested that more modest declines in lake level are expected (Lofgren and Rouhana 2016). These more recent results are consistent with predictions based on historic, periodic lake level fluctuations (Lu and Nairn, in submission). With a lake level drop in Georgian Bay to 175.0 m (approximately 1 m below record), esocid habitat in Georgian Bay embayments should persist. The steeply sloping nearshore of NEGB and NGB is representative of much of the Georgian Bay shoreline and does not allow for drastic changes in the potential SAV zone. TAD, with its large, shallow southern basin, has the most SAV habitat to lose under lower lake levels but will continue to support suitable SAV habitat under any likely lake level scenarios. Similarly, lake level declines are not expected to lead to major losses in cooler water habitats, as long as there are sufficiently deep areas in each embayment where cooler water can persist. The combination of warmer and lower water could result in habitat loss in shallower embayments, like the north basin of NEGB.

Ultimately, anthropogenic impacts appear to be a more immediate threat to esocid habitat in Georgian Bay embayments. Georgian Bay as a whole is oligotrophic (Weiler 1988), but some protected embayments can become more productive if basin morphometry and shoreline configurations limit mixing with the main bay. Campbell and Chow-Fraser (2018) found that Sturgeon Bay (i.e. NEGB in this study) was oligotrophic due to a high density human footprint along the shoreline and limited mixing with Georgian Bay. This is consistent with the hypoxic conditions that we observed during this study and nuisance algal blooms that have occurred in recent years (Gartner Lee Limited 2008). Interactions between anthropogenic stressors and impacts of global climate change (lake level, warming, intensity and frequency of precipitation; reviewed in Collingsworth et al. 2017) are likely a greater concern than a direct loss of suitable thermal habitat for adult esocids. This is somewhat encouraging as it presents a more achievable goal for managers; limiting further development along embayment shorelines and remediating existing issues, like nutrient leaching from septic systems (Dillon et al. 1994). In contrast, actions to directly address warming temperatures and Great Lakes water levels are beyond the scope of most management agencies. Protected embayments in Georgian Bay should continue to support suitable habitat, providing coastal wetlands and abundant SAV in addition to water deep enough to stratify and provide access to cooler water for larger esocids. We consider vulnerable habitat to be embayments experiencing significant human development, particularly those with shallower depths that do not support cooler water habitat or may lose that habitat under future climate scenarios. Spatial modelling and evaluation tools to assess the amount (Weller and Chow-Fraser/CH3) and resilience (Weller and Chow-Fraser/CH5) of coastal wetlands, and trophic response of embayments (Campbell and Chow-Fraser 2018) would be well suited to identifying vulnerable habitats.

Acknowledgements

We are grateful for our many hosts who provided us accommodations and support: Mary Muter, Harvey and Lorna Meirke, Bill and Freda Klassen, Jerry Burke, Diana and Roy Schatz, Mark Trudeau and the Tadenac Club, Arunas Liskauskas and the staff of the Upper Great Lakes Management Unit. This project was funded in part by scholarships to JPL (Ontario Graduate Scholarship and Muskies Canada Inc.) and to JDW (NSERC Canada Graduate Scholarships-Master's, Ontario Graduate Scholarship, and Muskies Canada Inc), the Ontario Ministry of Natural Resources and Forestry through the Canada-Ontario Agreement, and in partnership with the Georgian Bay Musky Association. With regards to the DEM developed for this project, it was produced by McMaster University based on Canadian Hydrographic Service charts and/or data, pursuant to CHS Direct User Licence No. 2016-1121-1260-M. The incorporation of data sourced from CHS in this product shall not be construed as constituting an endorsement by CHS of this project. This product does not meet the requirements of the *Charts and Nautical Publications Regulations, 1995* under the *Canadian Shipping Act, 2001*. Official charts and publications, corrected and up-to-date, must be used to meet the requirements of those regulations.

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Table 2.1: Tracking and biological information of each esocid included in this study. Region of capture (TAD = Tadenac Bay, NGB = northern Georgian Bay, NEGB = northeastern Georgian Bay), species of tagged escoid (Muskellunge = M, Northern Pike = P), radio tag ID all contribute to a unique identification code for each individual (Fish ID). Weight and total length were measured at capture and "# of locations" is the total number of locations for each fish collected between June and August of the tracking year.

Region	Species	Tag ID	Fish ID	Tag Type	Sex	Weight (g)	Length (mm)	# of locations
TAD	P	11	TAD_11_P	ID	M	1540	632	16
TAD	P	12	TAD_12_P	ID	M	1150	583	11
TAD	P	13	TAD_13_P	ID	F	6930	962	11
TAD	P	15	TAD_15_P	ID	M	1170	563	17
TAD	P	18	TAD_18_P	ID	F	5200	913	3
TAD	P	20	TAD_20_P	ID	M	1520	620	14
NGB	M	2	NGB_2_M	ID/T/P	F	11400	1226	9
NGB	M	3	NGB_3_M	ID/T/P	F	9800	1010	11
NGB	M	4	NGB_4_M	ID/T/P	F	12600	1180	5
NGB	M	5	NGB_5_M	ID/T/P	M	8400	1000	11
NGB	M	6	NGB_6_M	ID/T/P	F	12800	1080	3
NGB	M	8	NGB_8_M	ID/T/P	M	5200	963	6
NGB	M	10	NGB_10_M	ID/T/P	M	9800	1060	8
NGB	M	11	NGB_11_M	ID/T/P	M	6800	975	6
NGB	M	18	NGB_18_M	ID/T/P	F	17300	1320	14
NGB	M	19	NGB_19_M	ID/T/P	M	6800	1030	12
NGB	M	20	NGB_20_M	ID/T/P	M	7000	1000	11
NGB	M	22	NGB_22_M	ID/T/P	M	11000	1160	12
NGB	P	9	NGB_9_P	ID/T/P	F	1800	750	9
NGB	P	11	NGB_11_P	ID	F	1700	650	7
NGB	P	12	NGB_12_P	ID/T	F	4600	830	13
NGB	P	13	NGB_13_P	ID/T	F	1300	620	12
NGB	P	16	NGB_16_P	ID/T/P	F	2000	670	13
NGB	P	17	NGB_17_P	ID/T	F	1800	605	7
NGB	P	21	NGB_21_P	ID/T	F	1800	680	12
NEGB	M	42	NEGB_42_M	ID	F	15800	1148	6
NEGB	M	44	NEGB_44_M	ID	M	11300	1105	10
NEGB	M	45	NEGB_45_M	ID	M	10800	1155	9
NEGB	M	46	NEGB_46_M	ID	F	14800	1249	7
NEGB	M	52	NEGB_52_M	ID	F	17300	1338	10
NEGB	M	54	NEGB_54_M	ID	F	16500	1296	9

NEGB	M	56	NEGB_56_M	ID	M	13500	1151	10
NEGB	M	58	NEGB_58_M	ID	M	15300	1205	8
NEGB	M	60	NEGB_60_M	ID	F	14800	1215	10
NEGB	P	20	NEGB_20_P	ID/T	M	3250	784	12
NEGB	P	36	NEGB_36_P	ID/T	M	7250	1010	7
NEGB	P	37	NEGB_37_P	ID/T	M	4250	880	7

Table 2.2: General thermal conditions in each region during monthly esocid tracking. Surface water temperature measurements were taken within the top meter of the water column at the deepest location in the embayment. Air temperatures were the daily maxima from the weather station at Parry Sound, ON operated by Environment and Climate Change Canada. Presented temperatures (°C) are means of daily measurements during the tracking window.

Tracking Window	TAD (2011)		NGB (2013)		NEGB (2016)	
	Surface	Air	Surface	Air	Surface	Air
June	21.1	20.8	19.0	22.1	19.2	23.6
July	26.4	27.8	24.1	25.3	23.9	25.0
August	24.4	27.4	23.4	25.8	23.7	24.6

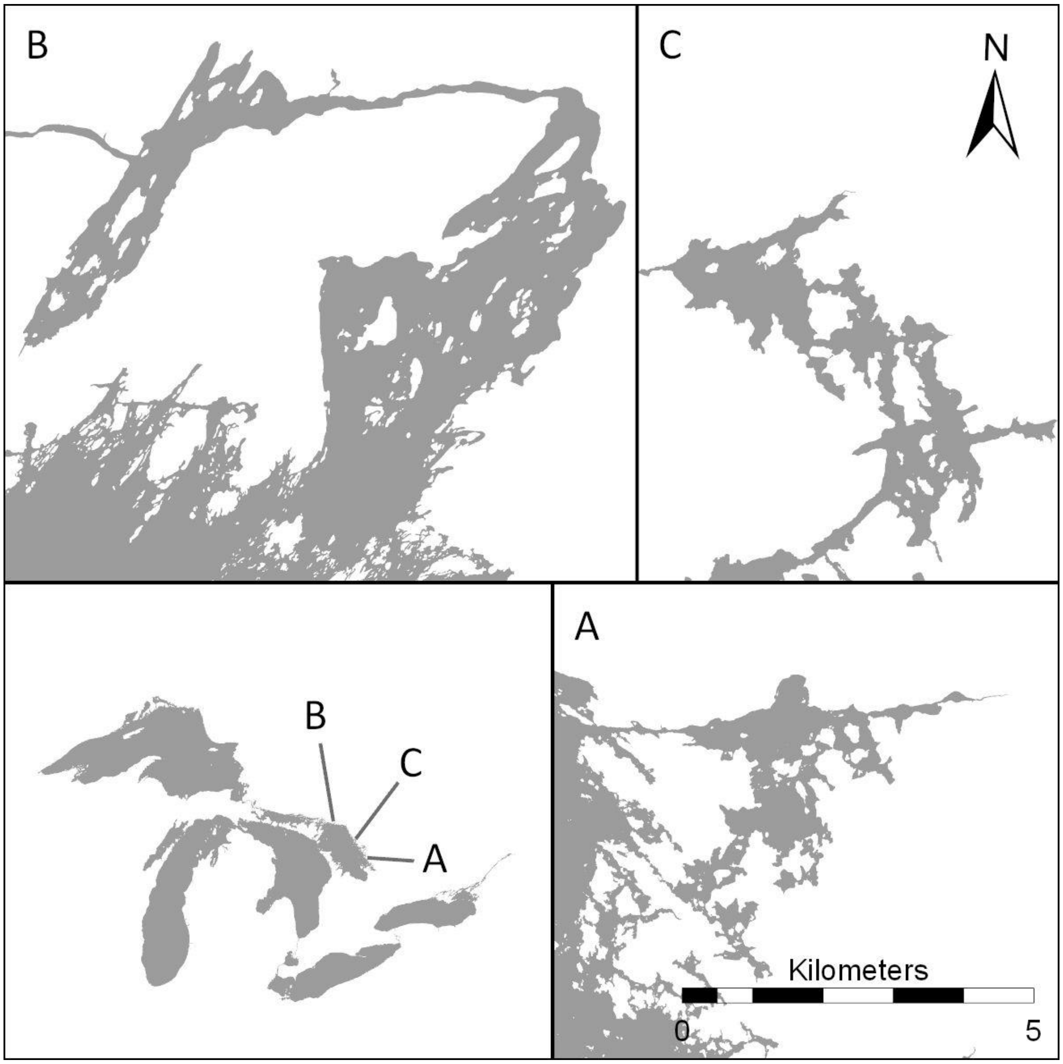

Figure 2.1: Location of each embayments in Georgian Bay where esocids were tracked (Great Lakes inset). Tadenac Bay (TAD) = A, northern Georgian Bay (NGB) = B, northeastern Georgian Bay (NEGB) = C.

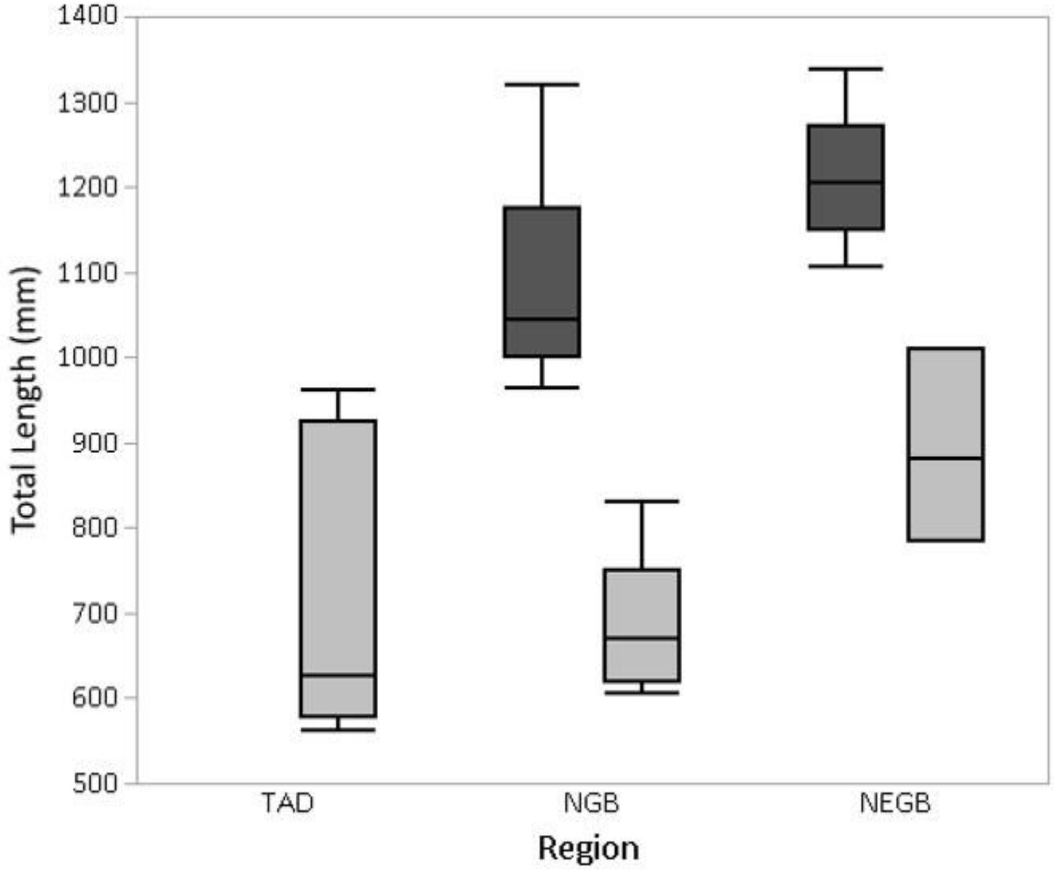

Figure 2.2: Comparison of length at capture (mm) of Muskellunge (dark gray) and Northern Pike (light gray) tagged and tracked in this study by region (TAD = Tadenac Bay, NGB = northern Georgian Bay, NEGB = northeastern Georgian Bay). Boxes show the median and interquartile range, whiskers are 1.5 x interquartile range. Length was used for size comparison instead of weight since most fish were tagged during spawning season, and weights could be biased by egg mass.

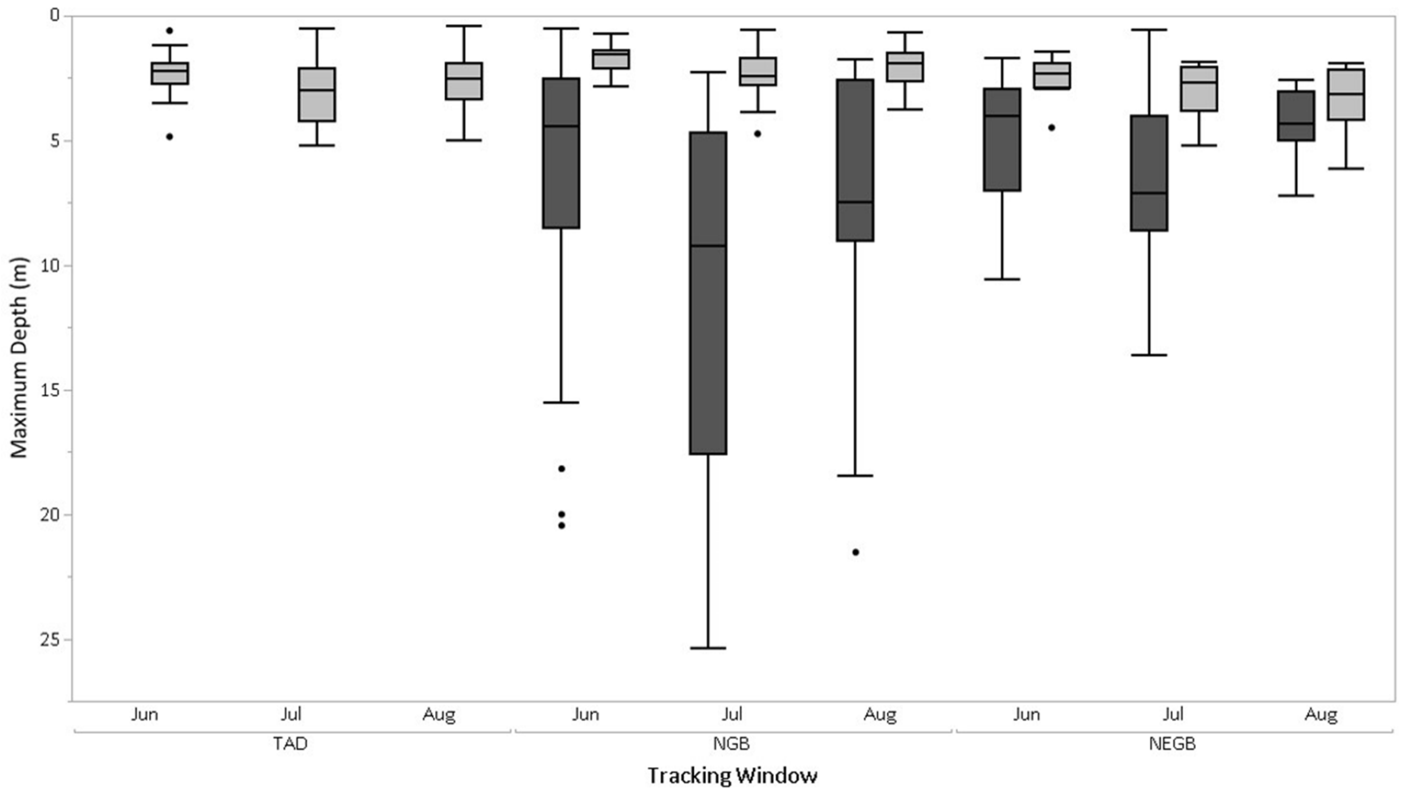

Figure 2.3: Maximum water depth at tracked Muskellunge (dark gray) and Northern Pike (light gray) locations collected during the monthly tracking window in each region (TAD = Tadenac Bay, NGB = northern Georgian Bay, NEGB = northeastern Georgian Bay). Tracking in each region was carried out in summer of different years (TAD = 2011, NGB = 2013, NEGB = 2016). Water depth was determined from a digital elevation model of each region. Boxes show the median and interquartile range, whiskers are 1.5 x interquartile range.

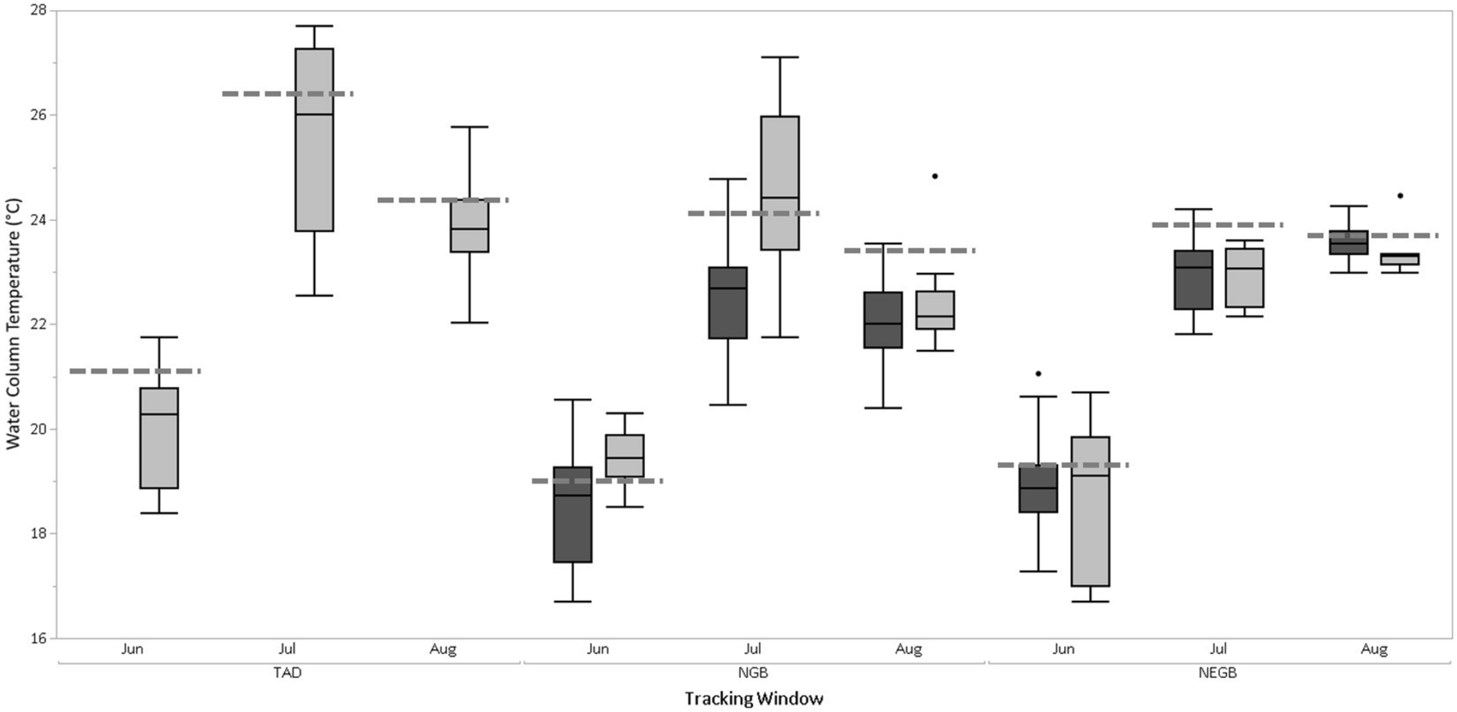

Figure 2.4: Water column temperature for tracked Muskellunge (dark gray) and Northern Pike (light gray) collected during the monthly tracking window in each region (TAD = Tadenac Bay, NGB = northern Georgian Bay, NEGB = northeastern Georgian Bay). Tracking in each region was carried out in summer of different years (TAD = 2011, NGB = 2013, NEGB = 2016). To approximate the temperature of habitat used, we calculated the mean temperature of the water column occupied by an esocid to a maximum depth of 10 m. Boxes show median and interquartile range, while whiskers are 1.5 x interquartile range. Dashed lines correspond to mean surface water temperature measured at the deepest area in each embayment.

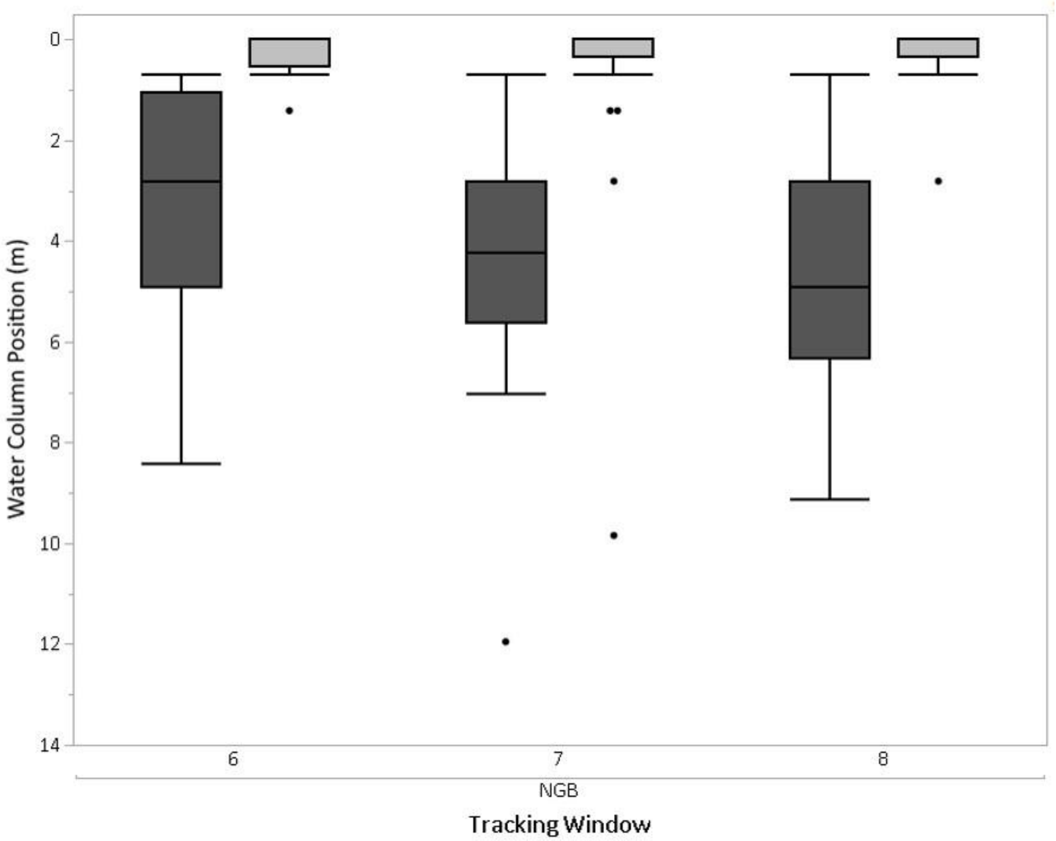

Figure 2.5: Estimated depth of Muskellunge (dark gray) and Northern Pike (light gray) in the water column from pressure-sensitive radio tags implanted in the body cavity. Pressure measurements were collected during monthly tracking windows in northern Georgian Bay (NGB). Only a subset of fish tagged in this study (14/37) were implanted with temperature sensitive tags. Boxes show median and interquartile range, while whiskers are 1.5 x interquartile range.

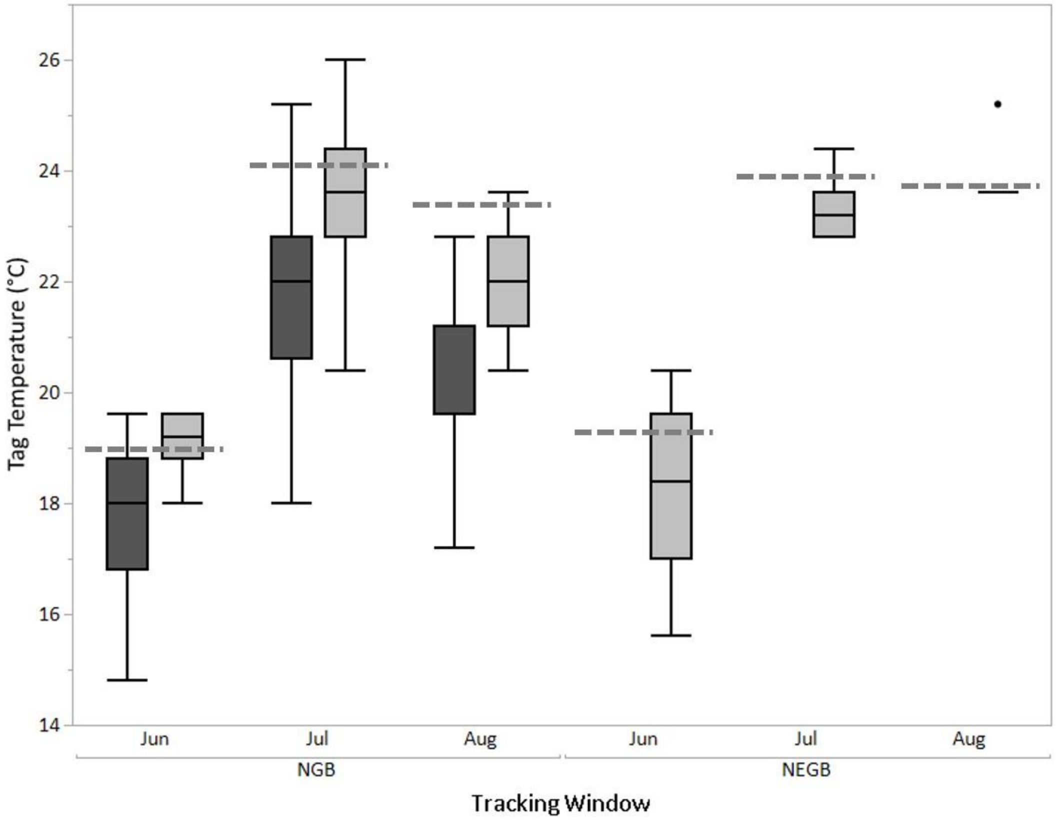

Figure 2.6: Temperature of Muskellunge (dark gray) and Northern Pike (light gray) from temperature-sensitive radio tags implanted in the body cavity. Temperatures were collected during monthly tracking windows in northern (NGB) and northeastern Georgian Bay (NEGB). Only a subset of fish tagged in this study (21/37) were implanted with temperature sensitive tags. Boxes show median and interquartile range, while whiskers are 1.5 x interquartile range. Dashed lines correspond to mean surface water temperature measured at the deepest area in each embayment.

