MANAGING EARLY-LIFE HABITAT OF THE GEORGIAN BAY MUSKELLUNGE

MANAGING SPAWNING AND NURSERY HABITAT OF THE GEORGIAN BAY MUSKELLUNGE (*ESOX MASQUINONGY*)

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 (2015) McMaster University
(Biology) Hamilton, Ontario

TITLE: Managing spawning and nursery habitat of the Georgian Bay muskellunge (*Esox masquinongy*)

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NUMBER OF PAGES: xviii, 200

LAY ABSTRACT

The following Ph.D. describes how a period of sustained low water levels and shoreline modifications in Georgian Bay, Lake Huron, have impacted the coastal wetland habitat used by muskellunge during their early life. To counteract these adverse effects, the thesis provides a definition of the wetland features that promote the survival of young-of-the-year muskellunge in Georgian Bay. Included is a proposed management tool in the form of an Index of Nursery Habitat Suitability (INHS) for muskellunge that can be used to identify high-quality, early-life habitat of muskellunge. Furthermore, the INHS can be used to predict how the quality of this habitat responds to different water-level scenarios and to shoreline modification in Georgian Bay, and to guide rehabilitative efforts of degraded wetland habitat.

PREFACE

The following Ph.D. thesis includes four chapters prepared as manuscripts for publication in peer-reviewed journals. To place this research into context a General Introduction is provided. *Chapter 1* has been published in the *Journal of Great Lakes Research*, and *Chapters 2* through *4* are presented as manuscripts but have not yet been submitted for publication. Completed references for all chapters, whether published or for submission, are found below. For all chapters, as first author, I analyzed the data and wrote all the manuscripts under the supervision of Dr. Pat Chow-Fraser. For *Chapters 1* and *2* Dan Weller collected significant supplemental information from southeastern Georgian Bay, while I was collecting data in northern Georgian Bay, and was included as a co-author. For the data collected in the field, I am grateful to many graduate and undergraduates students, and local stakeholders who are more formally recognized in the acknowledgement sections.

Leblanc JP, Weller JD, Chow-Fraser P (2014). Thirty-year update: Changes in biological characteristics of degraded muskellunge nursery habitat in southern Georgian Bay, Lake Huron, Canada. Journal of Great Lakes Research. 40: 870-878

Leblanc JP, Weller JD, Chow-Fraser P (2015, CH2). Similarities in fish communities between muskellunge nursery sites from two adjoining embayments in northern Georgian Bay, Lake Huron (Chapter 2)

Leblanc JP, Chow-Fraser P (2015, CH3). Nearshore ecosystem features predict suitability of muskellunge nursery habitats in Georgian Bay, Lake Huron (Chapter 3)

Leblanc JP, Chow-Fraser P (2015, CH4). Index of Nursery Habitat Suitability for muskellunge in Georgian Bay, Lake Huron (Chapter 4)

GENERAL ABSTRACT

The self-sustaining status of Georgian Bay's trophy muskellunge (*Esox masquinongy*) fishery is owed in part to the widespread distribution of high quality coastal wetlands used as nursery habitat. The specific wetland features that promote the recruitment of young-of-the-year (YOY) muskellunge in Georgian Bay have not been clearly defined, and without such information, it is unclear to what extent an unprecedented period of sustained low water-levels (*c.* 1999), and/or shoreline modifications, will continue to degrade the suitability of nursery habitats used by muskellunge throughout Georgian Bay. In this thesis, I use data from two years of intensive sampling in two embayments of northern Georgian Bay to statistically differentiate between wetlands that were found with and without YOY muskellunge. By doing so, I have provided the first quantifiable definition of suitable nursery habitat for muskellunge in Georgian Bay. Muskellunge nurseries have a structurally complex community of submersed aquatic vegetation (SAV; e.g. *Potamogeton richardsonii*) within the water column (≤ 1-m depth) and a fish community that had abundant suitable prey (e.g. Cypinid species) and a scarcity of early-life predators (e.g. *Perca flavescens*). Some key aspects of the SAV community were governed by wetland's bathymetry, and this relationship makes it possible to model the effect of changing water-level scenarios on habitat suitability.

I translated these results into a management tool for fish management agencies by creating an Index of Nursery Habitat Suitability (INHS) that can be applied to other embayments in Georgian Bay to identify high quality early-life habitats for muskellunge.

I developed two INHS models and applied them to an independent dataset from other regions of Georgian Bay, and found them to differentiate between sites that were known to be used by YOY muskellunge and those where YOY were absent. These were also able to track deterioration in habitat quality associated with the recent decade of low water levels. Both INHS models rely on variables based on robust ecological relationships known to favour YOY survivorship that can be readily collected by fish management agencies, and one INHS model does not require detailed information of the aquatic plant community. Both models were also designed to minimize the frequency of false negatives (suitable nursery sites misidentified as unsuitable) and false positives (unsuitable nursery sites misidentified as suitable). These INHS models should become an important tool that will complement harvest regulations to promote this economically and ecologically valuable, self-sustaining muskellunge population in Georgian Bay.

ACKNOWLEDGMENTS

First and foremost, I must express my deepest thanks and gratitude to Dr. Pat Chow-Fraser for her exceptional mentorship during the past four years. Her ongoing encouragement, insight and passion have been an inspiration to me and made the pursuit of this degree a true pleasure. I feel blessed and privileged that she took a chance and accepted me as a student with no previous experience with aquatic research, let alone with fisheries, couldn’t swim and really wasn’t fond of touching fish. In spite of this, she gave me the opportunity to work in the wonder and remoteness of Georgian Bay on the elusive noble beast.

I am grateful to Dr. Graham Scott and Dr. Jon Stone for agreeing to serve as members of my supervisory committee. Both of whom provided the guidance and insight that shaped the thesis herein.

This thesis would never have been possible without the support of residents in Georgian Bay. I am thoroughly indebted to Harvey and Lorna Mierke and their family. They opened up their home in northern Georgian Bay and accepted me like family while I spent two summers collecting data from their “backyard”. I also have to include Bill and Freda Klassen, and other members of the northern Georgian Bay cottage association for their love and support. I was honoured by the knowledge and charity that Jerry Burke was willing to share. The insight of when and where to find muskies that Jerry provided (“pebbles and reeds”) made a huge difference towards success. Much of the same praise goes to Brenda and David Flowers who were paramount when working in southeastern

Georgian Bay. A special thanks to Mary Muter for being a persistent and convincing spokesperson for all issues Georgian Bay and liaison to our hosts in Georgian Bay.

I cannot speak highly enough to the kindness, passion and intelligence of those whom I have worked with in the Chow-Fraser lab. Thank you to Jon Midwood, Maja Cvetkovic, Bob Christensen, Amanda Fracz and Catherine Dieleman who first introduced me to field work in Georgian Bay, the invaluable protocols used, and their jovial attitude towards the work. Thank you to Chantel Markle, Dallas Taylor, Julia Rutledge and James Marcaccio for their comradery and help in the field. Gratitude to Chris Biberhofer for his unwavering assistance in the field, no matter how trying the task. I cannot thank Dan Weller enough; his efforts, friendship and support made it possible to collect data from two regions of Georgian Bay at the same time, and will one day produce a great PhD thesis for him. Dan's attitude, both in the field and when being "sociable", made working in remote locations of Georgian Bay a true pleasure for those typical 10 day work weeks consisting of 10 hours a day. Despite having little else to do after a day in the field, a trusted Fox would bring some refreshing JRs and Dan and I would banter about gremlins, "stra-nilla", and things to barter at the "Tickle-Trunk", but not the jippopatamus.

There are many more people and organizations that contributed to the success of my research. Specifically, thank you to Arunas Liskauskas of the Ontario Ministry of Natural Resources and Forestry for being instrumental in providing greatly needed logistical support. Additionally, Muskies Canada Inc. and the Georgian Bay Musky Association provided invaluable assistance. Unfortunately, there are far too many to thank individually, but to all of the undergraduate summer students, Georgian Bay residents, and volunteers who helped in the field, know that I cannot thank you enough.

My family has been a source of unwavering support throughout my academic career and I likely fail to express my sincerest appreciation and love they deserve.

Finally, thank you Allison Boyd, for not only being my best friend, but whose love and support made this all possible.