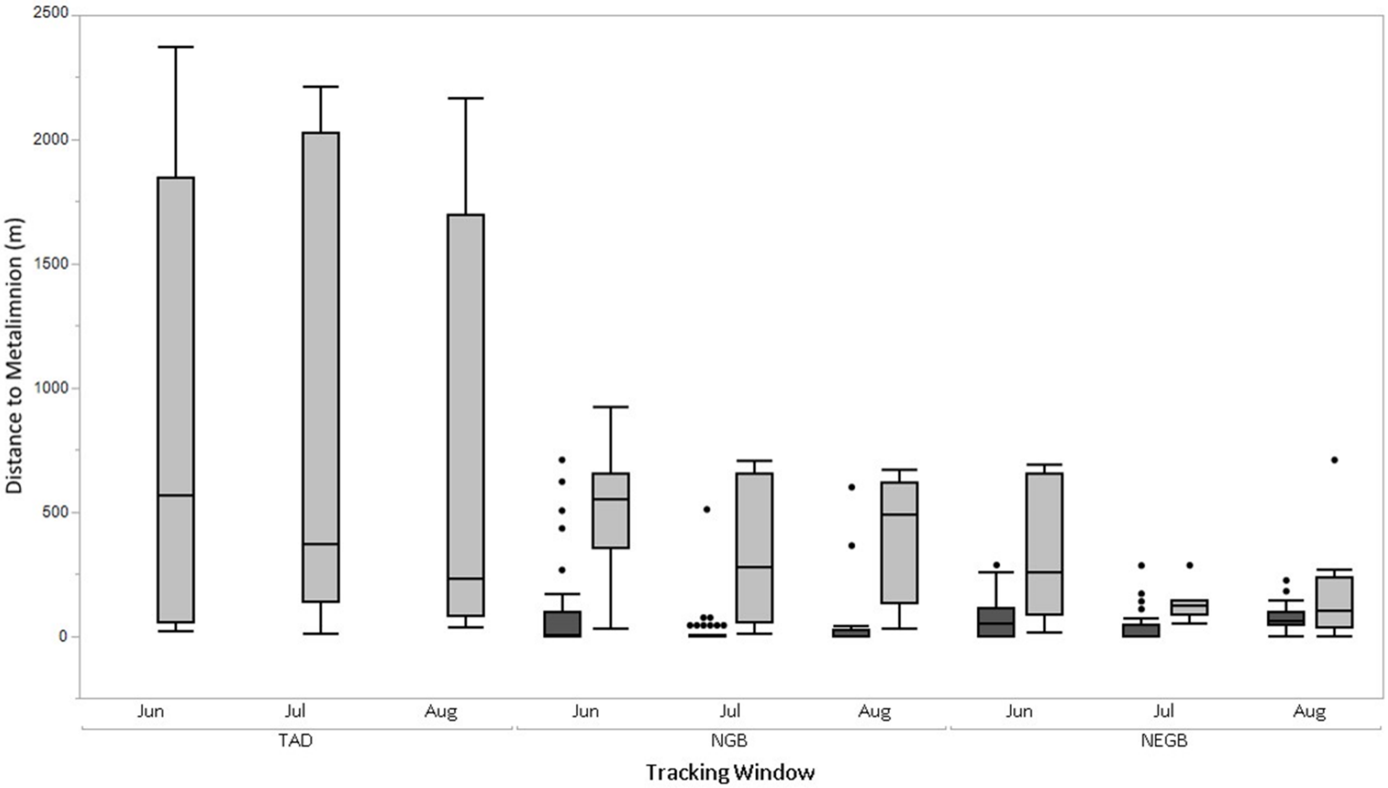

Figure 2.7: Two-dimensional distance between an esocid location (Muskellunge = dark gray, Northern Pike = light gray) to the upper boundary of the metalimnion. We use this to infer ease of access to cooler-water (i.e. deeper) habitat from each esocid location. Upper boundary of the metalimnion was estimated from water temperature profiles collected at the deepest location in the basin in July of the tracking year. Boxes show median and interquartile range, while whiskers are 1.5 x interquartile range.

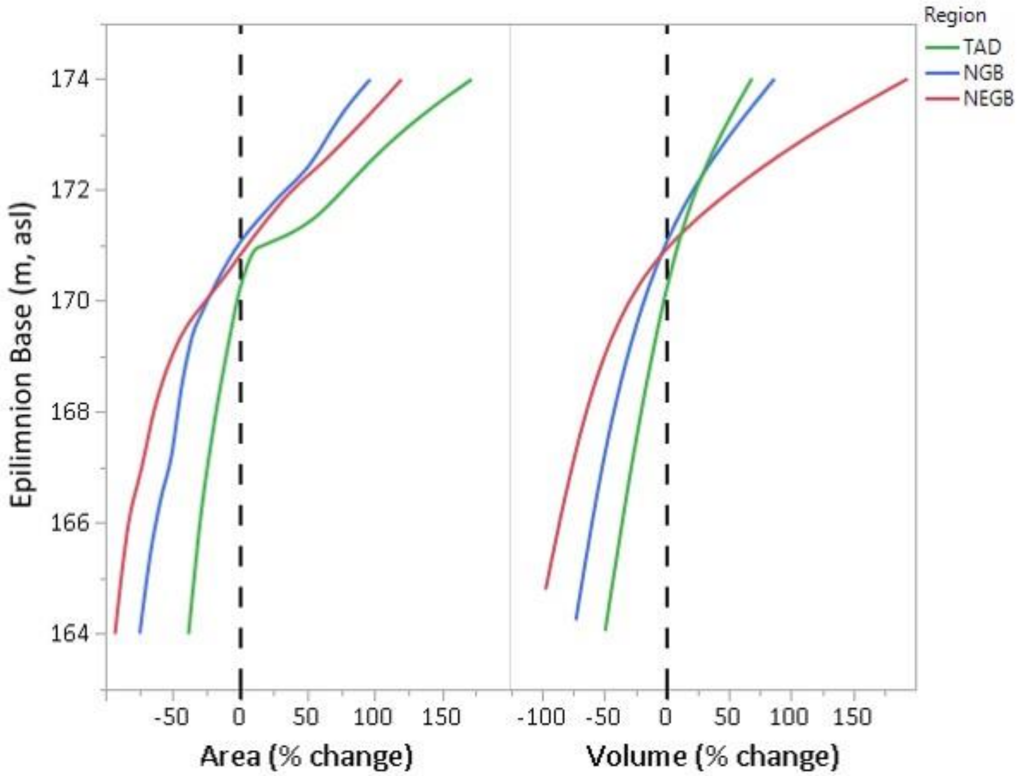

Figure 2.8: Change in availability of cool-water habitat in three embayments in Georgian Bay (TAD = Tadenac Bay, NGB = northern Georgian Bay, NEGB = northeastern Georgian Bay). Cool-water habitat was defined as total area and volume of water below the epilimnion in each embayment. Percentage change is relative to amount of habitat available during the July tracking window in each region.

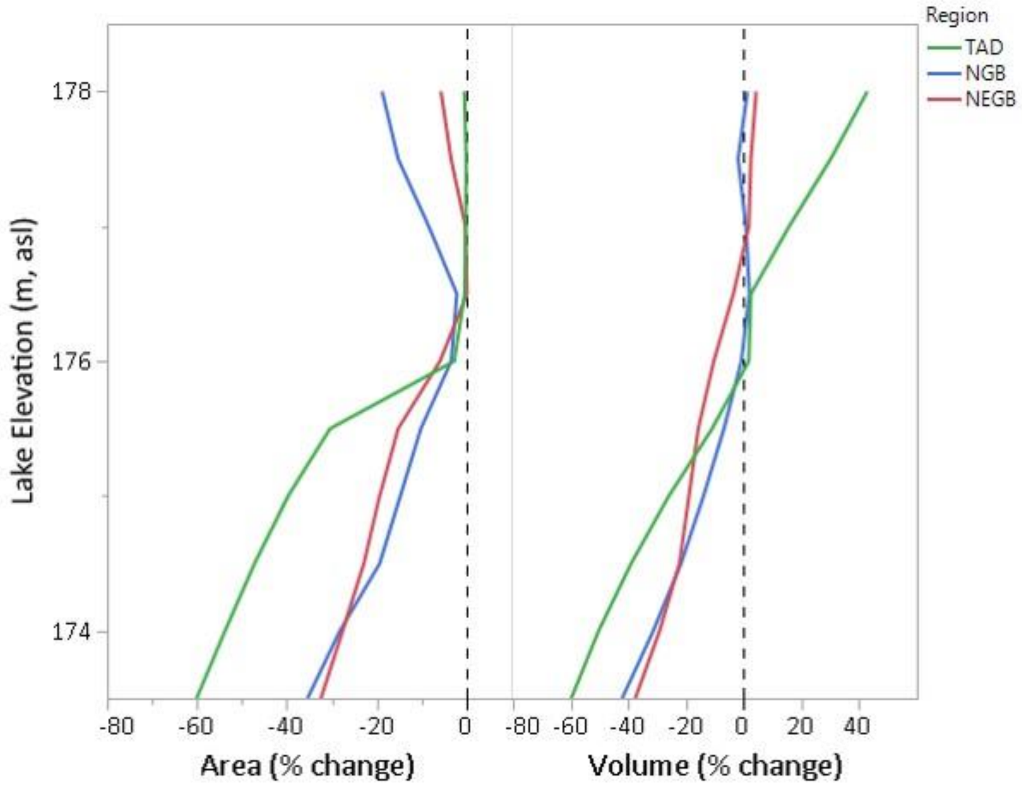

Figure 2.9: Predicted change in availability of SAV habitat as a function of changing lake levels in three embayments (TAD = Tadenac Bay, NGB = northern Georgian Bay, NEGB = northeastern Georgian Bay). We assumed that SAV would be able to grow in water up to a maximum depth of 5 m. Area and volume of the SAV zone was measured from DEMs to estimate the amount of potential SAV habitat under a range of possible lake levels.

Chapter 3

HYDROGEOMORPHIC MODELLING OF LOW-MARSH HABITAT IN COASTAL GEORGIAN BAY, LAKE HURON

In submission: Weller JD, Chow-Fraser P (2018/CH3) Hydrogeomorphic modelling of low-marsh habitat in coastal Georgian Bay, Lake Huron. Submitted to Wetlands Ecology and Management, submission ID: WETL-D-18-00080 (Chapter 3)

Abstract

Potential impacts of global climate change on the amount of low-marsh habitat in coastal wetlands of the Great Lakes are unknown, which has important implications for the Great Lakes fish community that use such habitat. We developed a generalized linear model that uses only hydrogeomorphic (HGM) features and lake elevations to predict the extent of low marsh in coastal wetlands of eastern and northern Georgian Bay. The McMaster Coastal Wetland Inventory was used as a reference dataset to train the model, while best available data were assembled to create a digital elevation model that was used to derive all HGM features at a lake elevation of 176.17 m (IGLD 1985). The best predictive model included depth, slope, and exposure as HGM variables, yielding an area under the curve (AUC) score of 0.83. We classified the model output into low-marsh and open-water habitat using a threshold value identified by maximizing the true skill statistic. The classified model output had sensitivity and specificity scores of 0.80 and 0.75, respectively, and correctly identified 81% of the low-marsh units present in the reference dataset with an average 60% areal overlap between the model prediction and reference dataset. We applied the model to two external datasets to check model performance, and found the lowest AUC to be 0.79, with associated sensitivity and specificity scores of 0.65 and 0.77, respectively. Applying this model with future water-level scenarios, should provide a cost-effective alternative for forecasting changes in the amount of low marsh-habitat in Georgian Bay.

Introduction

Coastal wetlands in the Laurentian Great Lakes are a valuable habitat type that can support impressive biodiversity and provide important ecosystem services (Brazner et al. 2001; Costanza et al. 1997; Environment Canada 2002; Sierszen et al. 2012). Low-marsh habitat in particular, the consistently inundated area of the wetland, provides critical habitat for most Great Lakes fish species (Jude and Pappas 1992; Randall et al. 1996; Wei et al. 2004). Despite their great economic and ecological value, much of the coastal wetlands in the Great Lakes basin has been degraded or destroyed due to anthropogenic activities (Environment Canada 2002; Jude and Pappas 1992; Mayer et al. 2004). In Georgian Bay (Lake Huron), there are thousands of coastal marshes (Midwood et al. 2012), that have remained largely undisturbed by anthropogenic influences (Cvetkovic and Chow-Fraser 2011). Although incremental human development pressure is an on-going concern, the more recent and immediate concern is that of uncharacteristic changes in lake levels, such as the drastic drop in lake levels (Assel et al. 2004) and persistent below-average lake levels that occurred between 1999 and 2014 (data from the Great Lakes Water Level Dashboard; Gronewold et al. 2013), that have threatened the long-term health of the region’s coastal wetlands (Fracz and Chow-Fraser 2013; Midwood and Chow-Fraser 2012).

Changes in lake-level fluctuations also pose a major threat to Great Lakes coastal wetlands as these communities are adapted to the disturbances brought about by continual changes in lake levels (Keddy and Reznicek 1986). Deviations from historic lake levels and lake-level fluctuations can have potentially detrimental impacts on the condition of coastal wetland habitat (Farrell et al. 2010; Leira and Cantonati 2008; Midwood and Chow-Fraser 2010; Mortsch 1998). There is a broad range of predictions as to how lake-levels will behave in the future (Angel and Kunkel 2010; Lofgren et al. 2002; Mortsch and Quinn 1996) but most studies agree that conditions outside historically observed norms are likely; therefore, scientists must develop approaches to assess how coastal wetlands may respond to these unprecedented changes in lake elevations.

Past studies have favored use of a hydrogeomorphic (HGM) scheme to classify Great Lakes coastal wetlands (Albert et al. 2005; Ingram et al. 2004; Keough et al. 1999; Minc 1997). Albert et al. (2005) defined coastal wetlands as “lacustrine systems” that are predominantly influenced by lake-level fluctuations and the geomorphic characteristics of the shoreline. Geomorphic characteristics of the shoreline affect how protected or exposed a particular site is to lake processes (e.g. wind waves, ice scour) and those characteristics can themselves be affected by lake level (e.g. exposure of shoals under low water conditions). The HGM classification has been an effective framework because it encompasses many of the major processes that affect coastal wetland distribution and composition. Lake-level fluctuation is a well-documented driver of wetland vegetation diversity (Keddy and Reznicek 1986; Leira and Cantonati 2008; Mortsch 1998; Wilcox and Meeker 1991) and wetland extent (Fracz and Chow-Fraser 2013; Mortsch 1998; Wei and Chow-Fraser 2008). Geomorphic characteristics such as substrate slope (Duarte and Kalff 1986; Duarte et al. 1986) and exposure (Angradi et al. 2013; Fonseca et al. 2002; Keddy 1982, 1984a, 1984b) are important drivers shaping community processes within the wetland. Such wide-spread adoption of the HGM framework for classifying wetlands provides a strong rationale for using HGM variables to model response of coastal wetlands to changing water-level conditions.

The literature has identified several useful HGM predictors, including fetch (Lemein et al. 2017) and geomorphic type (Albert et al. 2005), which were particularly useful for characterizing emergent and meadow vegetation communities throughout the Great Lakes. Water depth and exposure were found to be significant predictors of the cover of submerged aquatic vegetation (SAV; Angradi et al. 2013) in a Lake Superior estuary. Hebb et al. (2013) incorporated water depth into their wetland community modelling, as have Wilcox and Xie (2007). In these cases, HGM features were always considered amongst a suite of other environmental variables like land cover, water quality, or previous vegetation communities.

In this study, we propose to use only HGM features to model the extent and distribution of low-marsh habitat. We will develop this model for the eastern and northern shores of Georgian Bay, Lake Huron, where an existing inventory shows that there are thousands of coastal marshes (Midwood et al. 2012), many of which provide important spawning and nursery habitat for fish (Cvetkovic and Chow-Fraser 2011; Midwood and Chow-Fraser 2012; Leblanc et al. 2014). Given their ecological importance, our goal is to develop a model that can be applied to different water-level scenarios to assess the potential impacts of global climate change on the extent of low-marsh habitat throughout Georgian Bay.

Methods

Study Area

The geographic focus of our modelling efforts extends along the eastern and northern shoreline from Severn Sound in southeastern Georgian Bay to McGregor Bay in the northwest (Figure 3.1). This region has remained mostly undisturbed relative to the lower Great Lakes, where human impact has been limited to recreational (e.g. cottages, boathouses, marinas) and residential development. The bedrock is primarily granitic Canadian Shield and the coastal zone is characterized by a highly complex shoreline that consists of many small islands and protected embayments that provide habitat for fish, birds, and other wildlife.

Lake levels in Georgian Bay fluctuate regularly by up to 2 m between extreme highs and lows, but between 1999 and 2014, there was an unprecedented period of sustained low water levels that hovered near record lows. Between 2015 and 2017, lake levels rebounded to above-average levels, with the result that many coniferous trees and perennial shrubs that established in the wet meadow zone during the prolonged drawdown period began to occupy low-marsh habitat and slowly perished (Boyd 2017). These erratic inter-annual fluctuations are unprecedented and thought to be mediated by global climate change (Lofgren et al. 2002).

Hydrogeomorphic Parameters

For our modelling, we chose three parameters based on their well-established relationships with wetland vegetation: water depth, substrate slope, and wave exposure. Since data for these parameters are not available for the entire region of interest, we had to derive them from a digital elevation model (DEM) that we assembled for Georgian Bay, using the best available elevation data in terms of both coverage and resolution. The DEM was built by importing and manipulating relevant spatial data in ArcMap 10.5 (ESRI, Redlands, California). These data included navigation charts produced by the Canadian Hydrographic Service (CHS), which were used to derive elevation data below the low water chart datum of 176.0 m (all elevations are referenced to the International Great Lakes Datum 1985). The vertical and horizontal positional accuracy (95% confidence interval) for the hydrographic survey data within our study area did not exceed 0.5 m and 5 m, respectively (CHS 2013). Although navigation charts ranged in scale from 1:200,000 (i.e. full Georgian Bay chart) to 1:1,200 (e.g. narrow channels), the majority of the study area was derived from 1:20,000 scale charts. Depth soundings, depth contour lines, and the shoreline elevation from each chart were converted to elevation values in meters above sea level (IGLD 1985). Elevation data derived from the charts were sequentially stacked from the coarsest to finest scale, with the finer-scale elevation data replacing the coarser-scale elevation data where the chart footprints overlapped. We used the Ontario Provincial DEM v3.0 (OMNR 2013) as the source for all elevation data above 176.0 m. The horizontal and vertical accuracy of the input data for our study area did not exceed 5 m and 2.5 m, respectively (OMNRF 2016).

We interpolated the Georgian Bay DEM using the Topo to Raster function in ArcMap 10.5 (based on the ANUDEM program; Hutchinson 1989) by pooling all elevation data extracted from the CHS navigation charts and the Provincial DEM. Input elevation data were identified as spot (i.e. point elevations) or contour where appropriate. The hydrology option was set to “Enforced” and the number of iterations set to 50. All other input parameters were left as defaults. Due to the volume of elevation data and geographic extent of the DEM product, we interpolated the final DEM as a series of 10 km^2 tiles with a 1-km overlap with all neighboring tiles. All tiles were then mosaicked together to form the completed Georgian Bay DEM (GB-DEM) with a pixel size of 10 m. Any areas with missing or insufficient elevation data were identified and excluded from further analyses.

We used the GB-DEM to derive all HGM feature layers: depth, slope, and exposure. The depth layer was calculated by subtracting the elevation value from our target lake level. We derived the slope layer using the average maximum technique (Burrough and McDonell 1998) through the Slope tool in ArcMap 10.5.

To develop the exposure layer, we used a 32-point direct fetch measurement as the basis for wave exposure, similar to the 16-point direct fetch measurement used by Keddy (1982). From a given point on the water's surface, 32 bearing lines were drawn from the point until they intersected land, starting at North (0°) with 11.25° spacing between bearings. The sum of the lengths of all 32 bearing lines was used as a wave exposure metric for that point; this calculation was performed with a custom-built tool in ArcGIS 10.5. The time-intensive computations could not be performed for all points within the study area. Instead, we selected a subset of representative sample locations to capture the variation in wave exposure values and interpolated between these points. Since Midwood (2012) found negligible amount of low marsh vegetation (i.e. SAV) below 5 m, we first bounded the study area to only water depths between the shoreline and the 5-m contour and then placed a sample point at the center of all spatially distinct 0 – 5-m depth zones within the study area. Sample points were placed around the perimeter of all islands to account for their ability to block incoming waves. Four points were placed around islands with perimeters < 500 m and eight around perimeters > 500 m. Finally, we iteratively filled the remaining study area with sample points until we achieved a maximum distance of 500 m between adjacent points. This threshold was a suitable compromise that allowed us to capture the regional variation in fetch without spending excessive time on computations. We calculated the 32-point direct fetch value at each point and then interpolated between them using a triangulated irregular network, which was then converted to a raster layer with the same resolution and cell alignment as the GB-DEM. This was used as our wave exposure layer for the study area.

Model Development and Evaluation

The McMaster Coastal Wetland Inventory (MCWI; Midwood et al. 2012) is a geodatabase of coastal wetland habitat in eastern and northern Georgian Bay, digitized manually from IKONOS and Quickbird satellite images acquired between 2002 and 2009, during a period of sustained low water levels with a calculated mean monthly water level of 176.17 m (SE = 0.05) across the image acquisition dates. The coastal marsh habitat was classified as low marsh, high marsh and upstream wetlands. We used the low marsh layer as our training dataset to develop the model, and converted the inventory file to a 10-m raster, coincident with the GB-DEM. We took the entire extent of low-marsh habitat in the MCWI (Figure 3.1; study area) and then removed any areas where the bathymetric data were insufficient or missing. We then restricted the remaining study area to water depths between shore and 5 m deep. Since the low-marsh habitat in the MCWI was delineated from satellite imagery, the lakeward boundaries had been estimated based on visible characteristics and shape of the wetland rather than on actual depth contours (Midwood et al. 2012). By restricting the extent of low-marsh habitat to the 5-m contour, we are operationally removing areal extent of low marsh in the MCWI that may have been overestimated. Hereafter we will refer to the area entrained by the shoreline to the 5-m depth contour as the “coarse study area”. We then determined the distribution of slope and wave exposure values and the upper 95th quantile for all remaining low-marsh areas. These values were used as thresholds to remove any outlying low-marsh areas. The depth, slope, and exposure cut-offs were used to delineate areas that were deemed to be suitable for development of low marsh; hereafter, we will refer to this as the “effective study area”, which can be further divided into low marsh or open water. Two-thirds of the classified low marsh and open water served as the training dataset, while the remaining third served as the test dataset.

We set our lake level to 176.17 m because that was the calculated mean monthly lake level when the imagery used to delineate the MCWI wetlands was acquired. We calculated the HGM feature values for every cell in the training dataset and used those as predictors in a series of generalized linear models run in JMP 13.0.0 (SAS Institute Inc., Cary, NC) to predict the probability of a location supporting low marsh or open water. The generalized linear model consists of a random component, a systematic component, and a link function (Quinn and Keough 2002). Since we had classified the training dataset into two habitat types (low marsh = 1, open water = 0), we used a logit link function that is used for modelling binary data. We used each HGM feature as a single predictor and each possible combination of features for a total of seven different model runs. The generalized linear models calculated the probability that low-marsh habitat was present at a particular location.

We used a receiver operating characteristics (ROC) plot to rate each model's performance since it provided a threshold-independent evaluation (Fielding and Bell 1997), that is, the discrimination between open-water and low-marsh habitat was not biased by the threshold used to differentiate between these classes (Deleo and Campbell 1990). The ROC plot consists of the sensitivity (true-positive fraction) plotted against 1 minus specificity (false-positive fraction) for all possible threshold values (Fielding and Bell 1997). The area under the curve (AUC) of the ROC plot is used as an index of overall model performance, regardless of threshold (Deleo 1993), where 0.5 indicates that the model performance is comparable to random (i.e. an event has a 50% chance of being correctly classified) and an AUC of 1.0 indicates that the model performs perfectly (i.e. 100% chance of an event being classified correctly).

We selected the best-fitting model based on the AUC values from the ROC plots. For the best-fitting model, we found the threshold value that maximized the true skill statistic and used that threshold to classify our model output into low-marsh or open-water habitat categories. The true skill statistic is calculated as the sensitivity plus specificity minus 1 for a given classification threshold, where values can range from -1 to 1. We used this metric to select a classification threshold because it maximizes both our true positive and true negative classification rates and is independent of prevalence (Allouche et al. 2006), which was important since our low-marsh habitat category made up only a small portion of our overall dataset. We used a confusion matrix to evaluate the performance of the classified model output.

We validated the model using the test dataset using the AUC score for the unclassified model output and a confusion matrix for the classified output. We then pooled the test and training datasets and repeated the AUC and confusion matrix evaluations on the full reference dataset (i.e. the effective study that was classified as low marsh or open water based off the MCWI).

Two large embayments in eastern Georgian Bay were excluded from the study area because of gaps in the bathymetric data available from the CHS navigation charts, Tadenac Bay and Sturgeon Bay (near Pointe au Baril, ON). Both embayments were mapped as part of the MCWI (Midwood et al. 2012) so reference habitat information was available. We constructed DEMs for each site using the same methods as for the GB-DEM, but substituted the bathymetric data from the CHS navigation charts with bathymetric data collected from an off-the-shelf sonar unit (e.g. Lowrance HDS7 or comparable; horizontal accuracy approx. 3 m, vertical accuracy approx. 30 cm) for unrelated survey work. We continued to use the Ontario Provincial DEM v3.0 (OMNR 2013) as the source of our elevation data above 176.0 m. All HGM feature layers were derived in the same manner as for the GB-DEM, and the MCWI reference data were limited to the same depth, slope, and exposure thresholds as the effective study area. We ran the best-fitting model with the HGM data from each embayment and evaluated the model performance and classified output using the same methods described above.

For the full dataset (i.e. test and training) we used a confusion matrix to evaluate the classified output from the best-fitting model within the effective study area. We included an additional category, "excluded", to denote any areas that had slope or wave exposure values above the 95th quantile and that had been removed while creating the effective study area. We made this evaluation relative to the coarse study area to evaluate how the model performed in response to the cut-offs in slope and wave exposure. We maintained the 0 – 5-m boundary of the coarse study area because that threshold was based on empirical field observations (Midwood 2012). We then overlaid categories from the confusion matrix over the study area to visually assess the accuracy of the classification and to look for possible reasons to explain errors. Since low-marsh habitat class had such low prevalence in the dataset, we were more concerned with omission or exclusion errors than with commission errors.