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GENERAL INTRODUCTION

Of the muskellunge (*Esox masquinongy*) populations in Ontario, those in Georgian Bay, Lake Huron are among the most prized because of their potential to reach world record sizes (Casselman et al. 1999; Kerr et al. 2011). Contributing to the legacy of muskellunge in Georgian Bay is also their longevity (up to 30 years; Casselman et al. 1999), and a population that is managed strictly by natural reproduction, without any supplemental stockings (Kerr 2011). Moreover, muskellunge in Georgian Bay are characterized by genetically distinct sub-populations that are separated by as little as 50 km of shoreline (Kapuscinski et al. 2013; Chris Wilson, pers. comm.; Ontario Ministry of Natural Resources and Forestry (OMNRF); Peterborough, Ontario), which is likely the product of high fidelity to specific early-life habitats (Crossman 1990; LaPan et al. 1996; Jennings et al. 2011).

The sub-populations of muskellunge in Georgian Bay bestow high economic and ecological value as apex predators. For this reason, government (e.g., OMNRF) and private organizations (e.g., Muskies Canada Inc.) have been judicious in their efforts to protect breeding adults to promote muskellunge fisheries that are self-sustaining (Kerr 2007; Farrell et al. 2007). Despite success at limiting exploitation of adults (e.g., from a harvest rate of 20% in the early 1980s to less than 1% today; Kerry 2007), muskellunge populations in Georgian Bay are still liable to collapse if their early-life habitats are lost or modified (Dombeck et al. 1986; Zorn et al. 1998; Rust et al. 2002; Kapuscinski et al. 2007). Thus, management agencies throughout the Great Lakes have made protecting coastal wetlands used by muskellunge as spawning and nursery habitats (Craig and Black

1986; Farrell and Werner 1999; Farrell 2001) a management priority in addition to harvest regulations (Farrell et al. 2007; Liskauskas 2007; Kapuscinski et al. 2014).

To implement this part of the management strategy, muskellunge spawning locations have been identified and intermittently monitored in Georgian Bay by the OMNRF since 1998 (Liskauskas 2007). Although, it is widely believed that muskellunge spawning and nursery habitats are spatially linked (LaPan et al. 1996; Farrell et al. 2007) and occur in wetlands at depths less than 1.5 m (Craig and Black 1986; Farrell and Werner 1999; Farrell 2001), both habitat types must be suitable for successful recruitment. In general, the suitability of the spawning habitat is ubiquitously defined by dissolved oxygen concentrations at the sediment-water interface that is at least 3.2 mg/L (Dombeck et al. 1984; Zorn et al. 1998). In Georgian Bay, there is little indication that dissolved oxygen is limiting to the early-life of muskellunge because majority of coastal wetlands have been assessed to be in reference condition (Cvetkovic and Chow-Fraser 2011) based on Water Quality Index scores (WQI; Chow-Fraser 2006).

On the other hand, much less is known of the wetland features that define suitable nursery habitat for muskellunge in Georgian Bay. Only a single study exist that described locations where young-of-the-year (YOY) muskellunge were found 30 years ago in southeastern Georgian Bay (Craig and Black 1986). This is in contrast to the lower Great Lakes (e.g., St. Lawrence River) that have developed a relatively sophisticated definition of suitable nursery habitat for muskellunge. From an ecological perspective, this includes structural complexity in the upper water column that allows the YOY to hide from predators (Murry and Farrell 2007; Kapuscinski and Farrell 2014; Wagner et al. 2015) while at the same time ambush their preferred prey (i.e., soft-rayed fusiform species; Wahl and Stein 1988; Kapuscinski et al. 2012). Georgian Bay, however, differs markedly from the lower Great Lakes with respect to its geomorphology (i.e., Precambrian Shield vs Sedimentary watersheds, respectively; Larson and Schaetzl 2001; DeCatanzaro and Chow-Fraser 2011) and eco-regions (i.e., Northern Forests vs Eastern Temperate Forests, respectively; CEC 1997). This likely makes it inappropriate to directly extrapolate the specific features defining suitable habitat from one region of the Great Lakes to another without proper field validation.