In addition to the pixel-based evaluation of the classified model output, we also assessed the ability of our model to identify units of low-marsh habitat (i.e. spatially distinct patches of low marsh) in the effective study area. We considered it a “match” when some portion of a reference low-marsh unit was classified correctly by the model. For each match, we calculated the percentage reference unit that was correctly classified. Using multiple cut-offs of minimum area, we calculated the sensitivity (i.e. fraction of correctly identified low-marsh units) and mean overlap (i.e. percentage reference low-marsh unit that was correctly classified) to evaluate if there is a minimum low-marsh unit that must be used to achieve acceptable model performance.

Results

Model Development and Evaluation

Once we removed areas with insufficient bathymetric data and further excluding areas deeper than 5 m, we obtained 3,619 ha of low-marsh habitat and 37,092 ha of open water. The effective study area, however, which is restricted to the upper 95th quantile of slope (7.096%) and wave exposure (71,464 m), only contained 3,259 ha of low-marsh habitat and 13,964 ha of open water.

We used our training data subset to run seven different generalized linear models, one for each permutation of the depth, slope, and wave exposure predictors (Table 3.1). For every model run, all predictor variables were negatively correlated with the probability of a location supporting low-marsh habitat. The best-fitting model with respect to the AUC scores was the full model that included depth, slope, and wave exposure as predictor variables. This was followed closely by the depth-slope model. Of the models with only a single predictor variable, the depth-only model performed best, followed by slope-only, then wave-exposure-only. The AUC score of 0.7627 for the depth-only model indicates that there is a 76% chance that the model will correctly classify a given point within the effective study area as low-marsh habitat, and is a good overall fit. Slope-only also performed well at 0.7095. Exposure-only fared much poorer with an AUC of 0.5697, indicating it was a weak predictor of low-marsh presence within the effective study area boundary. The performance of the single-predictor models provides a sense of the relative importance of each of the variables.

The equation for the full model is as follows:

$$P(LM) = \frac{1}{1 + Exp(-(0.94271 - 0.97224(D) - 0.42310(S) - 1.5013 * 10^{-5}(E))}$$

where P(*LM*) is the probability of low-marsh habitat occurring at a given location, *D* = depth, *S* = slope, and *E* = exposure. For this model, the true skill statistic was maximized at a P(*LM*) value of 0.203, indicating that any cell with a value equal to or larger than the threshold was classified as low marsh and any smaller value was classified as open water. Based on the classified output of the full model, there are 10,152 low-marsh units (i.e. spatially distinct patches of wetland habitat), comprising a total area of 6,166 ha within the effective study area.

The model output for the test, training, and full Georgian Bay dataset all had very similar sensitivity and specificity values of approximately 0.80 and 0.75, respectively (Table 3.2). Consistency in the performances of the training and test datasets justified re-combining them into the full Georgian Bay dataset for subsequent evaluations of model performance. For both of the external datasets (Sturgeon Bay and Tadenac Bay), the model performed comparably to the full

Georgian Bay dataset. Model performance for Tadenac Bay was marginally better than that for the full Georgian Bay dataset, and even though the model performed poorest in Sturgeon Bay, it still received a good AUC score of 0.785 (Table 3.2). Sensitivity of the classified model output was lowest for Sturgeon Bay; based on visual assessments, this can be attributed to the consistent underestimation of the lakeward extent of low marsh, and not to errors associated with classifying low-marsh units.

The model faithfully reproduced the MCWI reference layer (Table 3.3), correctly classifying 80% of the low-marsh habitat and 75% of the open-water area in the effective study area. Applying the slope and wave exposure thresholds excluded 23,128 ha of open water from the effective study area, but also 360 ha of low-marsh habitat. The model could not accurately discriminate between open water and low marsh along the lakeward boundary of correctly classified low-marsh units, and this resulted in both omission (false negatives) and commission (false positive) errors (Figure 3.2). Some low-marsh habitats were also misclassified along channelized areas bordering wetlands and in nearshore areas where true elevations were higher than indicated by the GB-DEM. The latter resulted in some low-lying areas being misclassified as low marsh that were in reality wet meadow, which should not have been excluded from the effective study area. Approximately 10% of the low-marsh area in the coarse reference dataset had been incorrectly excluded from the effective study area, which included very steep areas along the shoreline. In these areas, nearshore slopes had been overestimated in the GB-DEM due to resolution limits, such that a tall cliff face adjacent areas with a gradual nearshore slope appeared as a very steep slope. This typically resulted in omission of fringing wetland that is frequently found in such geomorphic settings. Similarly, we found that exclusion of low-marsh due to the wave exposure cut-off was largely attributable to the resolution of the GB-DEM. In southeastern Georgian Bay, there are areas with relatively high wave exposure but the water is relatively shallow in the nearshore (< 2 m) and often contain many shoals and rocks that can attenuate wave exposure; however, since these features occur at a spatial scale that is finer than our DEM can resolve, the calculated exposure for these areas tended to be overestimated and led to misclassification of low-marsh habitat as open water.

The MCWI reference dataset contained 2,840 low-marsh units within the effective study area (mean ± SE: 1.42 ha ± 0.23). The model correctly identified 81% of the reference low-marsh units with a mean overlap of 60%, when no minimum low marsh size threshold was applied. The model sensitivity and mean overlap improved as the minimum area threshold for low marsh units increased (Table 3.4). When only low-marsh units larger than 1.0 ha were considered, the model sensitivity was nearly 100% (only one fringing wetland occurring along a steep channel had been missed) with mean areal overlap of 74%.

Discussion

Overall, our full model performed remarkably well, yielding good AUC values for model runs with all datasets, including two independent datasets (Table 3.2), and acceptable performance of the classified model output (Table 3.3). Further, its ability to correctly identify low-marsh units from the reference dataset was impressive, correctly identifying over 99% of low marsh units from the MCWI that were larger than 1.0 ha (Table 3.4; for reference, with the 10-m resolution of the GB-DEM a 0.1 ha low-marsh unit was the equivalent of 10 pixels). The performance of the model at that scale is relevant since Midwood et al. (2012) found that the average low marsh unit in eastern and northern Georgian Bay had an area of 1.4 ha, and the Ontario Wetland Evaluation System indicates that provincially significant wetlands must be > 2 ha in size, either as a single wetland or a complex consisting of functionally-grouped set of smaller wetlands (OMNR 2014). Based on a simple visual assessment of the predicted low marsh area (i.e. Figure 3.2), the model capably differentiated between low-marsh and open-water habitat types. In cases where the model overestimated the lakeward extent of the low marsh area compared with the MCWI, we confirmed that the predicted extent was generally consistent with field observations (J.D. Weller, pers. obs).

Despite the promising model performance, there were still notable classification errors: the exclusion of 360 ha of low-marsh habitat from the effective study area, and the misclassification of 653 ha of low marsh and 3,560 ha of open water (Table 3.3). The most commonly misclassified area was along the lakeward edge of low marsh areas, but this is largely attributable to the nature of the reference dataset. The habitat types in the MCWI (Midwood et al. 2012) were manually delineated from satellite imagery and the lakeward extent of the low marsh zone was delineated without the benefit of bathymetric data. As pointed out by Midwood et al. (2012), a set of heuristic rules had been used to estimate the lakeward boundary of the low marsh zone based on the morphology of the site and observable wetland characteristics. These differences in ruleset is one of the main reasons for the lower areal estimate of low marsh in the MCWI relative to our model output.

Exclusion of 360 ha of low marsh corresponding to the effective study area accounted for nearly 10% of the total low-marsh area from the MCWI, which was already a small component of the total dataset. These exclusions are the result of overestimated slopes immediately along the shoreline in areas where the resolution of the GB-DEM was not sufficient to accurately capture the true landscape structure. Although this was a pervasive issue throughout the study area given the rocky nature of the landscape, mostly narrow bands of shoreward low-marsh habitat were excluded. Omission errors due to inflated exposure as a result of the inability of the GB-DEM to detect shoals in the shallow region of southeastern Georgian Bay (see Figure 3.2) will not be corrected until a finer-scale elevation becomes available. We acknowledge that the scale of evaluating these HGM features is important (Duarte and Kalff 1990) but incorporating different scales of HGM data into this modelling effort was beyond the scope of this study.

Many management agencies operationally define the lakeward extent of coastal wetlands to be the 2-m depth contour (Albert et al. 2005; Keough et al. 1999; OMNR 2014). In this study, we explicitly applied a 5-m depth limit because we wanted to ensure our region of interest included all depths where aquatic vegetation could potentially colonize. Even so, our classified model output predicted a total 6,166 ha of low marsh, of which 6,141 ha was in water < 2 m deep. In fact, < 0.4% of our total predicted low-marsh habitat occurred in depths outside the accepted lakeward extent; therefore, the model predictions are consistent with the generally accepted criteria for the lakeward boundary of coastal wetlands. Even though the total area of low-marsh habitat predicted by the model is nearly double that of the MCWI, we believe this to be an underestimate of its lakeward extent because the model was trained with a conservative dataset. Sonar logs collected from a set of coastal wetlands that were surveyed in southeastern and northern Georgian Bay (J.D. Weller unpublished; see Figure 3.3) support this observation, with SAV extending further lakeward than the predicted low-marsh extent.

Our model does not take into account lake-level fluctuation and assumes a static lake level. Water-level fluctuations are a key feature of Great Lakes coastal wetlands (Environment Canada 2002) and the role that water-level fluctuation plays in coastal wetland processes is well documented (Keddy and Reznicek

1986; Leira and Cantonati 2008; Mortsch 1998; Wilcox and Meeker 1991). Our model attempts to predict extent of low marsh, as a general habitat category, and we do not attempt to predict any level of community composition or structure within that habitat area. Further, our training dataset (MCWI; Midwood et al. 2012) was delineated from imagery captured at least three years into a period of sustained low water levels. Assuming there is a 2 to 3 year lag time for wetland communities to respond to a shift in water levels (Gathman et al. 2005; Quinlan and Mulamoottil 1987; Wilcox and Nichols 2008), the wetland community should have responded to the new water level conditions by the time the imagery had been acquired. We assume that our training dataset is representative of a low-marsh community that had adjusted to the stable water-level regime and in which different vegetation classes occupied their "optimal" depth range. Even though stable water levels have not occurred historically in Lake Michigan-Huron (Sellinger et al. 2008), some models predict that periods of stable water levels may become more frequent (Lu and Nairn, in submission). Although the scope of the present paper did not permit it, inclusion of prior hydrographic conditions in the model would be a worthwhile refinement for future consideration.

We restricted our model evaluations to the best-fitting model, which was the full HGM model. Our depth-slope model performed nearly as well as the full-model, with AUC scores of 0.825 and 0.8306, respectively (Table 3.2). This is a computationally simpler model without sacrificing much in terms of performance. Deriving the wave exposure layer was by far the most computationally demanding process. An exposure threshold is still necessary to delineate the effective study area, but a reduced exposure layer could be derived that simply aimed to classify areas as above or below the exposure threshold. The exposure-only model had an AUC of 0.5697, indicating that it was only marginally better than random as a predictor of low-marsh habitat within the effective study area. Nevertheless, the value of the exposure layer was in delineating the region of interest that contained potential low-marsh areas. The majority of 23,128 ha of open water that were excluded from the effective study area (Table 3.3) can be attributed to applying the wave exposure threshold.

Inventories of coastal wetland are required to evaluate how these habitats may change over time and this HGM modelling approach is a practical way to address current data gaps and limitations. Large-scale efforts to inventory wetland habitat typically rely on remotely-sensed imagery (i.e. aerial or satellite imagery) to identify and delineate wetland areas (Bourgeau-Chavez et al. 2015; Ingram et al. 2004; Midwood and Chow-Fraser 2010; Midwood et al. 2012). While this is certainly an effective approach, the spatial and temporal extent of the inventory is limited by available imagery. Given that it is not always possible to access suitable images to reflect past and future conditions outside the range of recently observed conditions, our HGM modelling approach only requires a suitable training dataset and an appropriate DEM. This approach was particularly well-suited to our Georgian Bay study area because of limited anthropogenic impact and the fact it is underlain by weather-resistant Canadian Shield. As such, we are confident that our GB-DEM is an acceptably accurate representation of the true elevation of the area for upwards of several decades into the past or future. This approach may be less appropriate in areas where the landscape is subject to change on a much smaller timescale (e.g. dredging, shifting sand bars) or would require additional calibration of the DEM.

Data availability was certainly the most significant obstacle to overcome in this study, and we would qualify our efforts as a “best-possible” effort for Georgian Bay. The Ontario Provincial DEM v3.0 more than met our requirements for spatial scale, but lacked desirable resolution. In contrast, the resolution of the CHS data was an improvement over the comparable open-source bathymetric data but the coverage was not comprehensive. The Georgian Bay archipelago contains thousands of islands and shoals and in many areas, a comprehensive bathymetric survey is not possible. We echo the calls from other researchers who have called for improved elevation data (Ciborowski et al. 2009; Hebb et al. 2013; Ingram et al. 2004) for all Great Lakes, not only those in settled areas of Ontario. A nearshore LIDAR survey would provide improved resolution and a consistent sampling method from the aquatic to the terrestrial zones. This would likely help address some of the classification issues previously discussed and allow for a greater exploration of the spatial scale at which HGM features should be mapped to appropriately represent the landscape processes that affect wetland development.

Deviations from historic hydrologic conditions in the Great Lakes have, and will continue to have, an impact on the amount and quality of coastal wetland habitat. The uncertainty about future lake levels necessitates a means to predict and evaluate how coastal wetlands may respond to these novel conditions. The HGM modelling approach that we have demonstrated in this paper should satisfy that need and serve as a jumping-off point for more refined analyses.

Acknowledgements

With regards to the DEM developed for this project, it was produced by McMaster University based on Canadian Hydrographic Service charts and/or data, pursuant to CHS Direct User Licence No. 2016-1121-1260-M. The incorporation of data sourced from CHS in this product shall not be construed as constituting an endorsement by CHS of this project. This product does not meet the requirements of the Charts and Nautical Publications Regulations, 1995 under the Canadian Shipping Act, 2001. Official charts and publications, corrected and up-to-date, must be used to meet the requirements of those regulations. This work was supported in part through an Ontario Graduate Scholarship for Dan Weller and a research contract from Environment and Climate Change Canada.

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Table 3.1: Predictor coefficients (±SE) and performance metrics for the seven generalized linear model runs with the training dataset. Models were evaluated and ranked from the area under the curve (AUC) value derived from their respective ROC plots.

Parameters	**Intercept**	**Depth**	**Slope**	**Exposure**	**AUC**	**Rank**
all	0.94271 (±6.036 E-3)	-0.97224 (±3.151 E-3)	-0.42400 (±1.773 E-3)	-1.50 E-5 (±1.6547E-7)	0.8306	1
depth-slope	0.62952 (±4.924 E-3)	-1.00638 (±3.162 E-3)	-0.39424 (±1.712 E-3)	NA	0.8250	2
depth-exposure	-0.01752 (±4.568 E-3)	-1.03345 (±3.138 E-3)	NA	-7.29 E-6 (±1.55 E-7)	0.7673	3
depth	-0.14162 (±3.748 E-3)	-1.04886 (±3.134 E-3)	NA	NA	0.7627	4
slope-exposure	-0.04430 (±5.103 E-3)	NA	-0.48001 (±01.762 E-3)	-2.19 E-5 (±1.57 E-7)	0.724	5
slope	0.55675 (±3.721 E-3)	NA	-0.43794 (±1.689 E-3)	NA	0.7095	6
exposure	-1.17352 (±3.603 E-3)	NA	NA	-1.44 E-5 (±1.48 E-7)	0.5697	7

Table 3.2: Performance of best-fitting model with different datasets. Training and test datasets were randomly selected subsets, 2/3 and 1/3 respectively, of each habitat type (low marsh and open water) from the effective study area dataset. Area under the curve (AUC) of the ROC plot for respective model runs was used as threshold-independent evaluation of the model performance. Model outputs were classified into open water and low marsh based on a threshold value of 0.203. Overall performance (total correct classification), sensitivity (true positive fraction), specificity (true negative fraction), and true skill statistic (TSS) were derived from confusion matrices.

Dataset	AUC	Overall	Sensitivity	Specificity	TSS
Training	0.831	0.755	0.799	0.745	0.544
Test	0.831	0.756	0.801	0.745	0.546
Full GB	0.831	0.755	0.800	0.745	0.545
Sturgeon Bay	0.785	0.739	0.654	0.765	0.419
Tadenac Bay	0.849	0.800	0.766	0.807	0.573

Table 3.3: Confusion matrix of the classified output of the best model (i.e. depth, slope, exposure) of the full Georgian Bay dataset within the effective study area. Area of each class (LM = low marsh, WTR = open water, EXCL = excluded) is reported in hectares (round brackets) and as a proportion of the reference class (square brackets). The excluded class indicates the area of low marsh and open water in the reference dataset that was in the 0 – 5 m depth zone but above the 95th quantile for slope and wave exposure. NA = not applicable.

		Full Model		
		LM (6,165.87)	**WTR** (11,057.28)	**EXCL** (23,488.30)
Effective Study Area (17,223.15)	**LM** (3,259.11)	2,605.89 [0.80]	653.22 [0.20]	360.14 [NA]
	WTR (13,964.04)	3,559.98 [0.25]	10,404.06 [0.75]	23,128.16 [NA]

Table 3.4: Ability of the model to identify low marsh units ("Match" = correctly classify some portion of a low-marsh reference unit), with the mean proportion of overlapping area for matched units and the fraction of correctly classified units from the reference dataset. Multiple minimum area cutoffs were included to evaluate model performance at different spatial scales.

LM Unit Size (ha)	# of Units in MCWI	# of Matches	Mean Proportion Overlap (± SE)	Sensitivity
all	2840	2294	0.60 ± 7.96E-3	0.81
> 0.1	1441	1374	0.67 ± 7.96E-3	0.95
> 0.2	1072	1035	0.68 ± 9.17E-3	0.97
> 0.5	622	615	0.71 ± 1.10E-2	0.99
> 1.0	389	388	0.74 ± 1.28E-2	1.00

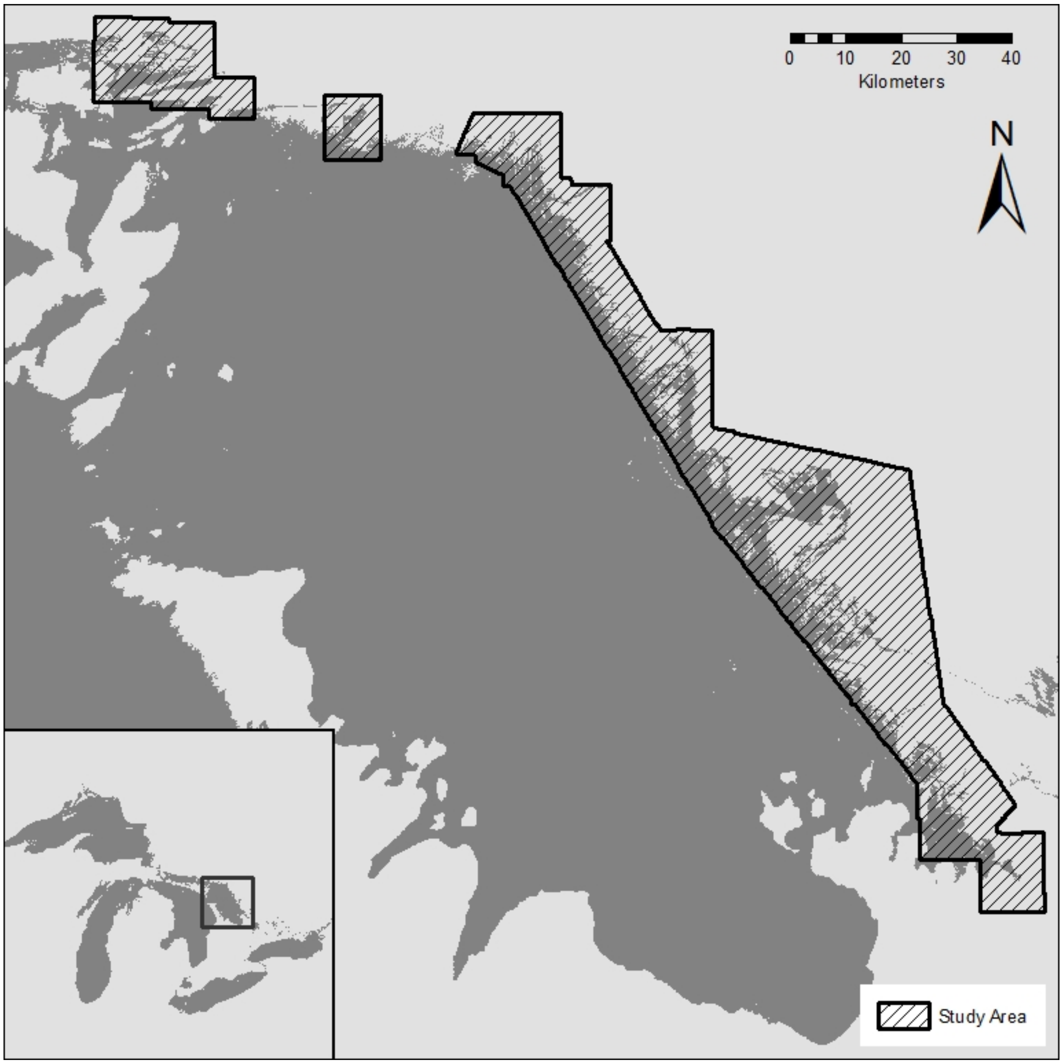

Figure 3.1: Location of study area in Georgian Bay (relative to Great Lakes; inset). Cross-hatched study area indicates simplified extent of study area for low-marsh modelling efforts. Areas where insufficient elevation data were available for modelling were removed from the indicated study area.

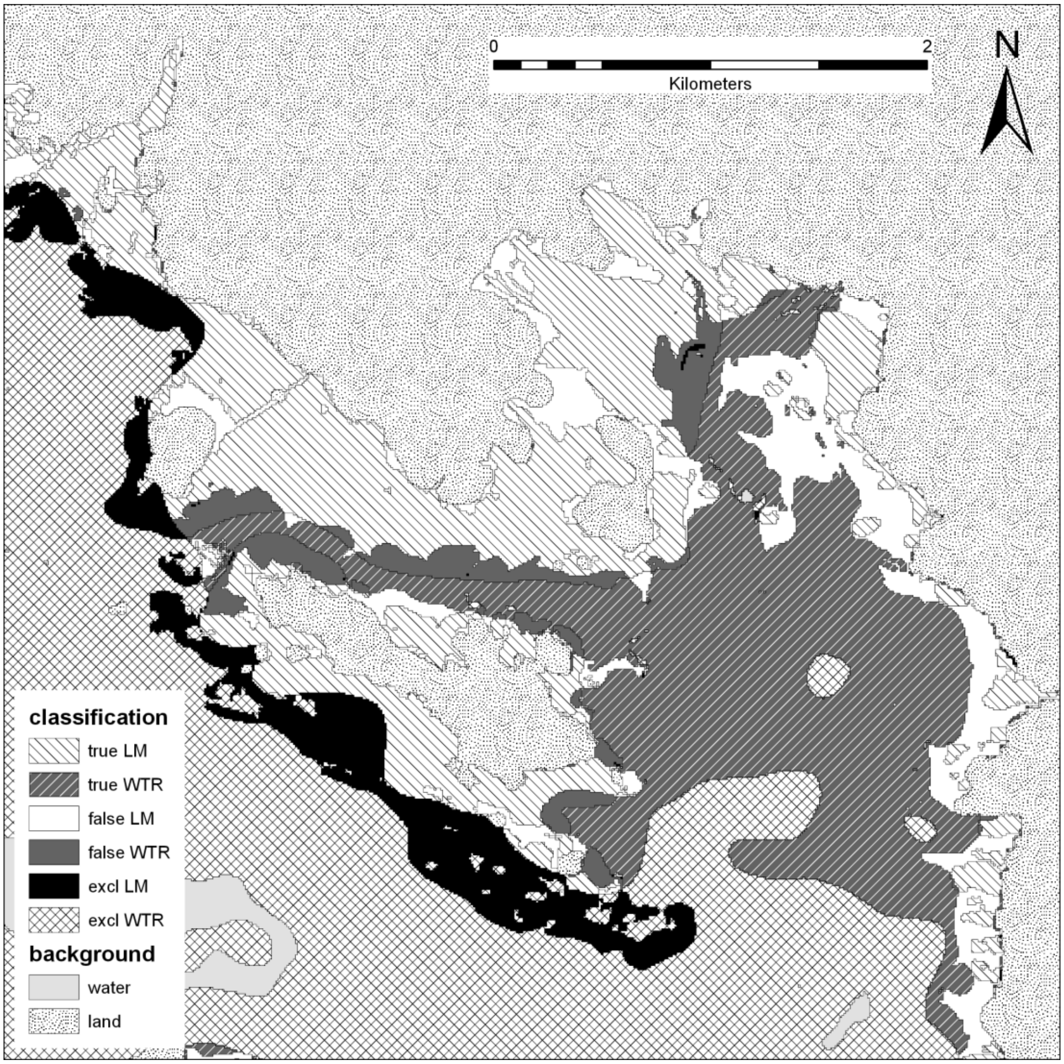

Figure 3.2: An area in southeastern Georgian Bay that is representative of the typical classification successes (true) and failures (false) of the model in predicting the presence of low marsh (LM) and open water (WTR) relative to the reference dataset. Excluded (excl) categories indicate LM and WTR that were present in the reference dataset but outside the effective study area of the model.

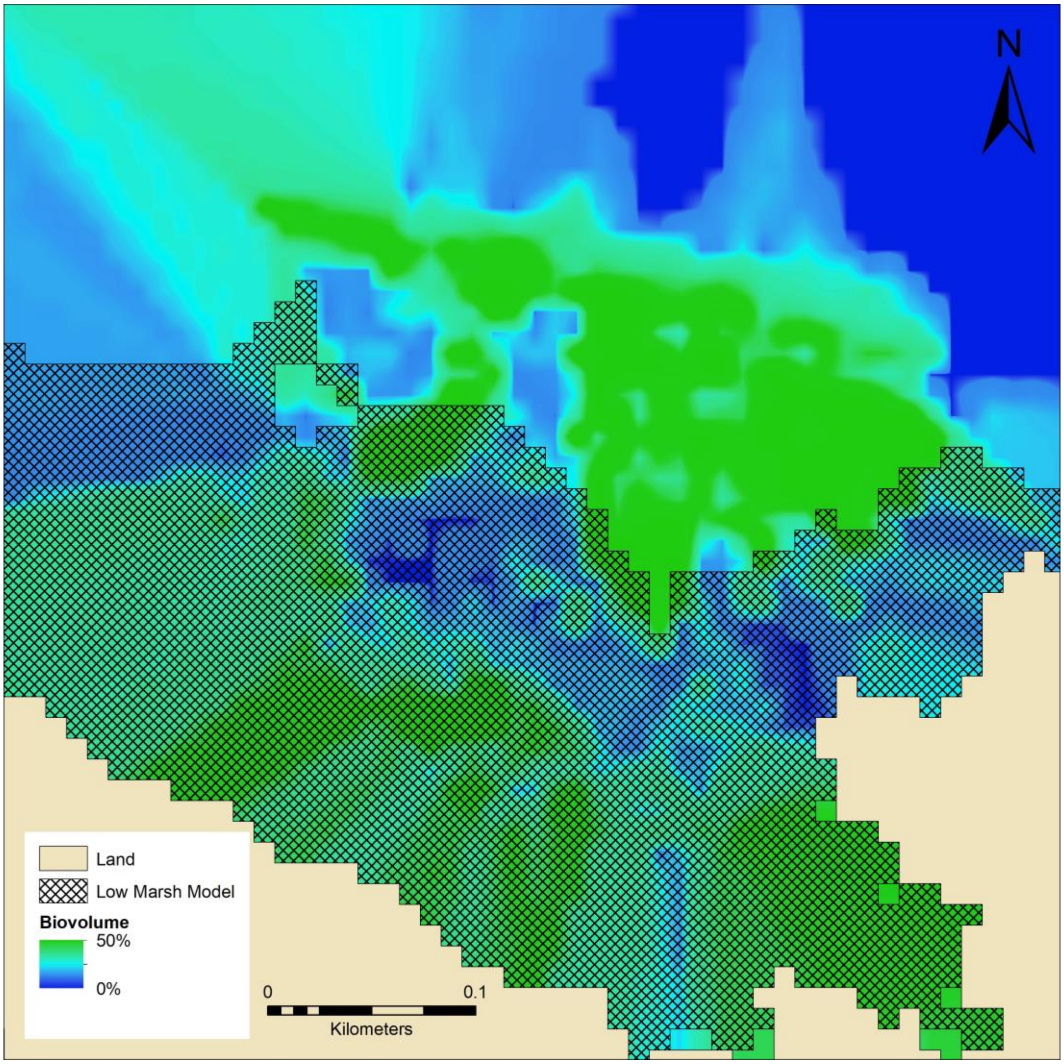

Figure 3.3: Comparison of modelled low marsh (hatched area) to aquatic vegetation data collected using sonar at a lake level of 176.75 m. Sonar data is expressed as biovolume (percent of the water column occupied by aquatic vegetation), where 0% is bare substrate and 25 – 50% approximates moderate density aquatic vegetation. The model underestimates the lakeward extent of the low marsh vegetation and does not capture the patchiness of aquatic vegetation within the wetland.

Chapter 4

SIMULATED CHANGES IN EXTENT OF GEORGIAN BAY LOW-MARSH HABITAT UNDER MULTIPLE LAKE LEVELS

In submission: Weller JD, Chow-Fraser P (2018/CH4) Simulated changes in extent of Georgian Bay low-marsh habitat under multiple lake levels. Submitted to Wetlands Ecology and Management, submission ID: WETL-D-18-00081 (Chapter 4)

Abstract

The extent of coastal wetlands in Georgian Bay is controlled primarily by the water level of Lake Huron, which directly affects the amount of critical habitat available for fish and wildlife communities. Lake-levels have historically fluctuated by nearly 2 m and that range could increase in the future, which prompted us investigate how quantity and quality of wetland habitat in Georgian Bay may be affected by different lake-level scenarios. The extent of low-marsh habitat was modelled with a generalized linear model that used hydrogeomorphic features (i.e. depth, slope, and exposure) as predictors. We ran projections between 175.5 m and 177.5 m, at 0.5-m increments, and found that the total area of low marsh peaked at 176.0 m (7,113 ha) and declined sharply as lake levels increased or decreased. In contrast, low-marsh volume was highest at 176.5 m ($3.84 * 10^7$ m^3) but remained relatively stable across all modelled lake levels. We derived an average elevation profile for low-marsh habitat across the study area that showed a shallow “step” between 175.5 and 176.0 m, flanked by steeper upslope and downslope sections. At historically low lake levels low-marsh habitat would have been dominated by shallow (< 0.5 m) water, whereas at higher lake levels, it would have been dominated by deeper (0.5 – 2.0 m) water. The geomorphology at low lake levels (i.e. 176.0 m) appears to favour large areas of shallow habitat at the expense of deeper habitats that could have supported more structurally complex, submersed aquatic vegetation.

Introduction

Water levels in the Great Lakes naturally fluctuate on short-term scales of hours to days (Trebitz 2006), over seasons (Minc 1997), to annual and multi-decadal time frames (Baedke and Thompson 2000; Hanrahan et al. 2010; Quinn and Sellinger 2006). These fluctuations are largely driven by natural cycles of climate, precipitation, and evaporation. Beyond these natural fluctuations in lake level, there are also anthropogenic factors at play. Regulation of lake levels with dams and locks have dampened historic fluctuations; additionally, dredging of connecting channels like the St. Clair River has also led to increased erosion and outflow from Lake Michigan-Huron, while human-induced changes to climate have been linked to changes in evaporation (e.g. through warmer winters and less ice-cover; Mortsch and Quinn 1996). The long-term mean lake level in Lake Michigan-Huron from 1860 to 2017 is 176.6 m asl (Canadian Hydrographic Service dataset), with a range of approximately 2 m between extreme high and low waters (~ 175.5 – 177.5 m). The dynamic nature of lake-level fluctuations is a key feature of the Great Lakes ecosystem and plays an important role in shaping coastal habitats.

From 1999 to 2013, Lake Michigan-Huron entered a period of sustained low water levels that was a marked departure from historic patterns of lake-level fluctuation (Sellinger et al. 2008). Even though lake levels have rebounded to above-average elevations since 2014, a return to low water levels appears likely. There have been a wide range of predictions for what future water levels might look like in Lake Michigan-Huron, ranging from increases of over a meter to decreases of up to three meters over the next century (Angel and Kunkel 2010; Lofgren et al. 2002; Mortsch and Quinn 1996). These scenarios were based on global climate models to account for various climate-change scenarios. Lu and Nairn (in submission) modelled changes in lake levels by analyzing historic patterns in water-level fluctuations and projected that periods of low lake levels would be persistent through the next several decades. There is still much uncertainty regarding the future state of Lake Michigan-Huron water levels but sustained periods of low or extremely low water are most likely.

A wide array of potential impacts of low lake levels were identified by Hartmann (1990), including the loss of valuable coastal wetlands habitat. In the Great Lakes, coastal wetlands provide a wide array of ecosystem services and support high biodiversity (Environment Canada 2002). Low-marsh, the inundated component of coastal wetlands, provides habitat for the majority of Great Lakes fish species (Jude and Pappas 1992; Wei et al. 2004) and thus supports economically, recreationally, and culturally valuable fisheries. The aquatic vegetation that occurs in low-marsh habitat provides physical structure that supports macroinvertebrates and a diverse community of prey species, making it important foraging habitat for piscivores (Dibble et al. 1997; Eadie and Keast 1984). Since aquatic vegetation community is a determinant of fish assemblages (Cvetkovic et al. 2010), the amount and type of available low-marsh habitat is a key consideration for Great Lakes fisheries. No other region exemplifies this better than the eastern and northern shores of Georgian Bay (Lake Huron), where there are thousands of high quality coastal marshes (Cvetkovic and Chow-Fraser 2011; deCatanzaro and Chow-Fraser 2011; Midwood et al. 2012) that have remained relatively free from human disturbances.

The impact of varying lake levels on wetland vegetation dynamics has been well documented. Persistent lake-level fluctuations are necessary to maintain high diversity in the wetland plant community (Keddy and Reznicek 1986), and periods of stable water levels in a typically dynamic water-level environment can lead to a loss of diversity and dominance of certain plant species (Midwood and Chow-Fraser 2012; Wilcox and Meeker 1991; Wilcox and Nichols 2008), which in turn can lead to subsequent shifts in the wetland fish community (Midwood and Chow-Fraser 2012; Wilcox and Meeker 1992). The types of vegetation present within a wetland have also been documented to change with water level; submersed aquatic vegetation (SAV) tends to dominate in periods of high water as the emergent and meadow species are inundated and die back, whereas under low water, the opposite occurs, with amount of SAV declining as emergent and meadow vegetation expand into the new areas released by the receding water levels (Hudon et al. 2005; Lyon and Drobney 1984; Williams and Lyon 1997). Ultimately, the structure of coastal wetland vegetation is closely linked to lake levels and their fluctuations.

Given the importance of low-marsh habitat and the uncertainty in future water-level trends, managers need to understand how amount and distribution of low-marsh habitat might change over the next few decades. The McMaster Coastal Wetland Inventory (MCWI; Midwood et al. 2012), the most comprehensive estimate of amount of wetland habitat in eastern and northern Georgian Bay, was derived from high-resolution satellite imagery acquired primarily during a period of low water levels in the early-mid 2000s. There is no comprehensive inventory of wetland habitat under other historic water-level conditions, nor for lake levels outside the historic range. Weller and Chow-Fraser (2018/CH3) developed a generalized linear model (GLM) to predict the presence of low-marsh habitat in eastern and northern Georgian Bay as a function of hydrogeomorphic features (i.e. depth, slope, exposure). That model was trained using data from low water levels, but can be applied to other lake levels. In this paper we used the low-marsh GLM developed by Weller and Chow-Fraser (2018/CH3) to simulate changes in the extent of low-marsh habitat in response to a range of potential lake levels in Georgian Bay.

Methods

The generalized linear model (GLM; Weller and Chow-Fraser 2018/CH3) used hydrogeomorphic features (i.e. depth, slope, wave exposure) derived from a digital elevation model (DEM) to predict the presence of low-marsh habitat. A threshold value was used to classify the probability outputs as either “low marsh” or “open water”. The model was trained with data from the MCWI (Midwood et al. 2012), a spatial inventory of coastal wetland habitat in eastern and northern Georgian Bay delineated from IKONOS satellite imagery acquired during the summer months of 2002, 2003, 2005, and 2008. Mean monthly water levels in Lakes Michigan-Huron at the time ranged from 176.04 m to 176.33 m, a mean of these being 176.17 m. The model was validated with a subset of MCWI data that had been withheld, and with independently acquired DEMs of two sheltered embayments in eastern Georgian Bay. The GLM performed well (area under the curve of 0.831), and the classified model correctly identified 80% of low marsh and 75% of the open-water habitat. Full details of the development and validation of the model can be found in Weller and Chow-Fraser (2018/CH3).

We maintained the same study area used by Weller and Chow-Fraser (2018/CH3): Severn Sound in the southeast to MacGregor Bay in the north (Figure 4.1), excluding areas with insufficient bathymetric information. Two stretches along the north shore of Georgian Bay were excluded because of gaps in the MCWI coverage (Midwood et al. 2012): French River to Beaverstone Bay and Killarney to MacGregor Bay.

We used ArcMap 10.5 (ESRI, Redlands, California) to run the GLM models and perform spatial analyses at five lake-level scenarios; 175.5 to 177.5 m (IGLD 1985) in 0.5 m intervals. This range of lake levels encompassed the historic highs and lows that have been recorded in Lake Michigan-Huron (1860 - 2017; Great Lakes Water Level Dashboard, Gronewold et al. 2013). Furthermore, this range includes lake levels that are likely to occur over the next century (Angel and Kunkel 2010; Lu and Nairn, in submission). For each lake level, the depth, slope, and wave exposure parameters were derived from the DEM as described by Weller and Chow-Fraser (2018/ CH3). The GLM produced a probability surface that was then classified as either low-marsh or open-water habitat based on a threshold value. To address errors stemming from inaccuracies in the DEM, we used several mask layers to exclude areas that should have been outside the target elevation range (i.e. 0 – 5 m below the lake level) but which had been incorrectly classified as low marsh or open water.

Although majority of the shoreline within the study area was undeveloped land, some built-up areas were present, most notably in Severn Sound and Parry Sound. We used the “Community/Infrastructure” classification from the Ontario Land Cover Compilation v2.0 (OMNRF 2016) and a 10-m buffer around the Ontario Road Network (OMNR 2009) to clip out these built-up areas. We excluded these because they were either areas occurring at a higher elevation than our DEM indicated or were built-up areas that would have been protected or hardened against high-water conditions. We also used the Wooded Area dataset (OMNR 2006) to clip out forested area (i.e. trees or shrubs > 2 m in height). We assumed that forests should normally occur above the high-water mark for Georgian Bay and are therefore outside our range of target elevations. We removed all masked areas from our habitat projections for each lake-level scenario.

We divided the modelled low marsh into 0.5 m depth zones between shore and 2 m deep, and considered 2 - 5 m deep as a single depth zone. We then derived hypsographic curves for the total low-marsh area and volume for each scenario. To estimate the average elevation profile, we rescaled the low-marsh area from each scenario to approximate a fringing wetland (i.e. a rectangle) where the length of the shoreline and each depth zone was held constant. Essentially we stacked the hypsographic area curves from each scenario using elevation values that corresponded to the respective depth measurements (e.g. 0 m for the 176.0 m scenario would correspond to 0.5 m contour for the 176.5-m scenario; the curve for the 176.0-m scenario was shifted laterally and vertically to align these points). All five hypsographic curves were aligned then smoothed to produce a representative elevation profile.

For each lake-level scenario, we calculated the total area and volume of the low marsh within the study area. Absolute and proportional area and volume were calculated for each depth zone. The depth zone analysis provided a coarse proxy for depth tolerances associated with different aquatic vegetation in the low-marsh habitat (i.e. emergent vegetation would occupy the upper 0.5 m, while submersed vegetation would occupy deeper zones).

We further broke down our study area into three regions (Figure 4.1) to investigate differences in low-marsh habitat across the study area. The areas were grouped according to the tertiary watershed boundaries (OMNR 2010). Watersheds for Nottawasaga and Black River Lake Simcoe have been consolidated into the “South” region (essentially Severn Sound), where nearshore areas are more gently sloping than the rest of the study area and support some of the largest coastal wetland units in Georgian Bay. The Muskoka and Magnetewan watersheds were grouped into the “Central” region, spanning the eastern shore of Georgian Bay from north of Severn Sound to Key River. The French River, Killarney, and Manitoulin Island watersheds were grouped into the “North” region, which contained the shoreline along the north shore of Georgian Bay between French River and the North Channel. For each region, we 1) evaluated the proportional depth zone composition, 2) calculated the area of low-marsh habitat per shoreline length, and 3) determined the mean slope. The area-to-shoreline ratio provided an estimate of the length of the average elevation profile in each region (i.e. distance from shore to lakeward extent of low-marsh).

Results

There were marked changes in the morphological structure underlying the simulated low-marsh habitat across the five lake-level scenarios. Between 176.0 m and 177.5 m, there was a shift from predominantly shallow (< 1-m deep) to deeper (> 1-m deep) low-marsh area (Figure 4.2). At 176.0 m, over 60% of the low-marsh area occurred at depths between 0 and 0.5 m, with each subsequent 0.5-m depth zone making up a progressively smaller proportion of the total area. In contrast, at 177.5 m, the majority of low-marsh habitat (50% by area and 65% by volume), occurred below the 1.5-m depth contour. At the intervening lake levels of 176.5 m and 177.0 m, the majority of the low-marsh area occurred at intermediate depth zones, 0.5 – 1.0-m and 1.0 – 1.5-m, respectively. At 175.5 m, there was a relatively even distribution of low-marsh area between shore and the 1.5-m depth contour, with the majority of habitat volume occurring below the 1-m depth contour.

Changes in depth-zone composition with lake level were consistent with the average elevation profile derived from the hypsographic curves (Figure 4.3a). There was a gradually-sloping section between 176.0 m and 175.5 m that essentially formed a “step” in the elevation profile. The upslope of the step (176.0 – 177.5 m) increased progressively with each scenario, which resulted in a greater proportion of deeper habitat (1.5 – 2.0 m) at higher lake levels. The downslope of the step was less steep and resulted in a more even distribution of low-marsh in the 175.5-m scenario. The position of the step relative to the lake level was an important factor determining whether composition of the depth zone was predominantly deep, intermediate, or shallow (Figure 4.3b, 4.3c, 4.3d, respectively).

In addition to shifts in morphology of the low-marsh habitat with different lake levels, we also projected large changes in overall low-marsh area (Figure 4.4). At the approximate long-term mean lake level (176.5 m), we projected a total area of 5,201 ha. We found that total area peaked at 7,113 ha under the 176.0 m scenario and was smallest at 1,752 ha under the 177.5 m scenario. Relative to the long-term mean, this amounted to a change in areal cover of low marsh by + 37% and - 66%, respectively. These are the corrected low-marsh areas that excluded built-up or forested areas. Progressively more low-marsh area had to be excluded as lake level increased (min: 5.8 ha at 175.5 m; max 340 ha at 177.5 ha).

The total volume of low marsh was relatively consistent across the lake-level scenarios (Figure 4.4). Total volume was greatest under the 176.5 m scenario ($38.4*10^6$ m^3). Total volume did not drop below 90% of the maximum volume under other lake levels, except at 177.5 m where the volume was 58% of the maximum. The 176.0 m scenario was associated with the second smallest volume, but the greatest low-marsh area. At 176.0, majority of low-marsh area was shallow (< 1 m), whereas at higher lake elevation, the low-marsh habitat was dominated by deeper water (> 1 m). The volume of low marsh appeared consistent across water-level scenarios because losses in area at higher lake levels were offset by the shift to a predominantly deeper low-marsh habitat. Area and volume of low-marsh habitat were most reduced at 177.5 m but the ratio of volume to area was highest at 1.28. The smallest volume-to-area ratio was 0.49, which corresponded to a lake level of 176.0 m.

The proportional area and volume for each depth zone was relatively consistent between the South, Central, and North regions of the study area (Figure 4.5). Despite differences in absolute area and volume of low marsh among regions, the consistent proportional composition by depth zone suggests that the average elevation profile (Figure 4.3a) is applicable to all three regions in study area. Mean slope of the low-marsh zone was consistently steepest in the Central region, followed by the North, then South regions; the only exception was at 177.5 m, where the mean slope for the North was lower than that for the South (Table 4.1). Given there are differences in mean slope among regions, the average elevation profile would have to be laterally stretched or compressed to appropriately represent the different regions. The area-to-shoreline ratios (i.e. length of the average elevation profile) were highest in the South and lowest in the Central region (Table 4.1). The elevation profile lengths were consistent with mean slope calculations. For a given lake level, the length of the average elevation profile in the South region was approximately twice that in the North region, and three times that in the central region.

Discussion

A basic assumption of our simulations is that marsh zonation is largely dependent on water depth, corrected for wave exposure and slope (Weller and Chow-Fraser 2018/CH3). The position of the step in the average elevation profile (Figure 4.3) relative to the lake level was the key determinant of the areal cover of low marsh. The literature has generally upheld the notion that under low water-level conditions, low marsh (aquatic habitat) would retreat in favor of high marsh (terrestrial habitat), given that emergent and meadow vegetation would colonize previously inundated areas (Hudon et al. 2005; Keddy and Reznicek 1986; Lyon and Drobney 1984). During the sustained low water period in Lake Michigan-

Huron (1999 – 2013), Fracz and Chow-Fraser (2013) raised concerns that the low lake levels would result in a loss of access to wetland fish habitat in Georgian Bay, notably fish spawning and nursery, as water levels decreased below the rock sill opening of protected wetlands. Further concerns were spurred by observations that the plant and fish assemblages during prolonged draw down in Georgian Bay wetlands had changed significantly to ones dominated by dense floating vegetation and fish communities that are tolerant of dense vegetation (Midwood and Chow-Fraser 2012). Leblanc et al. (2014) also documented changes in wetland vegetation and fish communities in wetlands in southeastern Georgian Bay that were attributed to the sustained low water conditions.

Simulations from our modelling can now provide a more complete understanding of what might happen. At 176.0 m, (a value that is slightly lower than the mean lake level during the 1999 – 2013 period), the area of low marsh was actually greater than those corresponding to higher and lower levels. Since total low-marsh area did not decline with water level but instead pivoted around 176.0 m, the total *area* of aquatic habitat may not be appropriate to assessing impacts of declining waters. Rather, we propose that the elevation profile is more appropriate for explaining why both fish and plant communities were less diverse after prolonged exposure to water levels at or near 176.0 m (Midwood and Chow-Fraser 2012). Under the 176.0 m scenario, over 60% of the low-marsh area occurred in less than 0.5 m of water, whereas under higher lake levels, the aquatic habitat was dominated by deeper waters (i.e. > 0.5 m). We hypothesize that during the sustained-low-water period from 1999-2013, there was loss of overall high-quality habitat for fish that depend on structurally complex SAV that require deeper water to flourish.

Low-marsh habitat is fundamentally a three-dimensional environment and most structurally-oriented fish use and move through it in three-dimensions. The depth zones provided a coarse approximation of the types of wetland vegetation that might be present as well as the sort of structure that might be used by fish. Intermediate densities of submersed aquatic vegetation promote the greatest diversity of fish species (Dibble et al. 1997; Eadie and Keast 1984; Smokorowski and Pratt 2007) and we would expect to see more of this vegetation type in deeper areas of the wetland (i.e. > 0.5m), whereas emergent and floating vegetation would be more prevalent in shallower waters (i.e. < 0.5 m). We observed a tradeoff between area and volume as a result of the low-marsh geomorphology; as lake levels approached the step at 176.0 m, total low-marsh area increased but the inundated area was shallower, resulting in lower volume. At this lake elevation, with 60% of the low-marsh area below 0.5 m, the SAV community would have been compressed to a very small area, while dense floating vegetation would have dominated. These conditions are known to be favorable to benthic-oriented species (e.g. Yellow Perch *Perca flavescens*, Brown Bullhead *Ameiurus nebulosus*, and Round Goby *Neogobius melanostomus*). Therefore, consistent with Midwood and Chow-Fraser's (2012) findings, during the period of sustained low water levels in Georgian Bay, there was loss of suitable high-quality fish habitat, even though there had not been loss in areal extent of low-marsh habitat.

The above observations are consistent with the response of wetland communities to water level stabilization in other areas (Keddy and Reznicek 1986; Leira and Cantonati 2008; Mortsch 1998; Wilcox and Meeker 1991). We propose that the stability of the lake levels occurring at a low lake level (i.e. 176.0 m) exacerbated these effects, as they relate to suitable fish habitat. Submersed aquatic vegetation provides more complex structure than floating or emergent vegetation, and intermediate densities of submersed aquatic vegetation maximize fish species richness (Eadie and Keast 1984). At low lake levels the low-marsh bathymetry favored the establishment of shallower-growing vegetation (i.e. floating and emergent), which provide less complex structure, and the lack of lake level fluctuation allowed the subsequent homogenization of that community, which likely further reduced the structural complexity and fish habitat quality. Under normally-fluctuating lake levels, low water conditions would support a more diverse array of vegetation types as individual species responded to the changing lake levels (Gathman et al. 2005). The shallow-dominated bathymetry at low lake levels would have a small volume-to-area ratio of low-marsh habitat, but would still represent a volume 90% of average lake levels (i.e. 176.5 m) and support a more structurally complex vegetation community than under stable lake levels. Further, the abundance of shallow habitat area under low lake levels facilitates the establishment of invasive species including *Phragmites australis*

(Tulbure and Johnston 2010) and *Typha X glauca* (Lishawa et al. 2010), which can form large, persistent stands that limit the establishment of higher quality fish habitat.

Our modelling does not take into consideration interannual fluctuations in lake levels since the GLM was developed with a dataset derived from a period of sustained low water levels (Weller and Chow-Fraser 2018/CH3). Lake-level fluctuations play a key role in structuring wetland vegetation communities (Keddy and Reznicek 1986; Leira and Cantonati 2008) so we must be cautious interpreting our simulations. Since the wetland inventory used to train the GLM was derived from imagery acquired between 2002 and 2008 (Midwood et al. 2012) and the sustained-low-water period began in 1999, the model assumes that lake levels had been stable for at least three years. A three-to-five-year lag time has been observed for wetland vegetation communities in response to changes in lake level (Gathman et al. 2005; Quinlan and Mulamoottil 1987; Wilcox and Nichols 2008), so we assumed that our training data (MCWI; Midwood et al. 2012) are representative of a vegetation community that had adapted to a lower water regime. Functionally, this means that our low-marsh projections for each lake level assume that the lake level has been stable for at least three years and that vegetation classes in the community had shifted laterally to their optimal depth zones. Given that stable, low lake levels are expected to be more frequent in the future (Angel and Kunkel 2010; Lu and Nairn, in submission; Mortsch 1998), we believe our simulated low-marsh extents are valid.

Periods of low lake levels occurred in the 1930s and 1960s, but the low water period from 1999 – 2013 was the longest period of stable lake levels on record (1860 – present). Considering the lagged response of wetland vegetation, if lake levels shifted from low to high then we would expect our simulated low-marsh extents to be underestimates since the lakeward edge of the low marsh at the lower water level would not yet have shifted shoreward. If lake levels shifted from high to low then our modelled extent would be an overestimate since lakeward boundary of low-marsh vegetation would not yet have shifted to the new outer depths. We felt it necessary to acknowledge this limitation since lake-level fluctuations are such a fundamental aspect of coastal wetland systems.

We limited our lake level evaluations to historically observed lake levels and those likely over the next century. Lower, more stable lake levels appear to be the most consistent prediction for future lake levels (Angel and Kunkel 2010; Lu and Nairn, in submission). Fracz and Chow-Fraser (2013) predicted massive losses of coastal wetland area as lake levels fell from 176.5 m to 173.0 m, because of limited space to shift lakeward or a loss of hydrologic connection to Georgian Bay proper. We did not directly calculate the amount of low marsh that would be lost due to the stranding of wetland habitat, but our low-marsh simulations only included areas that had a direct surface-water connection to Georgian Bay proper. Between our 176.5 m and 175.5 m low-marsh simulations there is evidence of protected-embayment wetlands that have been stranded as a result of the low water levels. The loss in overall habitat area that we modelled from 176.0 m to

177.5 m can be attributed to a loss of wetland area due to stranding and from the reduced habitat area as the low-marsh zone advances over the lakeward edge of the step in the average elevation profile. While we did not consider any lower lake levels in this paper, we would expect to see substantial declines in low-marsh area due to drying or stranding of wetlands, consistent with findings by Fracz and Chow-Fraser (2013). In the case of fringing wetlands, those less susceptible to stranding, we expect some capacity for them to shift lakeward as deeper, submersed vegetation species occur beyond the lakeward boundary of coastal wetlands (i.e. 2 m), and at depths of up to 5 m in Georgian Bay (Midwood 2012). However, the loss of access to some wetlands due to stranding may have consequences for fish habitat for species that exhibit some level of site fidelity during certain life stages, notably important sport-fish (e.g. muskellunge spawning; Weller et al. 2016/CH1).

This is the first attempt at modelling changes in low-marsh habitat across different lake levels in Georgian Bay at a regional-scale. Mapping efforts for coastal wetland vegetation have been achieved with satellite imagery (Midwood and Chow-Fraser 2010; Midwood et al. 2012; Rokitnicki-Wojcik et al. 2011; Wei and Chow-Fraser 2007) as well as site-specific bathymetry-based modelling (Boyd 2017; Fracz and Chow-Fraser 2013). Most wetland vegetation modelling that has incorporated hydrogeomorphic parameters focused on finer-scale vegetation modelling (e.g. Hebb et al. 2013; Wilcox and Nichols 2008) but we have not seen it applied at a broader-scale. The GLM that we used for our modelling was established as effective for a lake level of 176.17 m (Weller and Chow-Fraser 2018/CH3). The low-marsh projections for our lake level scenarios were largely consistent with expectations from field observations and comparison with satellite imagery, suggesting good model performance at other lake levels. The vertical and horizontal accuracies of the data used for the DEM were better for the bathymetric data (i.e. < 176.0 m) than for the topographic data (i.e. > 176.0 m), which is why we used the mask layers to exclude any erroneous elevations in the DEM. While higher resolution elevation data for this modelling effort would have been ideal, the DEM that was derived by Weller and Chow-Fraser (2018/ CH3) was the best available for the study area. The increasing amount of low-marsh habitat removed by the masks at the higher lake levels can be attributed to resolution issues in the underlying data. Projections to lower lake levels (< 176.0 m) should be more accurate due the higher-resolution data, and should be valuable for modelling possible future, low-water scenarios. The low-marsh projections for the higher lake levels (176.5 – 177.5 m), while less accurate, are still a useful tool for evaluating low-marsh extent at historic lake levels. If and when higher-resolution DEM becomes available, it would be useful to incorporate them and rerun our model.

One of the most important findings in this study is that habitat volume was a more informative parameter than habitat area in understanding the impact of water levels in Georgian Bay, especially in reference to suitable fish habitat. It is apparent from our work that the interaction between lake level and the nearshore geomorphology is a key driver determining low-marsh size and composition. The range of likely lake levels that have been forecast over the next century are largely within the range of historic observations (1860 – 2017), and possibly just beyond recorded extremes. With respect to fish habitat, it appears the greater concern is the *quality* of available low-marsh habitat and rather than the total areal cover of low marsh. Sufficient low-marsh habitat should persist through this range of lake levels but the hydrographic regime may ultimately determine the suitability of that habitat for Georgian Bay fish species.