More importantly, during the course of this study, Georgian Bay experienced an unprecedented period of sustained low water levels since 1999 (Sellinger et al. 2008). These low water levels have reduced the number of coastal wetlands that are accessible to fish (Fracz and Chow-Fraser 2013), while many of the remaining wetlands have experienced a decline in fish species diversity resulting from a less diverse and less structurally complex macrophyte community (Midwood and Chow-Fraser 2012). Considering that water levels and shoreline modification influence the diversity of the macrophyte community in wetland habitats (Keddy and Reznicek 1986; Wilcox and Meeker 1991), there is uncertainty of how the suitability of muskellunge nursery habitats have been and will be impacted by the sustained low water levels and increases in shoreline modifications. It is therefore timely to conduct a proper investigation to identify what features of a wetland promote muskellunge recruitment in the under-studied region of Georgian Bay. Moreover, it is important that fishery managers are provided tools that can be used to identify these limiting early-life habitats and predict how the suitability of these habitats will respond to different water-level scenarios and disturbances from shoreline modifications.

Thesis Objectives

In Chapter 1, I examine how the low water levels and shoreline modification have affected previously identified early-life habitats of muskellunge in southeastern Georgian Bay. I hypothesize that muskellunge recruitment is sensitive to the conditions of their nursery habitat, and predict that changes in the wetland macrophyte and fish communities induced by low water-levels and shoreline modification (Keddy and Reznicek 1986; Midwood and Chow-Fraser 2012) will affect the quality of the wetland to the detriment of YOY survival.

After locating wetlands units that support YOY muskellunge from a region in northern Georgian Bay, I examine what aspects of the wetlands differed between the locations with and without YOY. In Chapter 2, I investigate how the fish community may influence the suitability of muskellunge early-life habitat. Because YOY muskellunge growth and survival appears related to higher abundances of species considered their preferred prey (Wahl and Stein 1988; Kapuscinski et al. 2012) and limited numbers of early-life predators (Wahl and Stein 1989; Murry and Farrell 2007); I predict that muskellunge nurseries will be associated with higher abundances of prey and lower abundances of potential predators than sites without YOY muskellunge.

In Chapter 3, I expand the comparison between wetlands with and without YOY muskellunge by focusing on differences in the macrophyte community and physical features of the wetlands. Given that YOY preferentially inhabit the upper portion of the water column and are ambush predators (Wahl 1995), I predict that wetlands with YOY muskellunge will be associated with metrics related to habitat complexity from macrophytes that grow throughout the water column. I will also use a Discriminant Function Analysis to differentiate between habitat features of the aquatic plant community at sites where YOY muskellunge occur and where they are absent. I will consolidate these habitat features related to the fish and plant communities to propose a holistic definition of suitable nursery habitat for muskellunge in northern Georgian Bay.

Finally, I will create a Georgian Bay explicit Index of Nursery Habitat Suitability (INHS) for muskellunge in Chapter 4 to allow fishery managers the ability to assess the suitability of nursery habitats that are located near known spawning sites. The INHS will be developed based on the ecological relationships that define suitable nursery habitat identified in Chapters 2 and 3, and include variables considered mostly accessible to fishery managers. The INHS will be philosophically consistent in its development with Habitat Suitability Index models (US Fish and Wildlife Service 1981) that are familiar to fishery managers (De Kerckhove et al. 2008). The transferability of the INHS throughout Georgian Bay is also tested by applying it to independent data of muskellunge nurseries from other regions of Georgian Bay.

Results from this thesis will provide the first quantifiable definition of suitable nursery habitat for muskellunge in Georgian Bay that will offer fishery managers a tool that will complement harvest regulations by identifying important early-life habitats that can be offered protection from shoreline modifications. Furthermore, the INHS will allow managers to monitor how the quality of the muskellunge nursery habitat is affected by different water level scenarios; while at the same time provide guidance towards rehabilitative and restorative actions as needed.

The Chapters presented in this thesis are linear in nature, such that information presented in earlier Chapters are directly related to those that follow. Thus, there will be overlap regarding introductory information, protocols used to collect data, and the literature cited among the Chapters. However, analysis, results and conclusion drawn are unique for each Chapter.