Acknowledgements

With regards to the DEM developed for this project, it was produced by McMaster University based on Canadian Hydrographic Service charts and/or data, pursuant to CHS Direct User Licence No. 2016-1121-1260-M. The incorporation of data sourced from CHS in this product shall not be construed as constituting an endorsement by CHS of this project. This product does not meet the requirements of the *Charts and Nautical Publications Regulations, 1995* under the *Canadian Shipping Act, 2001*. Official charts and publications, corrected and up-to-date, must be used to meet the requirements of those regulations. This work was supported in part through an Ontario Graduate Scholarship for Dan Weller and a research contract from Environment and Climate Change Canada.

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Table 4.1: Mean (± SE) slope (% rise) and average elevation profile length in simulated low-marsh zone for each lake level scenario and region of the study area. Average elevation profile was calculated as the low-marsh area-to-shoreline ratio and approximates the mean distance from shore to the lakeward edge of the low-marsh zone.

Lake Level (IGLD 1985)	**Mean Slope (%)**			**Average Profile Length (m)**		
	South	**Central**	**North**	**South**	**Central**	**North**
175.5	0.96 ± 2.11E-03	1.68 ± 2.36E-03	1.42 ± 3.43E-03	34.78	8.79	12.71
176.0	0.90 ± 1.99E-03	1.45 ± 1.99E-03	1.22 ± 2.77E-03	28.57	7.98	8.94
176.5	0.87 ± 2.36E-03	1.55 ± 2.15E-03	1.19 ± 2.94E-03	34.67	11.16	18.12
177.0	0.70 ± 2.43E-03	1.29 ± 2.38E-03	0.93 ± 2.82E-03	23.81	9.28	14.43
177.5	0.82 ± 3.99E-03	1.11 ± 3.34E-03	0.69 ± 3.28E-03	14.40	6.64	10.52

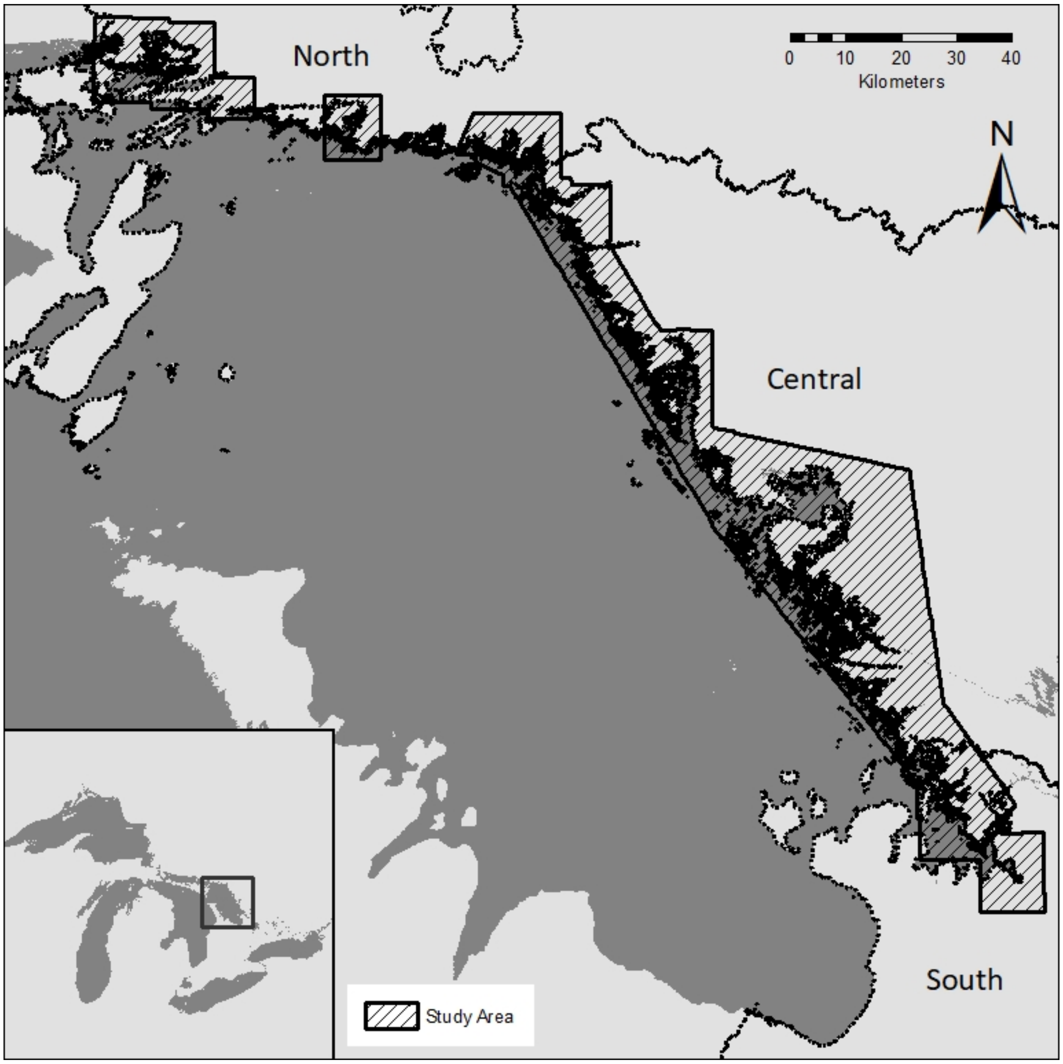

Figure 4.1: Simplified outline of study area (hatched area) along eastern and northern shoreline of Georgian Bay, Lake Huron (inset: Laurentian Great Lakes). Study area was divided into South, Central, and North to evaluate regional differences in simulated low-marsh habitat.

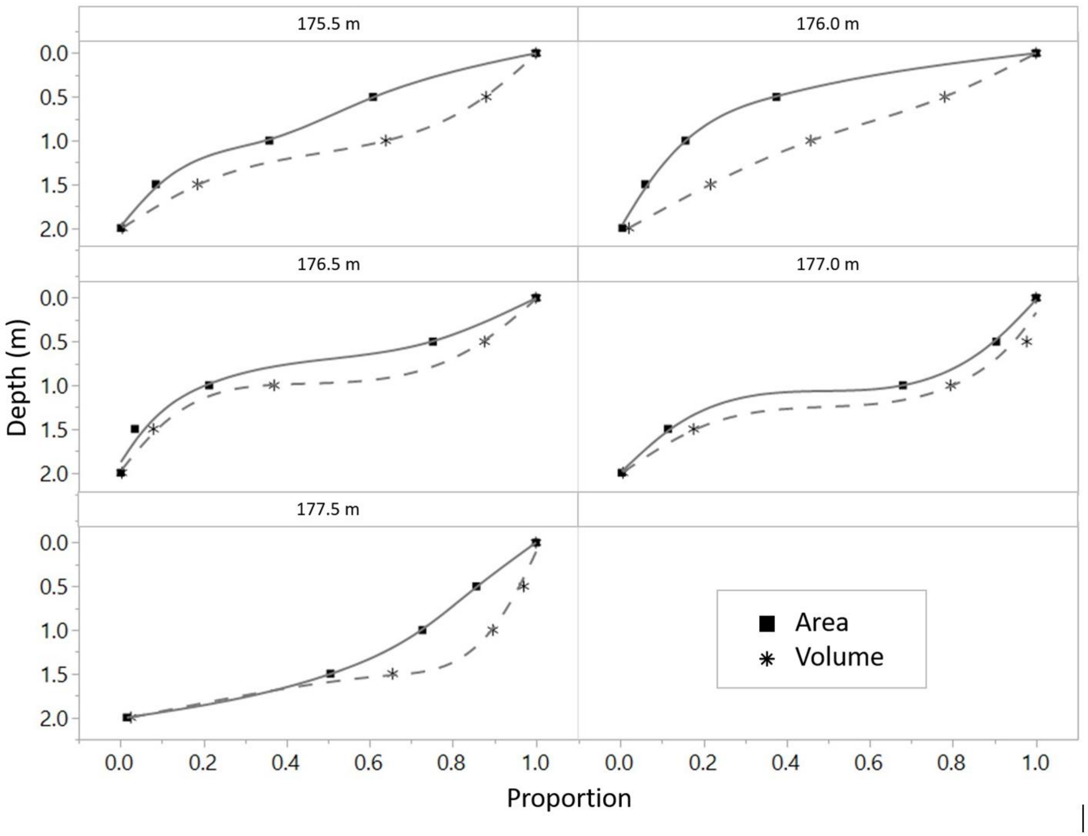

Figure 4.2: Smoothed hypsographic curves of proportional area (solid line) and volume (dashed line) of simulated low marsh under five lake-level scenarios (indicated at top of each panel; m IGLD85). Calculation of proportional area (squares) and volume (stars) were made at 0.5 m intervals from 0 – 2 m. The 2 – 5 m depth zone was omitted.

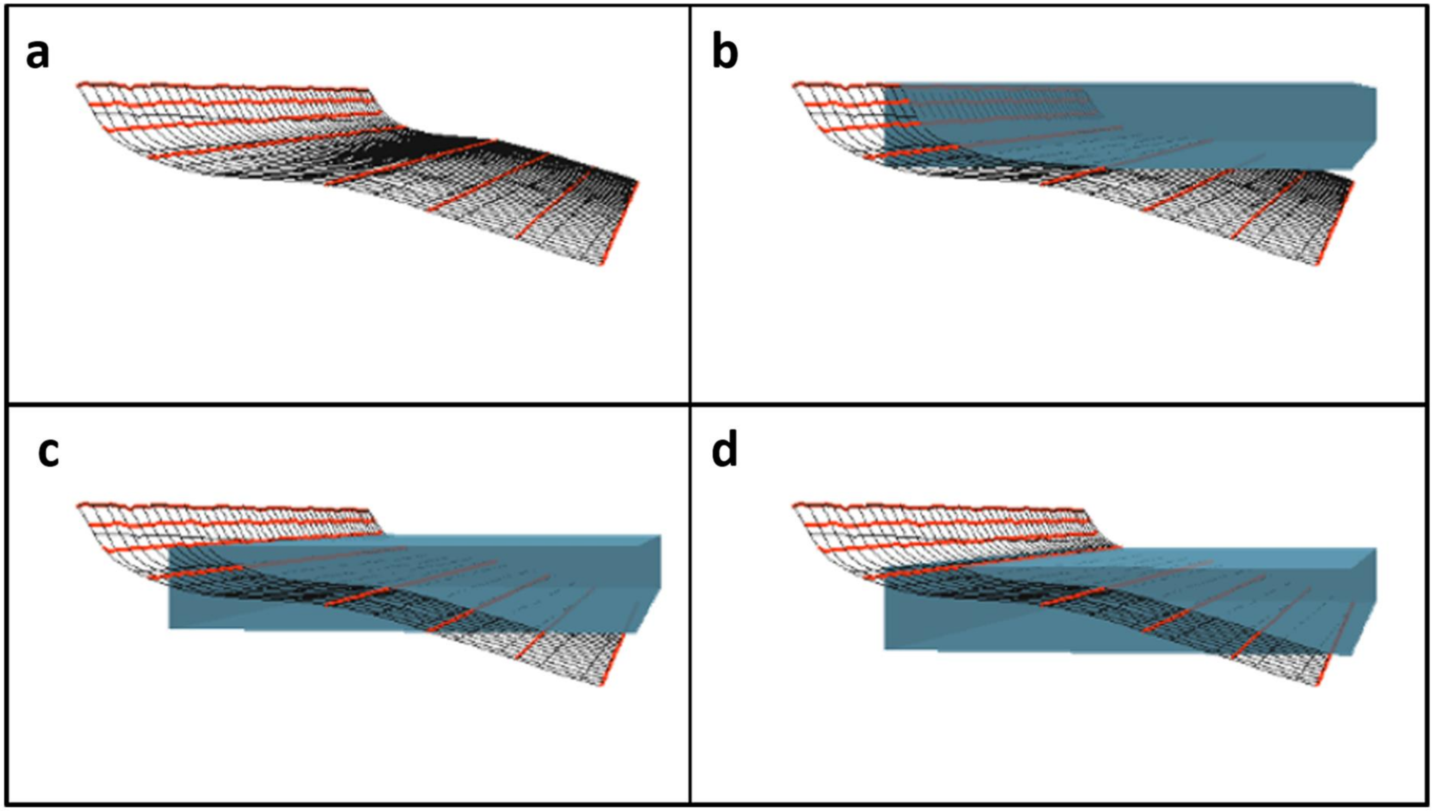

Figure 4.3: Average elevation profile for simulated low marsh in Georgian Bay. a) Wire-mesh surface illustrates the simplified geomorphology underlying simulated low marsh. Elevation contours (thick lateral lines) are in 0.5 m intervals between 177.5 m (top) and 174.0 m (bottom). Approximate depth window corresponding to low marsh habitat (0 – 2 m deep; polygon) illustrates shift in depth composition from b) deep-dominant (177.5 m), c) intermediate (176.5 m), to d) shallow-dominant (176.0 m).

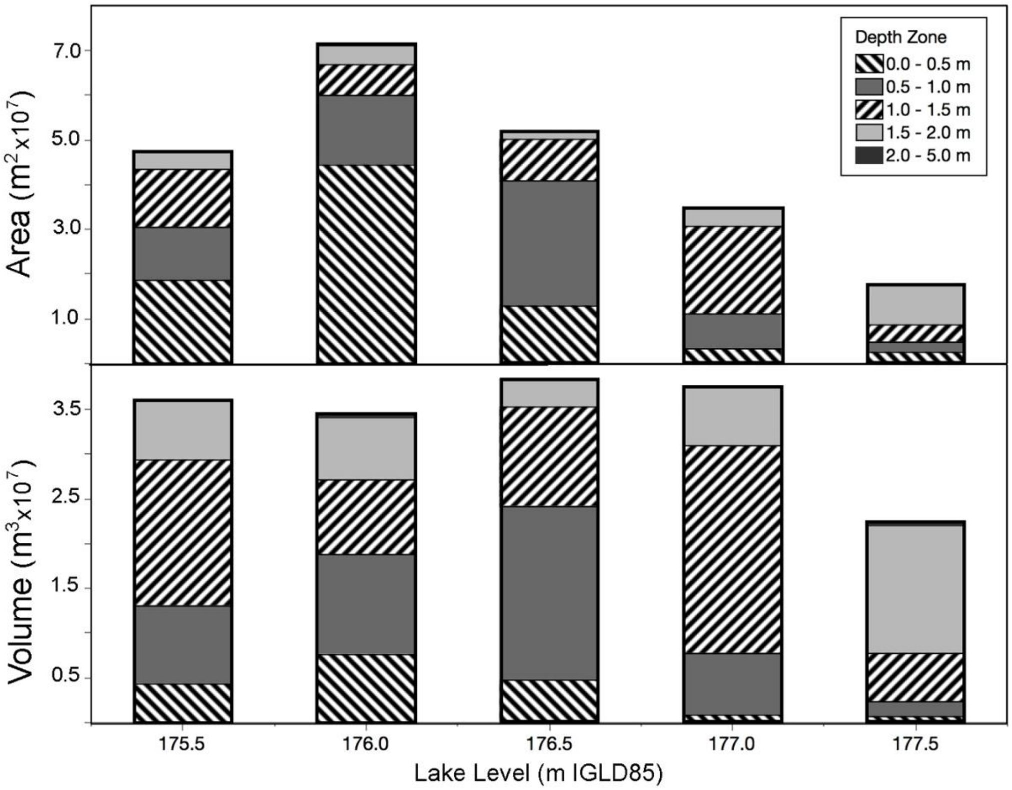

Figure 4.4: Total area (m^2) and volume (m^3) of modelled low marsh habitat across the Georgian Bay study area for five lake-level scenarios. Area and volume measurements are partitioned by 0.5 m depth zones between 0 and 2 m; depths from 2-5 m were treated as a single unit.

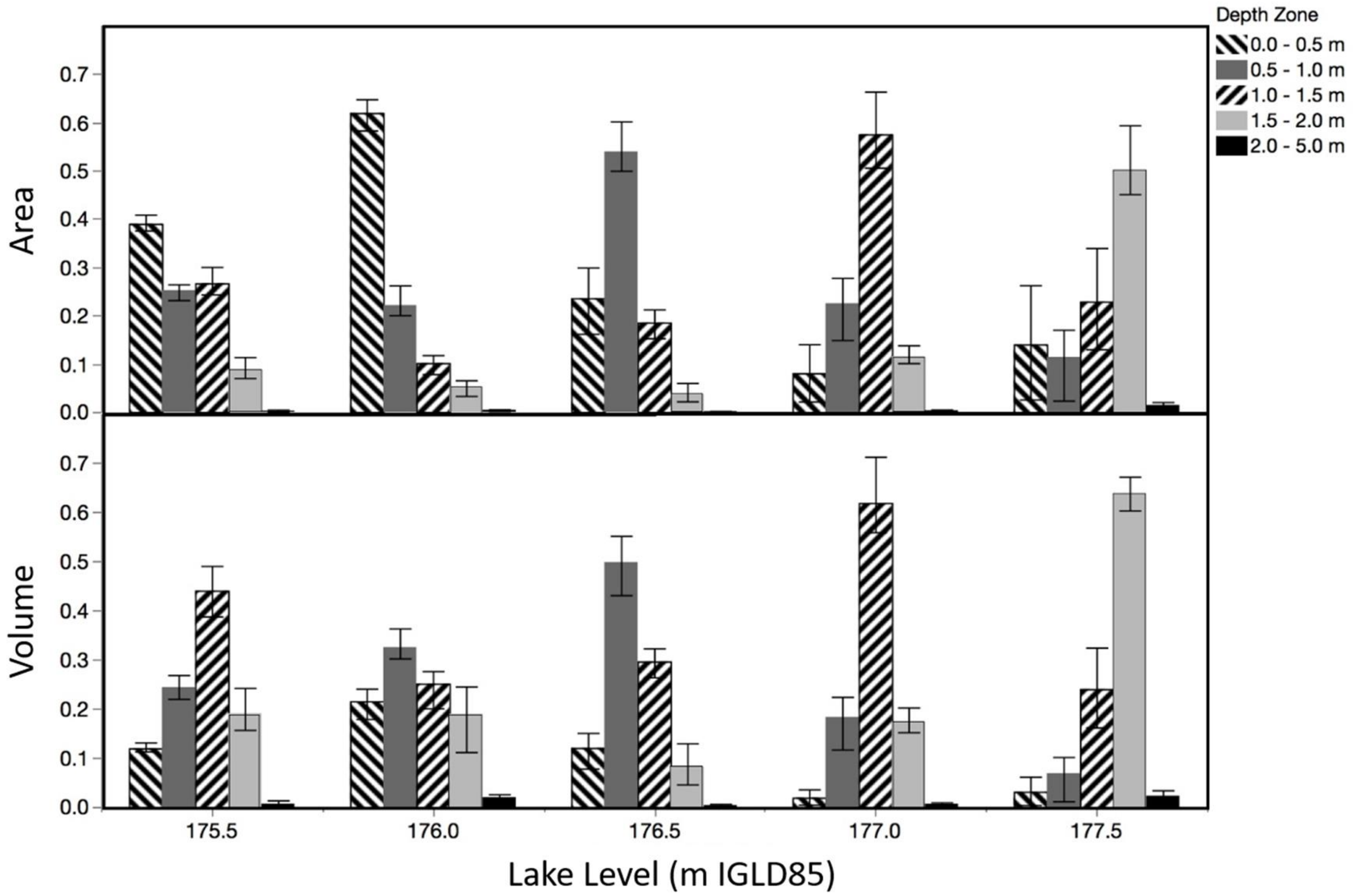

Figure 4.5: Proportional breakdown of low-marsh area and volume by depth zone for each lake level scenario. Displayed proportions are means of all three regions (South, Central, North), with range error bars

Chapter 5

DEVELOPMENT OF A MULTI-SCALE WETLAND RESILIENCE INDEX FROM MUSKELLUNGE NURSERY HABITAT IN GEORGIAN BAY, LAKE HURON

In submission: Weller JD, Chow-Fraser P (2018/CH5) Development of a multi-scale wetland resilience index from Muskellunge nursery habitat in Georgian Bay, Lake Huron. Submitted to Ecological Indicators (Chapter 5)

Abstract

In a 2012 study, no age-0 Muskellunge *(Esox masquinongy*) were found in any of 16 historic nursery sites in coastal marshes of southeastern Georgian Bay (SEGB), and this was attributed to sustained low water levels (1999-2013) that had altered the vegetation structure of nursery habitat. In the same study, age-0 Muskellunge were found in 16 coastal marshes surveyed in northern Georgian Bay (NGB), even though these sites had been subjected to the same water-level conditions. We hypothesize that hydrogeomorphic features of NGB sites made them resilient to effects of sustained low lake levels that made the SEGB sites unsuitable for age-0 Muskellunge. Compared to their SEGB counterparts, the NGB nursery sites were significantly steeper (Wilcoxon Rank Sum; $Z = -4.47$, $p < 0.001$), deeper (Wilcoxon Rank Sum; $Z = -4.73$, $p < 0.001$), and less sheltered (Wilcoxon Rank Sum; $Z = -3.30$, $p = 0.001$) under low water levels. We used these hydrogeomorphic features to develop a multi-scale Resilience Index (RI) for identifying coastal wetlands that are resilient to stable low lake levels. The RI correctly classified the NGB and SEGB nursery sites, with an area-under-the-curve score of 0.973. Coarser-scale variants of the RI provide a regional screening tool in the identification of resilient wetland habitat (e.g. potential Muskellunge nursery habitat), and a basin-wide approach to identify vulnerable wetland habitats. This multi-scale index, in conjunction with targeted field surveys, should provide managers a useful tool in the face of uncertain water level forecasts.

Introduction

Georgian Bay, Lake Huron supports a world-class, recreational Muskellunge (*Esox masquinongy*) fishery. The eastern and northern shorelines in particular are characterized by thousands of islands and small embayments that support a diverse collection of habitat types, including many high-quality coastal wetlands (Cvetkovic and Chow-Fraser 2011; Midwood et al. 2012). Coastal wetlands provide critical spawning and nursery habitat for many Great Lakes fish species (Jude and Pappas 1992; Wei et al. 2004), including Muskellunge, and those in Georgian Bay have remained largely unaffected by the types of anthropogenic disturbances that have been associated with loss or degradation of Muskellunge habitat in other regions (e.g. Dombeck 1986; Farrell et al. 2007; Rust 2002). Recently, however, age-0 Muskellunge could no longer be found in nursery sites of southeastern Georgian Bay (SEGB) that had been identified from field surveys 30 years earlier (Leblanc et al. 2014). Evidence from radio-telemetry (Weller et al. 2016/CH1) and genetic studies (Wilson et al. 2016) indicate that the Muskellunge of Georgian Bay exhibit spawning-site fidelity. Since spawning grounds were still active in SEGB (Weller et al. 2016/CH1), age-0 Muskellunge should have been found at the historic nursery sites unless the habitat had ceased to be suitable.

Leblanc et al. (2014) hypothesized that changes in the wetland fish and vegetation communities resulting from the preceding decade of sustained low water levels in Lake Michigan-Huron had reduced suitability of these sites for age-0 Muskellunge. The low water levels, however, did not seem to affect habitat suitability of coastal wetlands in northern Georgian Bay (NGB) since age-0 Muskellunge had been found there in 2012 and 2013 (Leblanc 2015). Given the differential responses of nursery sites in SEGB and NGB to the same lake levels, another variable must interact with water level to influence habitat suitability for age-0 Muskellunge.

The “typical” muskellunge nursery habitat in southeastern Georgian Bay has been described by Craig and Black (1986) as wetlands with high stem densities of emergent vegetation at the shoreline, becoming less dense out to 1 m deep (<100 stems/m^2), and having 40-50%cover of submersed aquatic vegetation (SAV) in more open water. Leblanc (2015) found that an important habitat features in nursery sites in NGB was a greater ratio of SAV stems within the upper water column relative to low-growing forms, such that almost 30-70% of the water column (i.e. biovolume) was occupied by SAV (Leblanc and Chow-Fraser 2017). Such descriptions of moderate densities of wetland vegetation providing complex, three-dimensional structure within the nursery habitat are broadly consistent across other study areas in the Great Lakes basin (Murry and Farrell 2007; Kapuscinski and Farrell 2014; Werner et al. 1996).

For age-0 Muskellunge, suitable habitat is a tradeoff between foraging efficiency and protection from predators (Crowder and Cooper 1982; Diehl and Eklov 1995; Gotceitis and Colgan 1989), factors that are critical for age-0 Muskellunge, but that are also important for diverse fish communities (Eadie and

Keast 1984; Tonn and Magnuson 1982). As such, suitable habitat for age-0 Muskellunge is likely to be high-quality wetland that is suitable for a wide spectrum of other fish species. An essential condition for maintaining structural diversity of the wetland plant community in such wetlands is interannual fluctuation of Lake Huron water levels. Although ecologists agree that dampening or stabilization of these fluctuations could reduce or eliminate habitat suitability for wetland fish (Gathman et al. 2005; Midwood and Chow-Fraser 2012; Wilcox 2004; Wilcox and Meeker 1991), sites can and do vary in response to these fluctuations depending on their geomorphology (Wei and Chow-Fraser 2008).

Site geomorphology can interact with lake level to determine the slope within a single wetland, and this in turn influences the amounts and types of aquatic vegetation found in littoral areas (Duarte and Kalff 1986; Duarte et al. 1986). Leblanc et al. (2014) reported that substrate slopes at SEGB sites had been steeper under high water levels, and appeared to be more similar to those in NGB (Leblanc 2015). In fact, site slope emerged as the main predictor of habitat suitability for all sites studied in Georgian Bay (Leblanc and Chow-Fraser 2017). Wind and wave exposure, which is subject to similar hydrogeomorphic drivers, also have documented effects on wetland vegetation (Duarte and Kalff 1990; Jupp and Spence 1977; Keddy 1982, 1984a, 1984b).

We hypothesize that differences in resilience of NGB and SEGB sites to sustained low water levels is primarily due to differences in local hydrogeomorphic features, in particular slope and wave exposure. An alternate hypothesis is that portions of SEGB wetlands had dried up or had become stranded by the low water levels, and were therefore no longer available as fish habitat (Fracz and Chow-Fraser 2013; Lyon and Drobney 1984). We will test these hypotheses by statistically comparing slopes, wave exposures, areal extents, and volumes of wetland habitats for both regions under high and low lake levels. We will identify hydrogeomorphic features that affect the resilience of Muskellunge nursery habitat to stable low water levels and ultimately develop an index of wetland resilience to remotely screen for age-0 Muskellunge habitat. Since wetlands that provide suitable habitat for age-0 Muskellunge should also be healthy wetlands suitable for a diverse fish community, we will apply this index more broadly as a management tool to identify regions of Georgian Bay with coastal wetlands vulnerable or resilient to water-level disturbances arising from global climate change.

Methods

Multi-scale Approach

Ecological processes can be influenced by factors at multiple spatial scales, which must be considered when developing and applying environmental indicators. Furthermore, the intended management applications of our Resilience Index each had unique objectives that span a broad range of spatial scales. As such, we have consciously developed several variants of the index to account for different spatial scales (and applications), rather than take a one-size-fits-all approach. We took this multi-scale approach to ensure that the index would be consistent across all spatial scales with respect to performance, feasibility and ability to provide meaningful information.

Index development and application were designed for three distinct spatial scales: **local**, **regional**, and **basin-wide**. The finest spatial scale we evaluated was at the **local** scale (~ 1 ha; i.e. a wetland unit); development of the **Resilience Index (RI)** at this scale was based on hydrogeomorphic features of nursery sites where age-0 Muskellunge had been confirmed from field surveys. We scaled up the RI for application at the **regional** scale (1,000 – 10,000 ha; i.e. a large embayment), by employing coarser-resolution hydrogeomorphic data (primarily to reduce computational demands) that could be used as a screening tool to guide targeted field surveys. Finally, at the **basin-wide** scale (i.e. eastern and northern shorelines of Georgian Bay), we again scaled up the RI to identify regions in the Georgian Bay coastline where wetlands have been assessed as being vulnerable to stable low lake levels. Our goal was to use basin-wide RI scores to classify shoreline stretches into vulnerability categories that can be used as a scientifically defensible way to select sites for monitoring in the era of unpredictable water-level fluctuations.

Local Scale: Habitat Characterization

Data for development of the local RI were obtained from published studies in two regions of Georgian Bay, southeastern Georgian Bay (SEGB) and northern

Georgian Bay (NGB; Figure 5.1), that had been sampled under two different lake-level scenarios. The two lake-level scenarios corresponded to 1981, when water levels had been relatively high (May to October monthly mean 176.8 m) and 2012, when water levels were almost a meter lower (May to October monthly mean 176.0 m). For RI development, we included 16 nursery sites in SEGB that had been identified in 1981 (Craig and Black 1986) and that had been re-sampled in 2012 (Leblanc et al. 2014); we also included 16 sites in NGB which had been sampled in 2012 and 2013 (Leblanc 2015). Note that the NGB sites had been sampled across two years (2012 and 2013) with similarly low mean water levels (approximately 8 cm difference).

We used a standardized protocol to delineate the boundary of a nursery site by applying a 100 m buffer around a confirmed capture location of an age-0 Muskellunge, and excluding areas deeper than 2 m. We excluded areas below the 2-m contour because we assumed that age-0 Muskellunge were using coastal wetlands as nursery habitat and the 2-m depth contour is the generally accepted lakeward boundary (Albert et al. 2005; Keough et al. 1999). If the capture site were located along a straight section of shoreline, then the nursery site would be delineated by a semi-circle with a 100-m radius, and exclude any area beyond the 2-m depth contour. We also assumed that age-0 Muskellunge would use wetland vegetation for protection and stay within it, rather than move between spatially distinct wetland patches. Therefore, only contiguous areas within the 0 – 2-m depth zone surrounding the capture location were considered nursery habitat

(Figure 5.2; cross-hatching, zone 1). This ruleset was applied to all capture locations to delineate the boundaries for nursery sites under both the high-water and low-water scenarios.

We did not use an existing wetland habitat layer (e.g. the McMaster Coastal Wetland Inventory (MCWI) from Midwood et al. 2012; low-marsh layer from Weller and Chow-Fraser (2018/CH3)) to restrict site identification, because several nursery sites used in this study occurred in areas that have not been classified as wetlands in available datasets. The misclassified wetlands were very small and we assume that these omissions in the independent wetland inventories were the result of detection limits or human error during manual delineation of wetlands (Midwood et al. 2012) or the coarse spatial resolution of modelling inputs (Weller and Chow-Fraser 2018/CH3). We have confirmed that all nursery sites in this study occur in coastal wetlands.

All spatial data processing and analyses were completed with ArcGIS Pro v2.1 (ESRI, Redlands, California). We used a digital elevation model (DEM) built for each of the NGB and SEGB regions to derive hydrogeomorphic features at each nursery site. The DEMs were assembled with bathymetric data from the Canadian Hydrographic Service navigational charts and topographic data from the Ontario Contour (OMNR 2009a) and Spot (OMNR 2009b) elevation datasets. We used the Topo to Raster tool in ArcGIS Pro (based on the ANUDEM program; Hutchinson 1989) to build a DEM for each region with a 5 m resolution.

We derived the shoreline and the 2-m depth contour for each region from its respective DEM. To improve calculation accuracy of nursery site area and the wave-exposure metric, we manually updated the shoreline using the most appropriate imagery to correct deviations from the true shoreline and to add small islands that had been missed in the DEM. In NGB, we used imagery from the Central Ontario Orthophotography Project (20-cm resolution; lake level ≈ 176.8 m) for the high-water scenario (176.8 m), and Quickbird imagery (60-cm resolution; lake level ≈ 176.2 m) for the low-water scenario (176.0 m). In SEGB, we used the digital terrain model (2-m resolution) derived from the South Central Ontario Orthophotography Project (SCOOP), which had been collected when the lake level was approximately 175.9 m, which is lower than both the low (176.0 m) and the high (176.8 m) lake-level scenarios. Therefore, the terrain model should accurately capture the shorelines for both scenarios since they would not have been obscured by water in the SCOOP imagery.

We classified our sites into four types: 1) **fringing** (occurring along a relatively straight section of shoreline) 2) **open embayment** (recessed into the shoreline with a large and exposed mouth), 3) **protected embayment** (embayment sheltered from most directions; i.e. accessible only through narrow channel(s) or protected by small islands), or 4) **archipelago** (amongst small shallow islands and lacking a clearly defined and persistent shoreline across lake levels). We measured five habitat features: area, volume, depth (volume/area), slope, and wave exposure at each nursery site corresponding to both lake-level scenarios based on boundaries of the nursery sites and the regional DEMs.

We derived hydrogeomorphic feature layers for water depth and slope from the DEMs and used the mean for all cells within the nursery-site boundary as a representative measure for each site. We calculated a Relative Exposure Index (REI; Fonseca and Bell 1998; Murphey and Fonseca 1995) as a metric of wave exposure. The formulation described by Malhotra and Fonseca (2007) was used to account for the effects of bathymetry on wave development. To determine fetch, lines radiating from sample points were extended until they intersected with the shoreline at increments of 11.25°. An inverse distance weighting function was then applied to each ray to account for the effects of bathymetry on wave development. A weighted average of neighboring rays was taken to determine effective fetch along eight bearings (N, NE, E…etc). The REI was calculated from the equation:

$$REI = (\sum_{i=1}^{8} E_i \times V_i \times D_i)\,/8$$

where E_i = effective fetch along the *i*th bearing, V_i = wind speed along the *i*th bearing, and D_i = duration of wind along the *i*th bearing. We used wind data from the US Army Corps of Engineers Wave Information Studies from Stations 93338 and 93370 for NGB and SEGB, respectively. Each station was approximately 10 km offshore of our nursery sites in each region and provided hourly hindcasts of wind speed and direction data from 1979 to 2014. We used wind data from a six month window (May to October) and only considered the highest 95% of wind speeds from each station (Fonseca and Bell 1998). The REI calculation was computationally intensive so we distributed sample points in a 10-m grid pattern within each nursery site and took the median REI of the sample points as our wave exposure metric for the site.

All statistical analyses were performed with SAS JMP 13.0.0 (SAS Institute Inc., Cary, NC), unless otherwise indicated. Our goal was to evaluate how the hydrogeomorphic features of each site differed between regions and lake-level, particularly if there were changes between the high- or low-water scenarios, or regional characteristics that would explain the apparent resilience of the NGB sites to the period of sustained low lake levels. We used a Wilcoxon Signed Rank test to compare the median values of each hydrogeomorphic feature between the high- and low-water scenarios. We then compared hydrogeomorphic features of nursery sites between regions and lake-level scenarios (i.e. SEGB high water, NGB low water) using a Kruskall-Wallis test, with a Steel-Dwass post-hoc test for multiple comparisons. We did not exclude any sites for this test. A Bonferroni correction of $\alpha = 0.01$ was applied to both tests.

Local Scale: Resilience Index

We used results from our nursery-habitat characterization to develop an index to score areas based on their likelihood of supporting wetland habitat that is resilient to stable low lake levels. The development of this index was based on the assumptions that suitable Muskellunge nursery habitat (i.e. age-0 Muskellunge were present) consisted of a structurally diverse aquatic vegetation community, and that under stabilized lake levels age-0 Muskellunge would only be found in resilient wetlands. Therefore, all NGB sites were considered “resilient” since age-0 Muskellunge had been found there under stable low lake levels. We selected the hydrogeomorphic variables that best differentiated the nursery sites in NGB from SEGB under the low-water scenario, and then developed a habitat suitability curve (HSC) for each variable using measurements from the NGB low-water scenario. We fitted a suite of candidate distributions to the data for each variable to use as the basis for the HSC, and then selected the best-fitting one based on Akaike's Information Criterion (AICc) scores and goodness-of-fit tests. The probability density function from the best-fitting distribution was re-scaled to values between 0 and 1 to arrive at the HSC. A bootstrapping protocol in R (R Core Team 2018) was used to estimate the confidence intervals for each HSC (Som et al. 2016). We calculated the score of our RI as the mean of the HSC scores from each selected variable at a given site. We evaluated the performance of the RI based on its ability to correctly differentiate the NGB (i.e. “resilient”) and SEGB (i.e. “not resilient”) sites, using the area-under-the-curve (AUC) of a receiver operator characteristic (ROC) curve, a threshold-independent evaluation of the model’s performance (Fielding and Bell 1997), and a confusion matrix with a binary classification (i.e. “resilient” or “not resilient”). To be conservative for the binary classification and to minimize omission of "resilient" habitats, we set the threshold value so that all NGB sites would be classified as "resilient".

For operational use, we split the RI scores into three categories: "most resilient", "moderately resilient", and "least resilient". We maintained the same threshold as the binary classification such that the "least resilient" category did not contain any of the NGB sites. We set an upper threshold to separate between "moderately resilient" and "most resilient", so that only NGB sites were included in the "most resilient" category. Functionally, this meant that the "least resilient" and "most resilient" classes exclusively contained SEGB and NGB sites, respectively. The "moderately resilient" class was where the lowest NGB scores and highest SEGB scores overlapped.

Regional Scale: Resilience Index

Our goal at the regional scale was to apply the local RI across a larger geographic area for use as a screening tool to identify broad areas (e.g. a large embayment) that support high proportions of resilient wetlands, and to guide targeted field surveys to identify Muskellunge nursery habitat. The local-scale methods described previously were too computationally intensive to apply at the regional scale, so we developed an alternative protocol using coarser-scale hydrogeomorphic measurements for the Regional RI.

We worked from the same 5-m resolution DEMs as described previously but did not make manual corrections to the shoreline, using the lake elevation contour as derived from the DEM. We maintained the study space extent as the 0 – 2-m depth zone within each region, but opted for coarser-scale measurement of the REI. We applied a tessellation of 1-ha hexagons over the 0 – 2-m zone and used the centroids as sample points. Any centroids on land were shifted to the nearest point along the shoreline. This amounted to a maximum spacing between points of about 60 m. We then interpolated a regional REI layer using a Triangulated Irregular Network. We used the Focal Statistics tool, essentially a moving window, in ArcGIS Pro to calculate a mean value for each hydrogeomorphic feature at a given location. A circle with a 100-m radius was used as the focal window for consistency with the local-scale delineation of nursery site boundaries. We compared the hydrogeomorphic feature measurements and RI scores between the two scales (i.e. local and regional) to verify that the index scaled-up appropriately, and that the three operational resilience categories associated with the local RI had been conserved.

We applied the RI across the entire NGB and SEGB regions, and a third region in northeastern Georgian Bay (NEGB), Pointe au Baril. There was only one confirmed Muskellunge nursery site in NEGB that could serve as a test site, so we also considered suspected Muskellunge nursery sites based on radio telemetry locations of adult Muskellunge during spawning season (Weller et al. 2016/CH1) as part of our index validation. Within each region we quantified the area of each resilience category for the total study space (i.e. 0 – 2-m depth) and for wetland habitats, based on the MCWI (Midwood et al. 2012).

Basin-wide Scale: Vulnerability Index

The **Vulnerability Index** (VIn) was essentially a coarser version of the regional RI with a reciprocal scoring system; an RI score of 0 would correspond to a VIn score of 1, indicating that a given area supported coastal wetlands that would be very vulnerable (i.e. not resilient) to wetland-community changes under stable low lake levels. Scaling up to a basin-wide RI required further simplification of the index. We excluded the wave exposure metric because it was the most limiting hydrogeomorphic feature with respect to computational demands. The performance of the regional RI against a version excluding wave exposure was checked to validate the appropriateness of this decision. We used a 10 m resolution DEM of Georgian Bay (see Weller and Chow-Fraser 2018/CH3 for full details) and the same protocols as the regional RI for measuring depth and slope. We calculated the RI for the 0 – 2-m depth zone across the eastern and northern shoreline of Georgian Bay (Severn Sound to MacGregor Bay) and subsequently considered only areas that had been identified as inundated wetlands area in the MCWI (low marsh; Midwood et al. 2012). We applied a tessellation of 10,000 ha hexagons across the Georgian Bay shoreline and calculated a representative RI score for each hexagon as the mean RI score for the entire wetland area within the hexagon. The representative RI scores were then converted to the corresponding VIn scores. So a hexagon containing 60 ha of wetland would be represented by 6,000 pixels with 10-m resolution (aligned to the DEM). The mean RI score of each of those 6,000 wetland pixels would be the representative RI score for the hexagon, which would then be converted to the corresponding VIn score.

We developed a ranking system to prioritize areas for management focus based on their VIn scores and total wetland area, such that hexagons with more wetland area received higher priority. For example, we determined that a hexagonal tile with only 1 ha of wetland and a VIn of 0.95 should have a lower priority than a tile with 100 ha of wetland and a VIn of 0.7. We independently ranked the hexagonal tiles in descending order according to VIn scores and wetland area so that tiles with the lowest mean was designated highest management priority.

Results

Local Scale: Habitat Characterization

Of the 20 SEGB sites, only one (SEGB 15) was classified as fringing and seven as open embayments, while the rest were protected embayments (n = 5) or archipelagos (n = 7). The shoreline configuration of the embayment sites afforded a greater level of protection from wave exposure than did the fringing site. The layout of the archipelago sites changed drastically with lake level; under the low-water scenario the sites were dominated by many small islands, which were fully or partially submerged under high water. This abrupt change in shoreline configuration resulted in less protection from wave exposure compared with that under the high-water scenario.

The SEGB sites had very gradual slopes under both high ($\bar{x}$ ± SE; 0.905% ± 0.151; n = 20) and low water-levels (0.778% ± 0.117; n = 16), and this resulted in an average lateral shift in shoreline position of 20 m (± 0.17) between lake-level scenarios, and in some cases up to 80 m. The shallow nature of these sites meant that the nursery-site boundaries of all but two (SEGB15 and SEGB05) were delineated by the 100-m buffer. Under high water, the site area was relatively large (2.21 ha ± 0.14; n = 20), whereas under low water, the area shrank (1.50 ha ± 0.13; n = 16) as the shoreline shifted lakeward while the lakeward site boundary remained static. The pairwise comparison of SEGB sites (n = 16) from the high-water to low-water scenario indicated that sites experienced significant decreases in area (S = -68.00, $p < 0.001$), volume (S = -68.00, $p < 0.001$), and REI (S = -68.00, $p < 0.001$), while slope remained unchanged (S = 28.00, $p = 0.1591$; Table 5.1). This amounted to an average loss of 33.6% (SE = 3.7) in area and 81.6% (SE = 3.2) in volume. The REI fell from an average of 1,692 (SE = 422) to 155 (SE = 66). The six sites with the most extreme decreases in REI were along the same stretch of shoreline. Most of these were archipelago sites, and the area offshore of the site boundaries was characteristically similar to the sites themselves (i.e. dominated by many small islands and shoals under low water, but submerged under high water).

By comparison, slopes of the NGB nursery sites were generally steeper, and the sites occurred along relatively straight stretches of shoreline. Of the 16 sites, 12 were classified as fringing, three were protected embayments sheltered by small islands, and one an open embayment. Regardless of water levels, the NGB sites were much steeper than their SEGB counterparts (9.01% ± 1.20 under high water and 6.13% ± 0.75 under low water). Thus, the lateral movement in shoreline position between lake-level scenarios was on average only 5.35 m (± 0.06) and no more than 35 m. The 2-m depth contour was encountered well within the 100 m buffer at almost all sites (n = 13), giving these the appearance of narrow bands along a straight shoreline. Areas of these nursery sites were relatively small regardless of water-level scenario (0.71 ha ± 0.14 vs 0.92 ha ± 0.12 in high and low water levels, respectively).

In pairwise comparison of NGB sites between high and low water levels, we observed a decrease in slope (S = -65, $p < 0.001$) and REI (S = -68, $p < 0.001$), an increase in site area (S = 60, $p < 0.001$), but no significant change in volume (S = 23.00, $p = 0.4332$; Table 5.1). The increase in area is consistent with the more gradual slope under the low-water scenario, while the volume remained the same because any increase in area was offset by a shift to shallower habitat. The shoreline configuration did not vary between lake levels, nor did it demonstrate the dramatic changes seen in parts of SEGB (i.e. emergence/submergence of many small islands), although the drop in lake levels dampened the depth-dependent component of REI calculations.

Substrate slope was the most distinguishing feature between NGB and SEGB sites; however, slopes did not change between lake-level scenarios (Table 5.2). The lateral movement of the shoreline between lake levels, essentially a function of the slope, and the use of a fixed lakeward extent for delineating site boundaries (i.e. 100-m buffer) explained the differences in area, volume, and depth, as described previously. This explains why the mean depth did not change significantly from high to low water in NGB (1.11 m vs 1.01 m; Steel-Dwass test: $Z = -0.508$, $p = 0.957$) because the steep slopes allowed the sites to shift laterally without encountering the maximum lakeward extent, whereas in SEGB the mean depth declined significantly (0.98 m to 0.27 m; Steel-Dwass: $Z = -5.078$, $p < 0.001$) as the more extreme lateral movement compressed the site boundaries against the fixed lakeward extent. Also of note is that low water levels resulted in much lower mean REI scores for SEGB sites compared with high water levels, and lower than the REI scores of NGB sites, regardless of lake elevation (Table 5.2).

Local Scale: Resilience Index

We selected slope, mean depth, and REI as the most appropriate hydrogeomorphic variables to develop the local RI for the Muskellunge nursery sites under low lake levels (Table 5.3). Measurements of each of these features were able to differentiate between the NGB and SEGB sites under the low-water scenario (Table 5.2) and were consistent with our initial hypotheses regarding habitat suitability under low lake levels. We opted to exclude wetland area because several of the NGB sites were very small (< 0.5 ha), and this made us question the appropriateness of using area as a criterion of suitability. We did not find significant differences in wetland volume between NGB and SEGB sites under the low-water scenario (Table 5.2). The HSC for each hydrogeomorphic variable was based on the probability density function of a 2-parameter Weibull distribution (Table 5.4), which had the lowest AICc score of the candidate distributions and acceptable goodness-of-fit (Cramér-von Mises W^2 test, $p > 0.05$). The probability density function fitted to the local measures (Figure 5.3) seemed appropriate (i.e. optimal scores and shape of the curves were consistent with hypotheses) and significant differences between SEGB and NGB sites were maintained (Table 5.4). The slope HSC scores most clearly differentiated between the two regions (AUC = 0.953) with all of the SEGB sites having scores below 0.31, while 11 NGB sites had scores above 0.75.

The NGB sites had significantly higher HSC scores for depth and REI (Table 5.4) but there was greater overlap with SEGB scores at intermediate scores (AUC: 0.949 and 0.750, respectively). The local RI performed well with an AUC score of 0.973. The threshold for the binary classification scheme was set at 0.42 and three SEGB sites were misclassified (RI, local scale; Figure 5.3). Of the 32 total sites, seven (three SEGB and four NGB) had intermediate scores, while the remaining sites separated out as expected (i.e. high NGB scores and low SEGB scores).

Regional Scale: Resilience Index

The local- and regional-scale hydrogeomorphic measurements were highly correlated for depth (Spearman's ρ > 0.97) and slope (ρ > 0.92). Differences in HSC and RI scores were largely attributed to the different protocols used. NGB 11 was the most obvious outlier with an increase in mean depth (+ 0.52 m) and a decrease in slope (- 6.93%) as product of the different rulesets (see Figure 5.2). The REI correlation between site and region measures was weaker (ρ = 0.37) and attributable to the set of archipelago sites in SEGB which relied on manual shoreline updates to accurately capture the many small islands that directly affected their REI measures. Exclusion of these sites (n = 5) improved the correlation to ρ = 0.83. Correlations between local and regional HSC values were consistent with the hydrogeomorphic measurements for depth (ρ = 0.94), slope (ρ = 0.90), and REI (ρ = 0.72), and correlations between the local and regional RI scores were highly correlated (ρ = 0.94).

The regional RI scores yielded an AUC of 0.975, and only one site was misclassified (SEGB03) based on the binary threshold, (Figure 5.4; RI, regional scale). Overall, the RI performed well and consistently at both the local and regional scale. For simplicity, we used one set of threshold values to define the operational resilience categories for both the local and regional RI. We set the lower threshold at 0.42 (between "least resilient" and "moderately resilient") and the upper threshold at 0.67 (between "moderately resilient" and "most resilient"). This ensured that all NGB sites were classified as "most resilient" or "moderately resilient” while minimizing the misclassification of SEGB sites. No SEGB sites were classified as “most resilient”.

Majority of SEGB was designated as “least resilient” (Table 5.5), with some narrow bands and small patches of “moderately resilient” or “most resilient” habitat towards the southern end of SEGB; the northern section of the region had a higher prevalence of resilient habitat, where the nearshore slope was steeper (Figure 5.5). NGB was primarily “moderately resilient” (Table 5.5), with only a few large wetland units that were considered “least resilient” (Figure 5.6). Similarly, majority of the NEGB was classified as “most resilient” or “moderately resilient” (Table 5.5), and all of the suspected nursery sites were classified as “most resilient” (Figure 5.7). The confirmed nursery site in NEGB had an RI score of 0.94.

Basin-wide Scale: Vulnerability Index

The basin-wide RI (i.e. based only on depth and slope) was highly correlated with the regional and local RIs ($\rho = 0.89$ and $\rho = 0.94$, respectively) for the SEGB and NGB nursery sites. This provided adequate rationale to use the basin-wide RI to develop the Vulnerability Index (VIn). Majority of the eastern and northern Georgian Bay shoreline currently support wetlands that have low or moderate vulnerability to stable low lake levels (Figure 5.8). The most vulnerable wetlands appear to be those in SEGB where there is a large amounts of wetland area with relatively high VIn scores (> 0.65). Isolated tiles with large proportions of highly vulnerable wetlands (VIn > 0.95) occurred along the northeastern and northern shoreline, but these tiles contained a very small total wetland area and therefore have low management priority (see area-vulnerability tradeoff; Figure 5.8, Appendix 1).

Discussion

The habitat requirements for age-0 Muskellunge appear to be highly prescribed and Muskellunge are sensitive to habitat alterations (Dombeck 1986; Farrell et al. 2007); a growing body of work have confirmed the importance of structurally diverse, aquatic vegetation within their nursery habitat (Craig and Black 1986; Kapsuscinski and Farrell 2014; Leblanc 2015; Murry and Farrell 2007; Werner et al. 1996). While previous studies have identified changes in the aquatic vegetation community as a probable cause of recruitment failure (Farrell et al. 2007; Leblanc et al. 2014), no study has yet shed light on the potential mechanisms driving these habitat changes. In this study, we have identified substrate slope and site exposure as key variables that are primarily linked to aquatic vegetation structure. We have shown that the interaction of these hydrogeomorphic variables with water level may explain how different types of aquatic vegetation respond to changing water depth (i.e. a deeper site can support more SAV and more diverse structure than can a very shallow site).

We assume that under historical (i.e. typical) lake-level fluctuations, the continuous change in water levels acts as a disturbance regime, promoting a higher diversity of plant species (Keddy and Reznicek 1986; Wilcox and Xie 2007), and a greater structural diversity that provide optimal fish habitat. In the absence of fluctuating lake levels, we should expect to see a homogenization of the plant community and a loss of diversity. This in turn should be expected to result in a subsequent shift in the fish communities present in those habitats (Cvetkovic et al. 2010; Eadie and Keast 1984; Midwood and Chow-Fraser 2012; Smokorowski and Pratt 2007; Weaver et al. 1997).

Our study confirms the importance of substrate slope by showing this as the key distinguishing feature between NGB and SEGB sites (Leblanc et al. 2014; Leblanc 2015). This also validates its use in development of habitat suitability index for age-0 Muskellunge (Leblanc and Chow-Fraser 2017). We are also encouraged by the convergence of results at multiple spatial scales in this study. Steeper sites appeared to be more resilient to stable low lake levels but the exact mechanism by which this occurs is unknown. Based on the strong predictive relationship between littoral slope and maximum biomass of SAV found by Duarte and Kalff (1986), more gradual slopes are capable of supporting greater SAV biomass than steeper slopes. This suggests that when released from the typical disturbance regime of lake-level fluctuations (Keddy and Reznicek 1986), our typically steeper NGB sites would have been unable to support as much SAV biomass as would the SEGB sites. We posit that the maximum SAV biomass supported by NGB slopes should correspond to a biovolume or structural configuration consistent with intermediate densities of aquatic vegetation. By comparison, when the SAV biomass increased in the SEGB sites, there was a corresponding increase in homogeneity and density of aquatic vegetation in some areas of Georgian Bay (Leblanc et al. 2014, Midwood and Chow-Fraser 2012). Similar to biovolume as a proxy measure of density, SAV biomass may be considered a proxy for vegetation structure (Leblanc and Chow-Fraser 2017; Valley et al. 2005).

We hypothesized that wave exposure promoted resilience of the NGB sites by acting as an alternative disturbance regime in the absence of fluctuating lake levels, essentially an example of the intermediate disturbance hypothesis (Grime 1973; Keddy 1984). Though there were differences between regions, substrate slope is the most pronounced feature, and the SEGB sites had lower REI scores under the low-water scenario (Table 5.2). Exposure is a difficult metric to interpret as it encompasses a range of conditions that can affect aquatic plant growth, such as sediment sorting, physical damage to plants, or uprooting (e.g. physical disturbance; Jupp and Spence 1977). Duarte and Kalff (1986) found that SAV biomass was negatively correlated with exposure (i.e. similar metric to the REI but without accounting for depth), but not at slopes in excess of 2.24%. This means that effects of exposure on vegetation may be a more important factor in SEGB than in NGB, and could in part explain the weaker discriminating power of the REI. The largest set of suitable nursery habitat with shallow slopes was from SEGB under the high-water scenario; nevertheless, we cannot draw conclusions because the typical lake-level fluctuations that prevailed during this period is a confounding factor.

It is difficult to assess if an alternative set of exposure HSCs tailored for gradual or steep slopes would have been useful. Under stable low water levels, there were only two Muskellunge nursery sites from NGB with gradual slopes (< 2.24%) and that had REI scores between 100 and 200; almost all of the SEGB sites (11/16) had REI scores of < 75. In shallow water (~1.0 m), wave exposure has been associated with SAV growth, presumably because the energy is required to remove fine sediments and to bring in associated nutrients (Duarte and Kalff 1988; 1990). This provides an alternative mechanism as to how physical disturbance of waves may act on SAV. The use of exposure is further complicated because the methods available to measure exposure are drastic oversimplification of complex processes including shoaling, breaking, and refraction (USACOE Shore Protection Manual 1977), and more accurate or appropriate measures involve the use of complex numerical models (e.g. SWAN, WeMo) which involve a level of computational power that makes them impractical to use at a large regional scale. While REI was not as useful in discriminating between our NGB and SEGB sites, we retained this variable in the RI because of its heuristic value; optimal values from its HSC made sense and we felt its ability to reduce scores at extremely high or low exposures was more evident when applied at a regional scale, and not just to the 32 sites that contributed to development of the index.

The significant decline in area and volume of nursery sites we found during low water levels (Table 5.1) are consistent with loss of wetland fish habitat reported by others for eastern Georgian Bay (e.g. Fracz and Chow-Fraser 2013; Midwood and Chow-Fraser 2012). However, we attributed this result to the nature of our site delineation, since we maintained a fixed buffer around the capture location as a maximum site extent. Recent models to simulate the response of coastal wetlands in Georgian Bay to low lake-levels suggest that low-marsh area actually increases under low-lake levels but that volume decreases as the habitat becomes dominated by shallower habitat (< 0.5 m; Weller and Chow-Fraser 2018/CH4). Based on our knowledge of the region's bathymetry, we would expect a similar result if using a strictly depth-dependent site boundary, but difficulties associated with accounting for the often large, lateral shifts in site position and extent precluded such an approach. Furthermore, Georgian Bay coastal marshes are typically quite small (< 2 ha; Midwood et al. 2012), including those found in NGB which are known to support age-0 Muskellunge. This supports our contention that the size of the available nursery habitat is less important than the types of structure within the habitat and its overall quality.

We stress the consideration of spatial scale when using the indices developed in this paper, particularly their respective purposes, limitations, and interpretations. The regional RI was one of the main products of this study, intended as a coarse-scale screening tool to remotely identify suitable Muskellunge nursery habitat before more targeted surveys are conducted, similar to those carried out by Leblanc and Chow-Fraser's (2017) Index of Nursery Habitat Suitability. Of Leblanc and Chow-Fraser's (2017) 37 "no-Muskellunge" sites used to develop the INHS, the regional RI only classified 5 as "least resilient" while the remained were evenly split between "moderately resilient" and "most resilient". We interpreted this poor classification of the "no-Muskellunge" sites as evidence that resilient wetland habitat alone does not guarantee the presence of age-0 Muskellunge and that other variables, hydrogeomorphic or otherwise, must be considered as well. Therefore we recommend using the regional RI to assess if a target region supports a high proportion of resilient wetlands that merit subsequent field surveys, or to prioritize sampling effort among larger wetland complexes (e.g. prioritizing based on resilience categories). Although the local RI provided finer resolution than did the regional RI, the much greater effort (both in terms of time and labour) required to produce the habitat layers are difficult to justify.

The VIn, and the priority rankings (Appendix 1), offers a relatively efficient means to identify the average vulnerability of wetlands over a broad area. We envision this being used in development of lake-wide sampling programs, possibly with subsequent, targeted use of the regional RI. We emphasize without hesitation, however, that such screening tools do not substitute for detailed field surveys that involve examining SAV structure and the fish communities, and that our hierarchy of indices must be used as intended (Table 5.3). The performance of these indices, particularly at the local and regional scale, depend on availability of fine-scale bathymetric information, which are currently lacking for most of Georgian Bay, and thus limits further improvements of the RI.

Although lake levels have rebounded from the unprecedented period of sustained low water levels in Georgian Bay (1999 – 2013), forecasts of future lake levels suggest that prolonged periods of stable, low lake levels may become more common (Lu and Nairn, in submission; Angel and Kunkel 2010), and could have far-reaching negative impacts on the quality and quantity of wetland habitat (Midwood and Chow-Fraser 2012; Wilcox and Nichols 2008; Wilcox and Meeker 1991). It is therefore necessary to have tools to identify wetlands that are most vulnerable to these conditions. The indices that we have proposed offers a relatively simple and effective means to gauge the resilience of wetlands to such water-level disturbance over multiple spatial scales. We recommend the RI be used to guide targeted field surveys or to identify areas that may be in need of restoration or protection as part of an overall strategy to sustainably manage the trophy Muskellunge fishery in Georgian Bay. Further we propose the broader use of the RI and VIn in developing a management strategy for Great Lakes coastal wetlands subject to lake level disturbances as a result of global climate change.

Acknowledgements

We would like to acknowledge the funding support of OMNRF COA, the Lake Simcoe Eastern GB Cleanup Fund, Muskies Canada, and an Ontario Graduate Scholarship for Dan Weller. With regards to the DEM developed for this project, it was produced by McMaster University based on Canadian Hydrographic Service charts and/or data, pursuant to CHS Direct User Licence No. 2016-1121-1260-M. The incorporation of data sourced from CHS in this product shall not be construed as constituting an endorsement by CHS of this project. This product does not meet the requirements of the *Charts and Nautical Publications Regulations, 1995* under the *Canadian Shipping Act, 2001*. Official charts and publications, corrected and up-to-date, must be used to meet the requirements of those regulations.

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Table 5.1: Comparison of medians for hydrogeomorphic variables of Muskellunge nursery sites in each region between high- (HIGH) and low-water (LOW) scenarios using Wilcoxon Signed Rank test. Measurements were derived from a DEM with manually corrected shoreline features. Bonferroni corrected of $\alpha = 0.01$.

Variable	Region	HIGH	LOW	S	*p*
Area (m^2)	SEGB	22,311	14,387	-68	< 0.001*
	NGB	4,546	8,852	60	< 0.001*
Volume (m^3)	SEGB	22,168	4,040	-68	< 0.001*
	NGB	4,917	7,235	16	0.4332
Depth (m)	SEGB	1.00	0.27	-68	< 0.001*
	NGB	0.99	1.04	-18	0.3755
Slope (%)	SEGB	0.63	0.62	28	0.1591
	NGB	8.46	5.84	-65	< 0.001*
REI	SEGB	554.93	59.21	-68	< 0.001*
	NGB	348.23	301.77	-68	< 0.001*

Table 5.2: Comparison of hydrogeomorphic variables for sites in all region-years (NGB or SEGB) at high- (HIGH) or low-water (LOW) levels. Kruskal-Wallis and the Steel-Dwass test were used to identify differences among groups. Groups sharing the same letter were statistically homogeneous.

Variable	Group	Mean	SE	χ^2; *p*	Statistical grouping		
Area (m^2)	SEGB HIGH	22,092	1,431	37.034; < 0.001	A		
	SEGB LOW	15,037	1,300			B	
	NGB HIGH	7,150	1,414				C
	NGB LOW	9,176	1,234				C
Volume (m^3)	SEGB HIGH	22,226	1,517	38.964; < 0.001	A		
	SEGB LOW	4,429	852				C
	NGB HIGH	8,125	1,821			B	C
	NGB LOW	8,344	975			B	
Depth (m)	SEGB HIGH	1.01	0.03	35.184 < 0.001		B	
	SEGB LOW	0.29	0.05		A		
	NGB HIGH	1.11	0.05			B	
	NGB LOW	1.01	0.08			B	
Slope (%)	SEGB HIGH	0.91	0.15	48.966; < 0.001	A		
	SEGB LOW	0.77	0.12		A		
	NGB HIGH	9.01	1.20			B	
	NGB LOW	6.13	0.75			B	
REI	SEGB HIGH	1608.31	421.50	25.713; < 0.001	A		
	SEGB LOW	155.27	65.94			B	
	NGB HIGH	401.22	59.02		A		
	NGB LOW	292.61	38.31		A		

Table 5.3: Summary of attributes and features of different Resilince Index scales, including target study area size (Size), resolution of digital elevation model used (DEM), included hydrogeomorphic features (HGM), and any other defining characteristics (Characteristics).

Scale	Size	DEM	HGM	Characteristics
Local	~ 1 ha	5 m	Depth Slope REI	Manually verified nursery site delineation REI samples: 10 m spacing
Regional	~1,000 – 10,000 ha	5 m	Depth Slope REI	Automated nursery site delineation REI samples: ~60 m spacing
Basin-wide	> 10,000 ha	10 m	Depth Slope	Automated nursery site delineation Inverted scoring system for Vulnerability Index

Table 5.4: Specifications for the habitat suitability curves (HSCs) for hydrogeomorphic variables associated with Muskellunge nursery sites. Local-scale data from the NGB sites under low-water (176.0 m) were used to fit a 2-parameter Weibull probability density function (Fitted PDF: α = scale parameter, β = shape parameter, W^2 = Cramér-von Mises goodness of fit) for each morphometric variable. The PDF was then re-scaled to values between 0 and 1, where 1 indicated the most suitable habitat (α and β parameters are from the original PDF, not the rescaled values). A Wilcoxon Signed Rank test (α = 0.05) was performed to confirm median HSC scores were significantly different between SEGB and NGB sites.

	Fitted PDF			Wilcoxon Signed Rank Test			
Variable	α	β	W^2	NGB	SEGB	Z	*p*
Depth	1.124	3.791	0.25	0.80	0.05	4.315	< 0.001
Slope	6.924	2.221	0.25	0.90	0.13	4.353	< 0.001
REI	331.711	2.113	0.25	0.77	0.24	2.393	0.0167

Table 5.5: Percentage area in each region for three resilience index (RI) categories. Percent breakdown by the entire region (0 – 2 m Depth Zone) and subsequent application of a wetland mask layer (Wetland Mask). Total area of each region is included in brackets.

	0 – 2 m Depth Zone			Wetland Mask		
RI category	SEGB (2,121 ha)	NGB (462 ha)	NEGB (236 ha)	SEGB (946 ha)	NGB (159 ha)	NEGB (66 ha)
Least Resilient	58	20	6	56	26	12
Moderately Resilient	28	50	32	27	47	33
Most Resilient	14	30	62	17	27	56

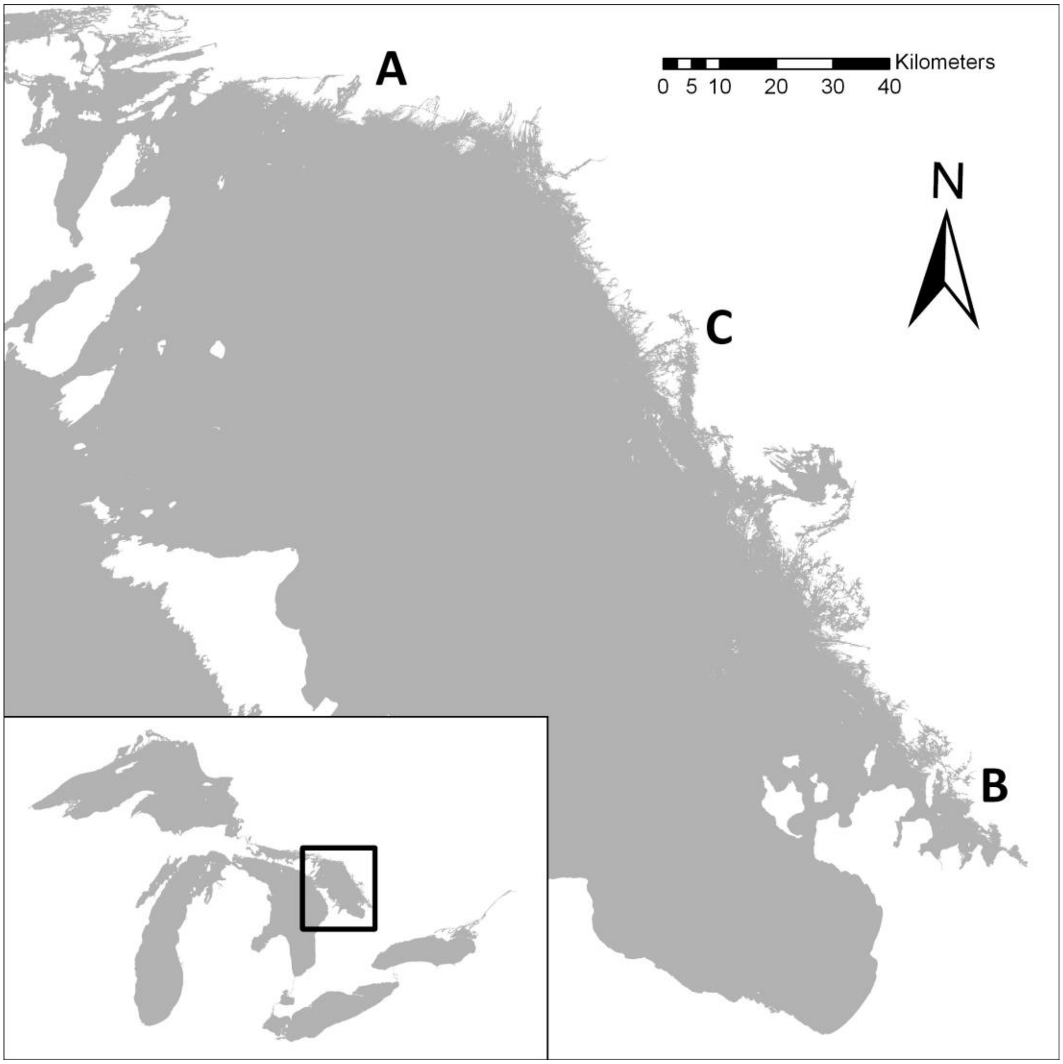

Figure 5.1: Georgian Bay, Lake Huron (inset: location relative to Laurentian Great Lakes) with main study regions indicated: northern Georgian Bay (A), southeastern Georgian Bay (B), and northeastern Georgian Bay (C).

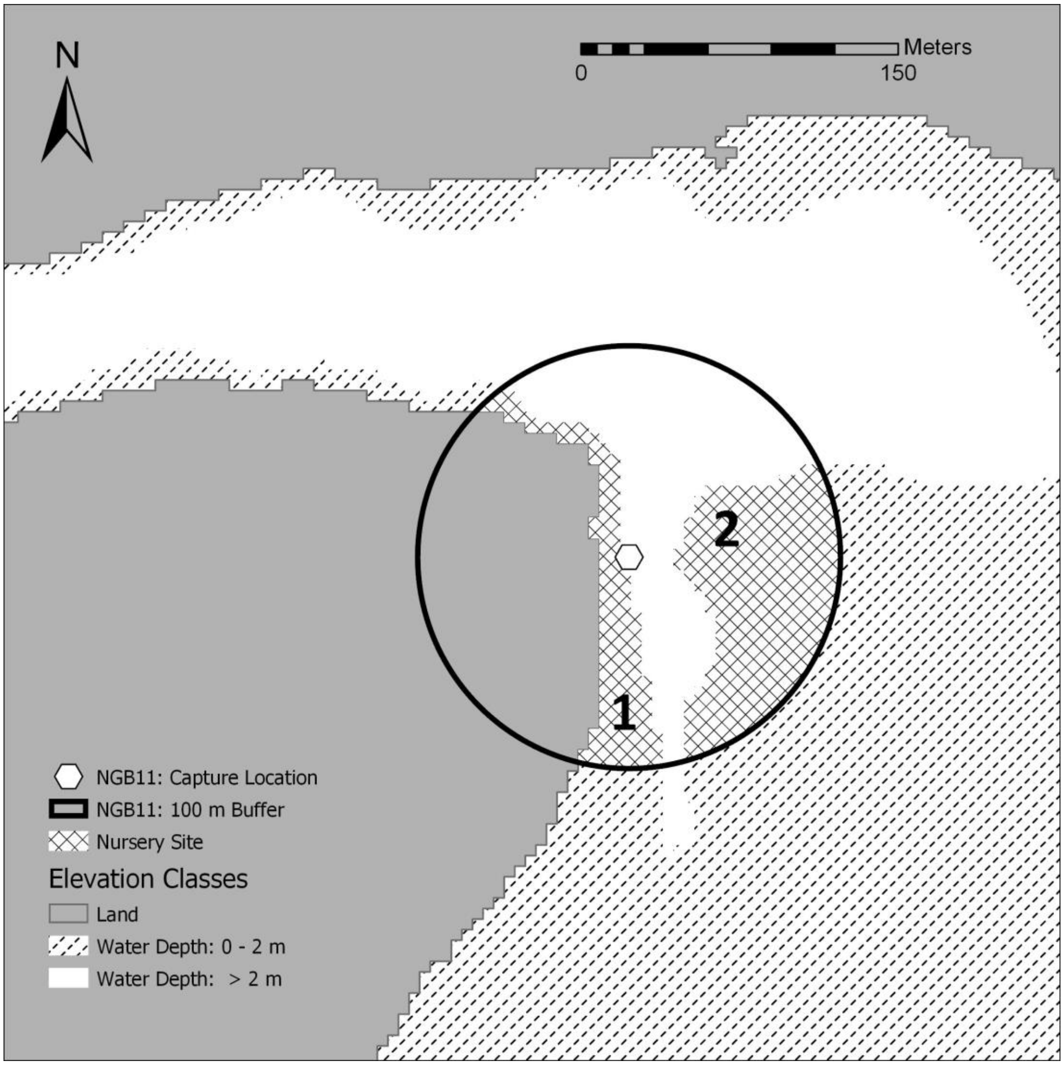

Figure 5.2: Nursery site NGB11 is used to illustrate occasional discrepancies between hydrogeomorphic measurement at the local and regional scales due to difference in site areas. The regional-scale extent (cross-hatching: 1 and 2) consists of all area between 0 – 2 m deep within the 100 m buffer. The local-scale site extent (cross-hatching: 1) consists of area between 0 – 2 m deep within the 100 m buffer that contains the capture location; discontinuous patches (i.e. 2) are excluded.

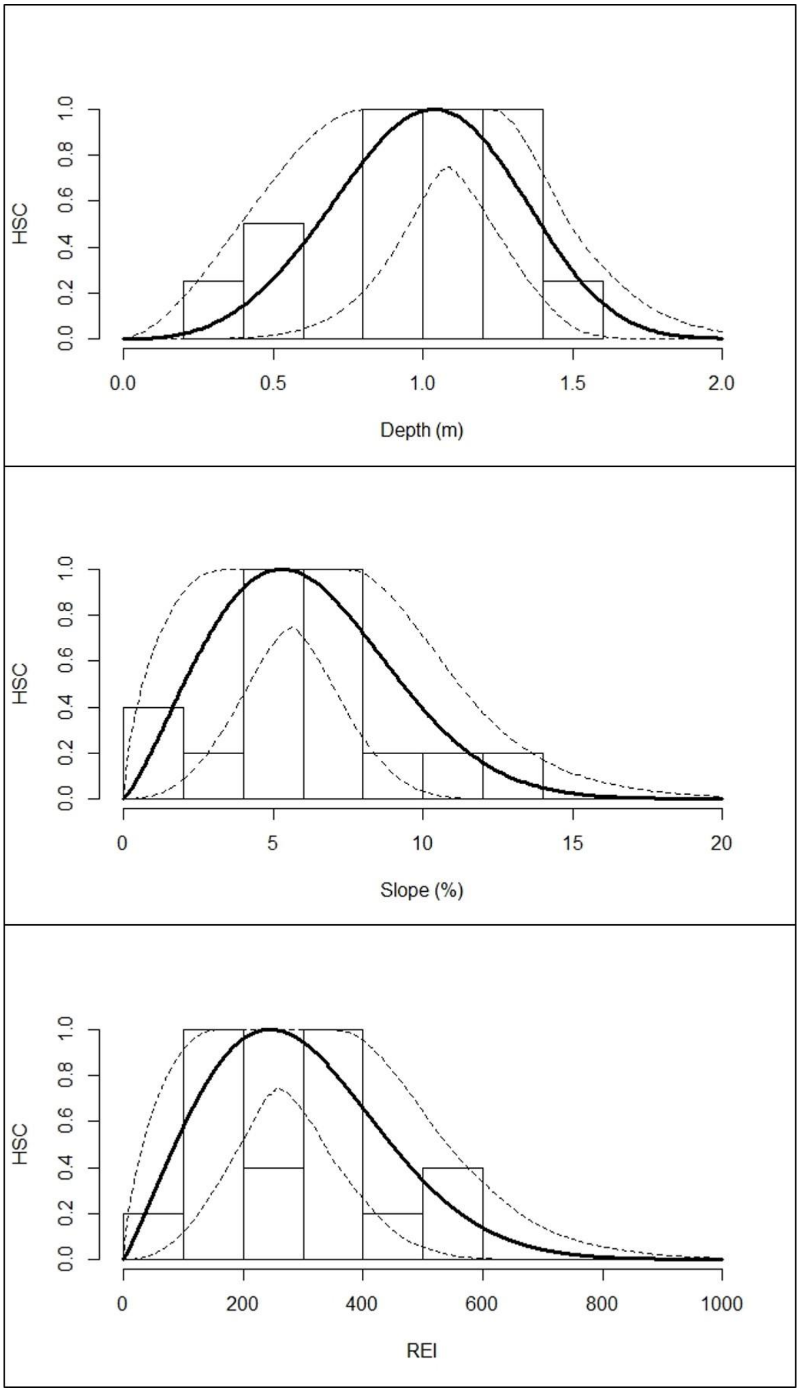

Figure 5.3: Habitat suitability curves (HSCs; solid line) bounded by 95% confidence interval (dashed lines) for hydrogeomorphic variables associated with Muskellunge nursery sites. A 2-parameter Weibull probability density functions was fitted to the data from northern Georgian Bay sites under low lake levels (n = 16). The HSC is the probability density function rescaled to values of 0 – 1.

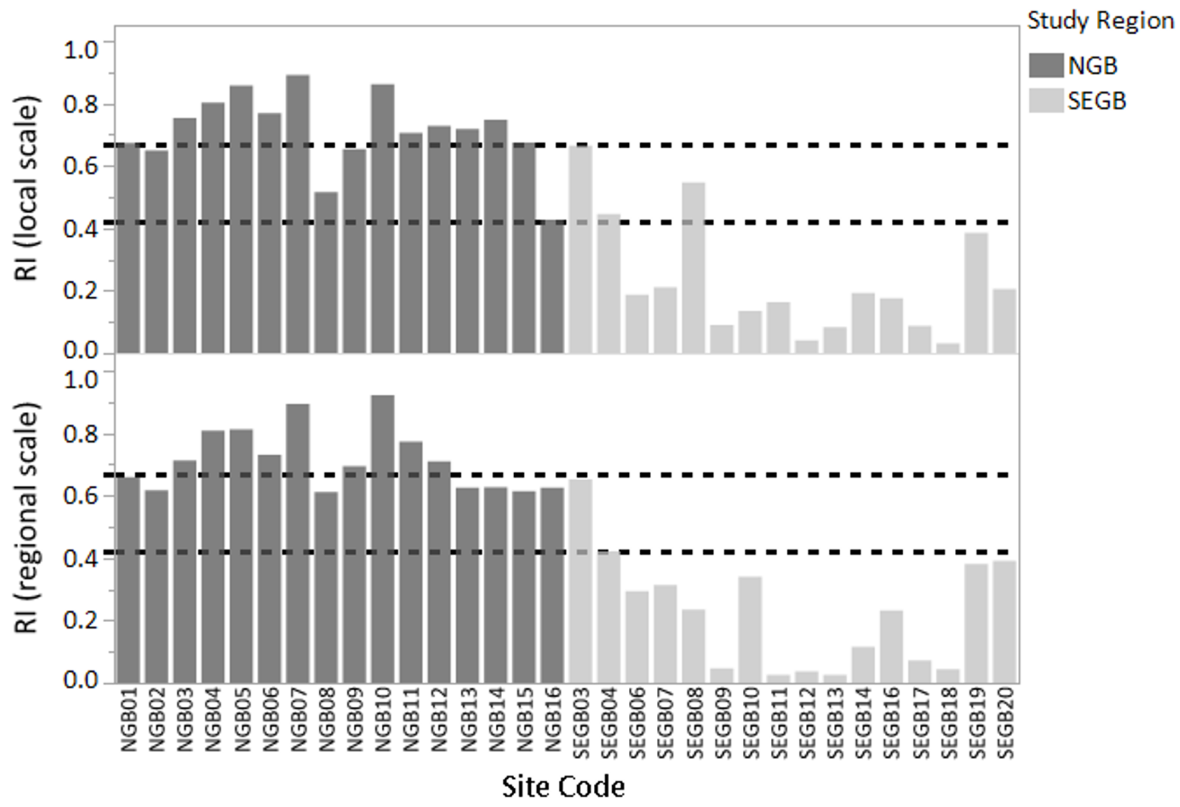

Figure 5.4: Resilience index (RI) scores for Muskellunge nursery sites in southeastern Georgian Bay (SEGB; n = 16) and northern Georgian Bay (NGB; n = 16) using local-scale and regional-scale hydrogeomorphic variables. RI scores were calculated for each nursery site under the low-water scenario (lake level = 176.0 m). Dashed lines indicate the thresholds for defined categories: most resilient (> 0.67), moderately resilient (0.42 – 0.67), and least resilient (< 0.42).

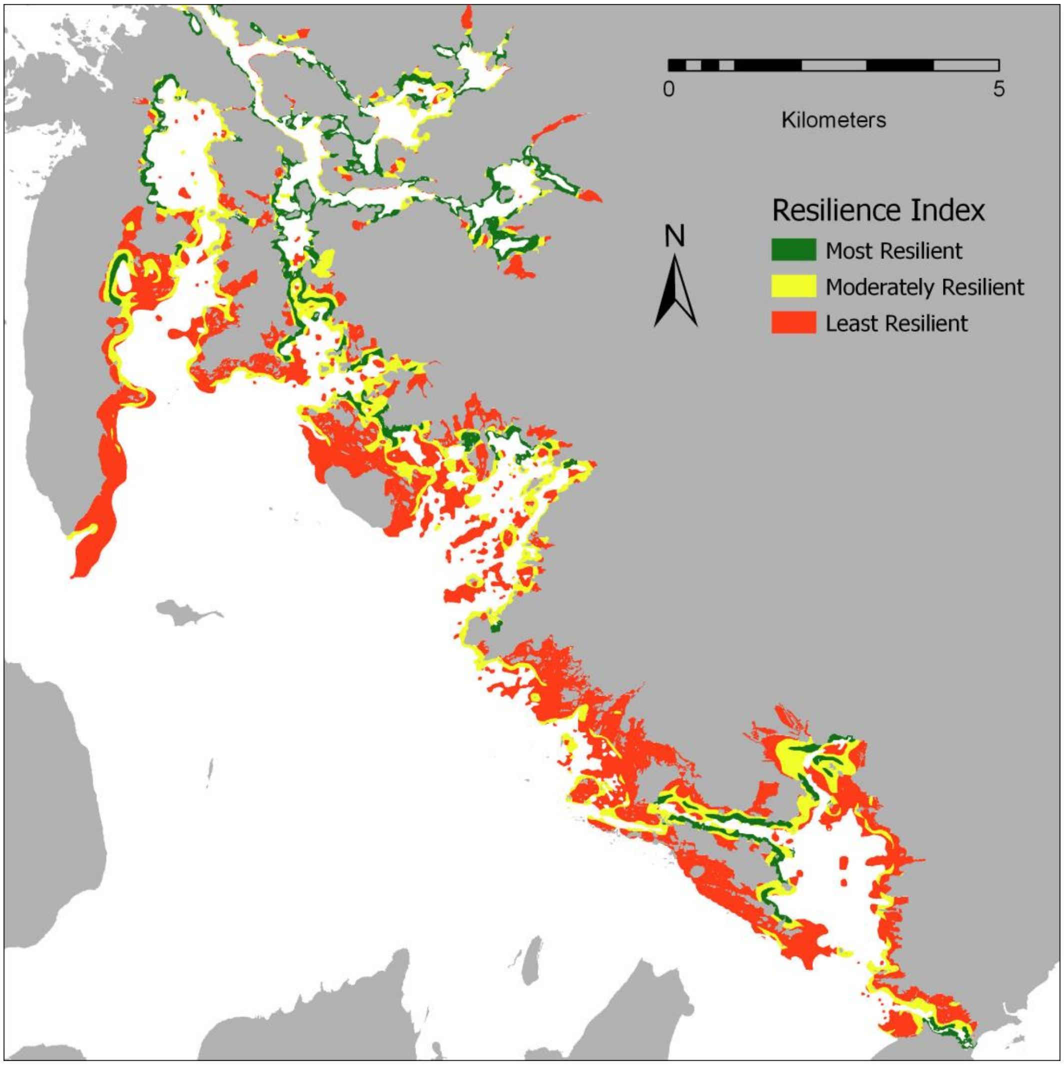

Figure 5.5: Classification of wetland areas into three resilience categories for southeastern Georgian Bay.

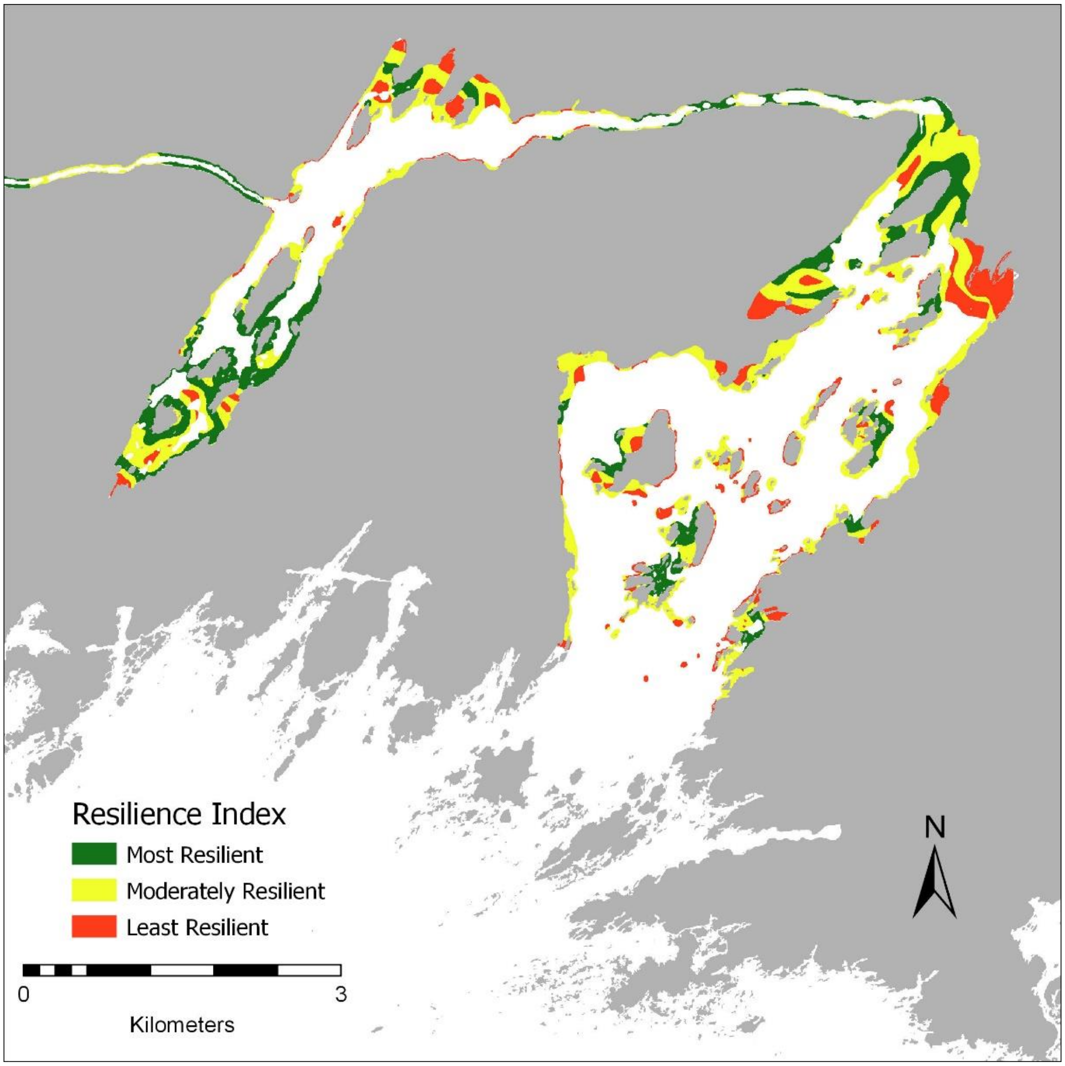

Figure 5.6: Classification of wetland areas into three resilience categories for northern Georgian Bay.

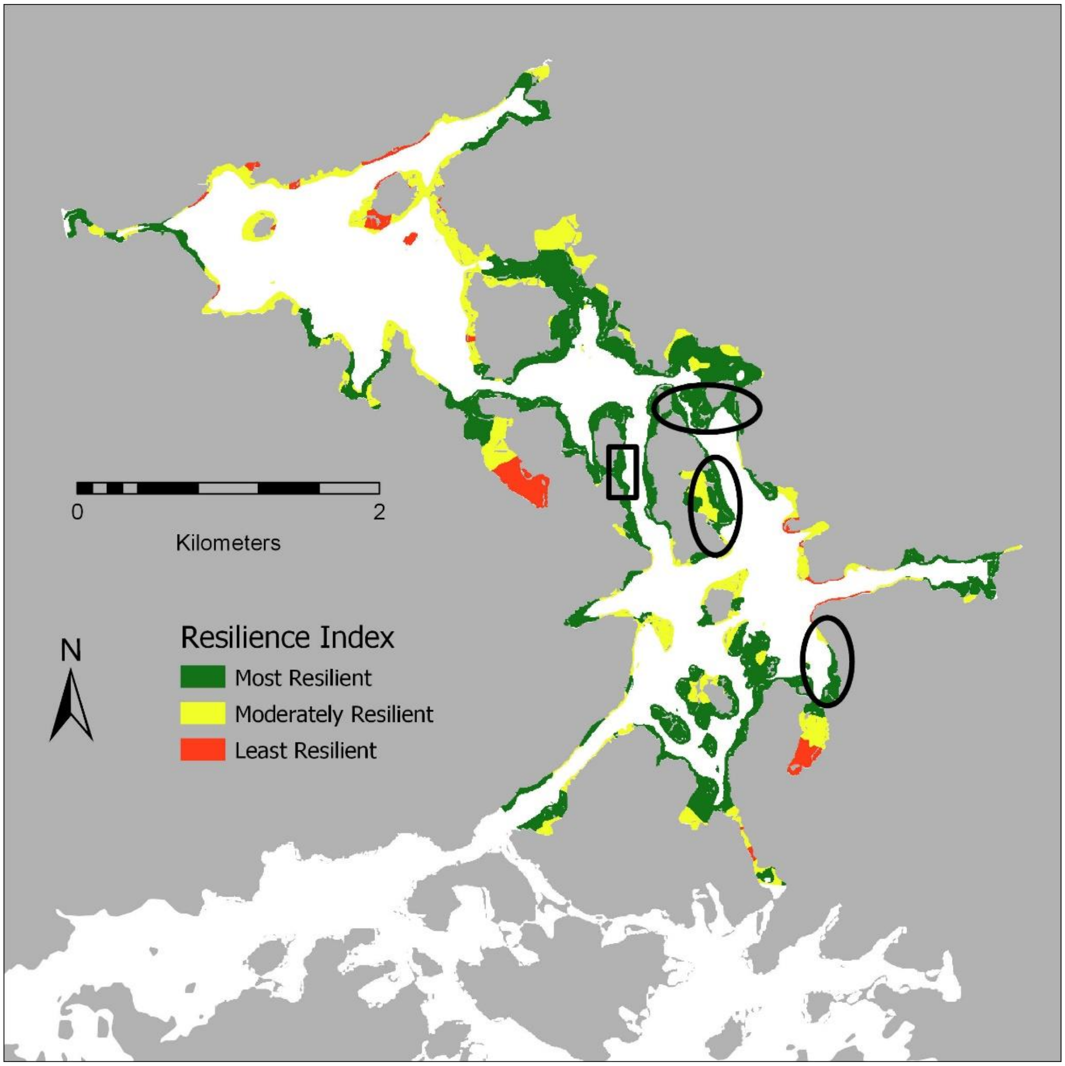

Figure 5.7: Classification of wetland areas into three resilience categories for northeastern Georgian Bay. Rectangle indicates confirmed Muskellunge nursery site (i.e. captured age-0 Muskellunge) and circles are suspected nursery sites based on radio-tracking of spawning adult Muskellunge.

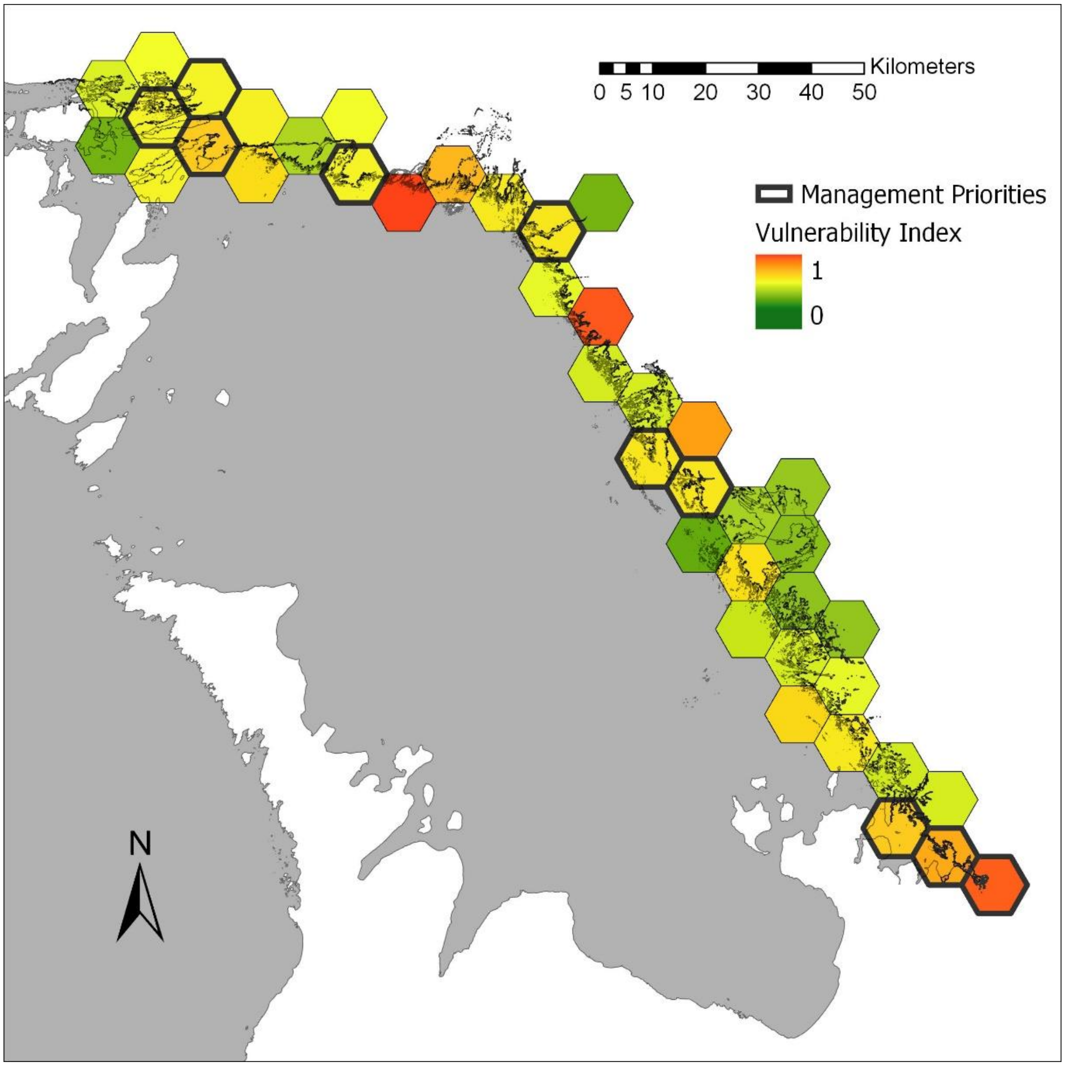

Figure 5.8: Vulnerability index (VIn) scores for the eastern and northern shoreline of Georgian Bay, calculated as the reciprocal of the mean basin-wide RI score for all wetland area contained within a hexagonal tile. Scores range from 1 (red) indicating most vulnerable to 0 (green) indicating least vulnerable. Priority tiles for management consideration (top 10, bold outline) were selected based on VIn score and total wetland area. Priority tiles support large wetland areas, many of which are considered vulnerable to community shifts under stable low water levels.

Appendix 1: Prioritized areas along the Georgian Bay shoreline for management focus due to vulnerability of wetlands to stable low lake levels. The study area is represented by 10,000 ha hexagonal tiles unique alpha-numeric identifiers (Tile ID). Latitude and Longitude (NAD 1983) indicate position of tile center. Priority ranking was based off vulnerability index (VIn) score and total wetland area within the tile (Area). For example, tile I-3 had the highest VIn score but small wetland area so it is of lower priority than tile O-8, which has a lower VIn score but more wetland area. The number of spatially distinct wetland units (Units) is included for additional context.

Tile ID	Longitude	Latitude	VIn	Area (ha)	Units	Priority
T-15	-79.73680	44.77563	0.75	743.92	135	1
U-15	-79.62037	44.72591	0.94	127.76	4	2
S-14	-79.85343	44.82522	0.66	201.19	100	3
E-2	-81.51189	45.99053	0.65	191.53	79	4
O-8	-80.31737	45.40932	0.58	214.4	48	5
D-2	-81.63259	46.03829	0.54	117.05	208	6
H-3	-81.15127	45.94322	0.53	84.62	42	7
L-4	-80.67160	45.84613	0.57	58.71	65	8
N-8	-80.43581	45.45833	0.58	48.89	79	9
E-1	-81.51278	46.08724	0.53	62.89	63	10
J-3	-80.91115	45.94329	0.71	18.09	122	11
P-10	-80.20050	45.26347	0.60	31.74	78	12
O-7	-80.31620	45.50604	0.78	8.6	4	13
I-3	-81.03118	45.89496	0.99	4.11	9	14
Q-11	-80.08423	45.11751	0.44	68.99	135	15
R-13	-79.96854	44.97142	0.57	34.15	111	16
F-3	-81.39139	45.94265	0.60	16.09	23	17
S-13	-79.85151	44.92194	0.43	78.04	230	18
T-14	-79.73468	44.87234	0.44	65.27	81	19
N-7	-80.43484	45.55505	0.44	54.2	99	20
D-1	-81.63370	46.13499	0.51	36.28	44	21
F-2	-81.39207	46.03937	0.55	22.59	29	22
M-5	-80.55291	45.70065	0.95	0.09	3	23
C-1	-81.75351	46.08591	0.46	46.74	63	24
H-2	-81.15153	46.03994	0.50	36.09	29	25
P-9	-80.19914	45.36019	0.34	65.28	59	26
D-3	-81.63149	45.94158	0.53	24.24	38	27
K-3	-80.79127	45.89477	0.57	9.25	39	28
Q-10	-80.08267	45.21422	0.29	66.87	191	29
Q-12	-80.08577	45.02079	0.62	0.67	4	30
Q-8	-80.07955	45.40765	0.31	48.35	33	31
G-2	-81.27156	45.99136	0.36	44.4	48	32

R-12	-79.96680	45.06814	0.47	14.63	33	33
L-5	-80.67217	45.74942	0.48	7.2	25	34
Q-9	-80.08112	45.31094	0.28	34.92	67	35
M-6	-80.55368	45.60393	0.44	3.7	13	36
R-11	-79.96505	45.16485	0.30	8.08	18	37
M-3	-80.55136	45.89408	0.24	7.53	5	38
P-11	-80.20185	45.16675	0.41	0.45	2	39
C-2	-81.75219	45.98921	0.23	3.83	13	40
O-9	-80.31853	45.31260	0.21	2.51	12	41

GENERAL DISCUSSION

Thesis Summary

The main objectives of this thesis were to improve understanding of habitat use by esocids in Georgian Bay (Lake Huron) and develop landscape-level tools for the identification and evaluation of suitable habitat. These objectives were intended to address management needs and priorities of esocid fisheries, notably Muskellunge and Northern Pike, and to be more broadly applicable to the conservation and management of coastal wetlands in general. In Chapter 1 and Chapter 2 we used radio telemetry to track adult esocids to identify important habitat areas and characteristics of suitable habitats. In Chapter 3 and Chapter 4 we used landscape-level features to model how different water levels may affect the amount of available low marsh habitat, an important habitat for esocids and many other Great Lakes fish species. Finally, in Chapter 5, we developed a Resilience Index from landscape-level features of Muskellunge nursery sites to evaluate the response of low marsh communities to stable low lake levels, which has been identified as one of the major threats facing coastal wetlands in Georgian Bay and the long-term sustainability of esocid fisheries.

Specifically, in Chapter 1 we identified coastal wetlands that are important Muskellunge spawning grounds in several regions of Georgian Bay and established that adult Muskellunge display high year-to-year fidelity for specific locations during the spawning season. The close proximity of these spawning-season locations to confirmed nursery habitat provides further corroboration of the close spatial linkage between Muskellunge spawning and nursery habitats.

This highlights the importance of identifying and protecting early-life habitat for Muskellunge since the fidelity for spawning grounds by adults appears to be independent of habitat suitability, and provides an explanation for the absence of age-0 Muskellunge from southeastern Georgian Bay (Leblanc et al. 2014).

In Chapter 2 we continued to use radio telemetry to identify habitat use by adult Muskellunge and Northern Pike during the summer when thermal habitat conditions are most likely to be limiting. We found that the availability of suitable, physical habitat structure was the primary driver of habitat use in both esocid species, which included SAV associated with coastal wetlands, sharp changes in bottom contours, and man-made structures (e.g. docks). Water temperatures were not found to be a limiting habitat features for either species but under possible global climate change scenarios involving lower lake levels and warming temperatures, shallow embayments with a high anthropogenic footprint could develop adverse conditions. This again highlights the importance of coastal wetlands as esocid habitat, beyond early-life stages, and the need to conserve these areas.

In Chapter 3 we developed a model to accurately predict the extent and distribution of low marsh habitat in eastern and northern Georgian Bay by using landscape-level features that can be readily derived from DEMs. This model can be used to assess how the availability of low marsh habitat may change under different lake levels scenarios and to better predict the response of fish habitat under novel lake level conditions. Low marsh is an important habitat for early-life and adult esocids (Chapter 1 and Chapter 2) so this is a useful tool for managing esocid habitat and coastal wetlands more broadly in Georgian Bay.

In Chapter 4, we used the low marsh model (Chapter 3) to evaluate how the extent of low marsh habitat changed under different lake levels. We found that the interaction between nearshore morphology and lake levels has important implications for the amount and suitability of low marsh habitat. Under low lake levels, similar to the sustained low water period from 1999 – 2013, we predicted the total area of low marsh was greatest but that it was primarily composed of shallow habitat (< 0.5 m) that is more conducive to emergent vegetation types. Under higher lake levels, total low marsh area was less but it consisted of deeper water habitats (0.50 – 1.5 m), which is more likely to support a SAV community that is suitable for esocids. This chapter showed the utility of the low marsh model, provided valuable insight as to how low marsh habitat may respond to changing lake levels, and highlighted the value of considering wetland habitat in three dimensions.

In Chapter 5 we used a similar suite of hydrogeomorphic features as the low marsh model (Chapter 3) to characterize the resilience of coastal wetlands to stable low lake levels. Using the presence of age-0 Muskellunge as an indicator of a resilient wetland, we identified differences in wetland depth, slope, and wave exposure that distinguished resilient from non-resilient sites. We used these features to develop a multi-scale Resilience Index (RI) to evaluate coastal wetland habitat in Georgian Bay, again using features that are readily obtained from a

DEM. Most relevant are the regional-scale RI that can be used as a screening tool to remotely identify areas for targeted field surveys of critical esocid habitat, and the basin-wide RI that can be used to identify relevant study sites for wetland monitoring and resilience assessment.

In summary, the results of this thesis address outstanding management needs and priorities for Georgian Bay esocids, including an improved understanding of habitat use and the development of a suite of easily-applicable management tools. More broadly, this work contributes to understanding the response and resilience of coastal wetlands to changing lake level conditions. The recommendations and future research directions described herein will help maintain Georgian Bay's esocid fisheries and develop adaptive management plans for Georgian Bay coastal wetlands in an uncertain future.

Recommendations

Based on the major findings described in this thesis, the following recommendations are proposed to aid management of esocid fisheries in Georgian Bay and more broadly the conservation and protection of coastal wetland habitat.

1) Identification and protection of esocid spawning and nursery habitat has been a longstanding management priority for good reason. The high fidelity for spawning habitat shown by adult Muskellunge suggests continued use of these habitats despite potentially degraded conditions in

nursery habitats. Human development pressure along the Georgian Bay shoreline is expected to persist and protection of wetland habitat is critical. Local environmental groups, townships, planning agencies, and citizens should be made aware of the value of coastal wetland habitats to ensure their protection.

2) Availability of suitable summer habitat for embayment-resident esocids was not found to be imminently at risk under likely climate change scenarios, but eutrophication from anthropogenic activities were considered to be more pressing concern. Embayments in eastern and northern Georgian Bay that are susceptible to eutrophication due to shallow maximum depths, limited mixing with the main bay, and a dense human footprint along the shoreline should be identified. Where possible, further development can be limited and existing properties should be upgraded or maintain to prevent additional nutrient inputs (e.g. leaking septic systems). Campbell and Chow-Fraser's (2018) anthro-geomorphic model is a landscape-level tool that leverages similar elevation data inputs as our low marsh model (Chapter 3), and could be used to identify currently or potentially vulnerable embayments.

3) Wetland habitat assessments often rely on *area* as a key evaluation metric, and the appropriateness of this approach has been discussed with respect to the typically small coastal wetlands in Georgian Bay (Midwood 2012). I stress the importance of considering wetland *volume*, particularly for fish

habitat. From the perspective of a fish, wetlands are a fundamentally three-dimensional habitat and should be considered as such to develop a more complete understanding of the suitability of that habitat for a given species or community. Appropriate depth information in wetlands, especially in Georgian Bay, is often unavailable but habitat area can be readily derived from aerial or satellite imagery. I recommend the collection of depth information from coastal wetlands and nearshore areas when conducting field surveys (e.g. dGPS, sonar) or at a broader scale (e.g. Light Detection and Ranging; LiDAR) to refine wetland habitat assessments.

4) The loss of natural lake level fluctuations has been identified as among the most pressing threats to Georgian Bay coastal wetlands and there is much uncertainty as to future lake level conditions due to global climate change. Some action to restore Georgian Bay lake levels and lake-level fluctuations to more natural conditions over the long-term is merited, such as some type of variable control structure at the St. Clair River to modulate the outflow of Lake Huron.

5) In Chapter 5 we based our classification of “resilient” and “not resilient” wetlands on the presence or absence of age-0 Muskellunge under stable low lake levels at a relatively small number of sites. Characterizations of the fish and aquatic plant communities at the sites were consistent with this classification scheme but additional work to validate and potentially refine the RI is recommended. Different responses to stable low lake levels have

been noted between wetlands in northern Georgian Bay and southern or eastern Georgian Bay in previous work (Midwood 2012), and these data sets should be used for further validation of the RI.

6) A suite of tools have been developed to evaluate coastal wetlands and nearshore areas in Georgian Bay, and Muskellunge habitat more specifically. I recommend integrating these individual tools into a comprehensive framework for Muskellunge habitat identification and assessment. The low marsh model (Chapter 3) can be used to predict the presence of low marsh habitat under a target lake level(s), and the RI (Chapter 5) can then be used to evaluate the resilience of that low marsh habitat to stable low lake levels. Targeted field surveys and application of the INHS (Leblanc and Chow-Fraser 2017) can be directed at the resilient wetlands and cross-referenced against the presence of known spawning populations (Spring Muskellunge Index Netting, A. Liskauskas unpublished data; Wilson et al. 2017), local knowledge, and limited anthropogenic disturbance (e.g. Campbell and Chow-Fraser 2018).

Future Work

The following are suggested topics for future study that arose during the course of this thesis and would advance the research presented herein. These include topics that I would have addressed given time and outstanding gaps in knowledge.

1) Spawning habitat characteristics for muskellunge are quite variable (Diana et al. 2017) and efforts to develop predictive models have been limited (Nohner and Diana 2015; Crane and Kapuscinski 2014). Nohner and Diana (2015) had some success using landscape features to predict spawning habitat in Wisconsin Lakes and a similar approach should be applied to Georgian Bay. Weller and Chow-Fraser (2017) did some preliminary work on this topic using the spawning-season locations from Chapter 1 and an additional season of tracking data in northeastern Georgian Bay to characterize *spawning grounds*, as opposed to the more specific *spawning sites* (see Crossman 1990 or Chapter 1 for further clarification). We found Muskellunge staging at the lakeward edge of coastal wetlands where we assume spawning took place and that they were associated with steeper slopes that may have been used a travel corridors. We also found male Muskellunge may have a minimum spawning ground area requirement and thus use multiple wetlands during the spawning season. These are characteristics that can be derived from a DEM, similar to our other landscape-level habitat models described in this thesis, and should be developed into a spawning-ground model that can act as an additional screening tool to identify spawning and nursery habitat.
2) The mechanism behind the spawning-ground fidelity observed in Muskellunge is unknown. Adult Muskellunge in Chapter 1 displayed

fidelity for locations that supported unsuitable nursery conditions, however genetic analyses show some limited mixing between sub-populations of Georgian Bay Muskellunge (Wilson et al. 2017). Identifying the mechanism by which Muskellunge demonstrate site fidelity, or when they do not, has important implications for fisheries management. This could affect selection of stocking locations of young Muskellunge, and the capacity of adult Muskellunge to seek alternate, more suitable spawning habitats.

3) In Chapter 2 we found that physical habitat structure appeared to be the primary driver of habitat use, not water temperatures. However, fish are ectotherms and water temperatures will have an effect whether or not that manifests in changing patterns of habitat use. Developing a water temperature model for Georgian Bay embayments would be a worthwhile effort to better understand how changing climate scenarios and lake level conditions could affect thermal habitat availability. This would allow for more detailed consideration of potential changes to water temperatures, duration of seasons, and stratification characteristics. This would be a useful tool for fisheries management planning in general, and could more specifically targeted towards a more refined evaluation of thermal habitat vulnerability for adult esocids, or potential effects on earlier life stages (e.g. spawning and nursery habitat considerations).

4) Our study of summer habitat use by esocids only focused on those that were resident in embayments during the summer season, but we had tagged esocids that left the embayments following the spawning season. Locations of some of these individuals were found opportunistically outside the embayment while tracking (e,g. Midwood and Chow-Fraser 2015) or from anglers, with individuals reported up to 30 km from their initial capture locations. Esocids are versatile predators and it would be interesting from an ecological perspective to understand what types of habitat these non-embayment esocids used during the summer, the extent of their summer ranges, and what types of prey they were targeting. Tracking in Georgian Bay outside of defined embayments is incredibly challenging due the large open-water areas and complex shoreline. Improving quality of batteries and miniaturization of telemetry equipment could provide a solution if a detachable data-logger tag, similar to those deployed on large pelagic fish, reach a size and resolution more suited to a large esocids. This information could be combined with our habitat use study of embayment-resident esocids to develop a habitat suitability model for adult esocids in Georgian Bay to augment our suite of tools to evaluate early-life habitat.
5) In Chapter 3 we showed that hydrogeomorphic features could be used to model low marsh as a general habitat class, but future research

should aim to refine this habitat modelling approach. Use of higher-resolution elevation data sets and wetland plant community surveys should be used to develop species distribution models, or coarser groupings based on structural characteristics (e.g. canopy SAV or dense emergents). This would provide another *ex situ* model to evaluate suitability of wetland habitat for esocids or other fish species.

6) Advances in remote sensing techniques and the increasing availability of new sensors can also contribute to more detailed mapping of aquatic vegetation communities in Georgian Bay. This includes the creation of detailed wetland habitat maps that could be used for standalone assessments or as part of long-term monitoring. This could also contribute to training and validation of the aforementioned hydrogeomorphic model which would still be necessary to consider novel environmental conditions (e.g. lake levels).

7) The response time of wetland vegetation communities in Georgian Bay to a change in lake levels is an area in need of further study and is especially relevant given the uncertainty regarding future lake levels conditions. For example, the expected 2-3 year lag time for a community response (Gathman et al. 2005; Quinlan and Mulamoottil 1987; Wilcox and Nichols 2008) was not borne out in Georgian Bay after 14 years of sustained low lake levels (Boyd 2017). If prolonged periods of stable lake levels are to become more frequent as some

models predict (Lu and Nairn, in submission) then a better understanding of the wetland community response is needed. Lake level variability and lag time should be incorporated into the low marsh model (Chapter 3) or finer-scale modelling efforts.

8) The low marsh model (Chapter 3) and RI (Chapter 5) were developed in the unique landscape of eastern and northern Georgian Bay, but are based on process that should be applicable in other large lake systems, if not more broadly. It would be interesting to see if the wetland evaluation tools developed in this thesis are directly transferable to other systems or provide a framework to develop similar tools that are tailored to particular areas.

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