References

Casselman JM, Robinson CJ, Crossman EJ (1999). Growth and ultimate length of muskellunge from Ontario water bodies. North American Journal of Fisheries Management 19: 271-290

CEC (Commission for Environmental Cooperation; Montréal, Québec)., & Secretariat. (1997). Ecological regions of North America: toward a common perspective. The Commission

Chow-Fraser P (2006). Development of the Water Quality Index (WQI) to assess effects of basin-wide land-use alteration on coastal marshes of the Laurentian Great Lakes. In: Coastal Wetlands of the Laurentian Great Lakes: Health, Habitat and Indicators. Authorhouse, Bloomington, Pp 137–166

Craig RE, Black RM (1986). Nursery habitat of muskellunge in southern Georgian Bay, Lake Huron, Canada. American Fisheries Society Special Publication 15, Pp. 79–86, *in* Hall

Crossman EJ (1990). Reproductive homing in muskellunge, *Esox masquinongy*. Canadian Journal of Fisheries and Aquatic Sciences 47: 1803-1812

Cvetkovic M, Chow-Fraser P (2011). Use of ecological indicators to assess the quality of Great Lakes coastal wetlands. Ecological Indicators 11: 1609–1622

De Kerckhove DT, Smokorovski KE, Randall RG (2008). A primer on fish habitat models. Canadian Technical Report of Fisheries and Aquatic Sciences 2817: vi + 65 p

DeCatanzaro R, Chow-Fraser P (2011). Effects of landscape variables and season on reference water chemistry of coastal marshes of eastern Georgian Bay. Canadian Journal of Fisheries and Aquatic Sciences 68: 1–45

Dombeck MP, Menzel BW, Hinz PN (1984). Muskellunge spawning habitat and reproductive success. Transactions of the American Fisheries Society 113: 205–216

Dombeck MP, Menzel BW, Hinz PN (1986). Natural muskellunge reproduction in Midwestern lakes. American Fisheries Society Special Publication 15, Pp. 122–134, *in* Hall

Farrell JM (2001). Reproductive Success of Sympatric Northern Pike and Muskellunge in an Upper St. Lawrence River Bay. Transactions of the American Fisheries Society 130: 796-808

Farrell JM, Klindt RM, Casselman JM, LaPan SR, Werner RG, Schiavone A (2007). Development, implementation, and evaluation of an international muskellunge management strategy for the upper St Lawrence River. Environmental Biology of Fishes 79: 111-123

Farrell JM, Werner RG (1999). Distribution, abundance, and survival of Age-0 muskellunge in Upper St. Lawrence River nursery bays. North American Journal of Fisheries Management 19: 309-320

Fracz A, Chow-Fraser P (2013). Impacts of declining water levels on the quantity of fish habitat in coastal wetlands of eastern Georgian Bay, Lake Huron. Hydrobiologia 705: 151-169

Jennings MJ, Hatzenbeler GR, Kampa JM (2011). Spring capture site fidelity of adult muskellunge in inland lakes. North American Journal of Fisheries Management 31: 461-467

Kapuscinski KL, Belonger BJ, Fajfer S, Lychwich TJ (2007). Population dynamics of muskellunge in Wisconsin water of Green Bay, Lake Michigan, 1989-2005. Environmental Biology of Fishes 79: 27-36

Kapuscinski KL, Farrell JM (2014). Habitat factors influencing fish assemblage at muskellunge nursery sites. Journal of Great Lakes Research 40: 135-147

Kapuscinski KL, Farrell JM, Murry BA (2012). Feeding strategies and diets of Young-of-the-year muskellunge from two large river ecosystems. North American Journal of Fisheries Management 32: 635-647

Kapuscinski KL, Farrell JM, Wilkinson MA (2014). Trends in muskellunge population and fishery characteristic in Buffalo Harbor (Lake Erie) and the Niagara River. Journal of Great Lakes Research 40: 125-134

Kapuscinski KL, Sloss BL, Farrell JM (2013). Genetic population structure of muskellunge in the Great Lakes. Transactions of the American Fisheries Society 142: 1075-1089

Keddy P, Reznicek A (1986) Great Lakes vegetation dynamics: the role of fluctuating water levels and buried seeds. Journal of Great Lakes Research 12: 25–36

Kerr SJ (2007). Characteristics of Ontario Muskellunge (*Esox masquinongy*) fisheries based on volunteer angler diary information. Environmental Biology of Fishes 79: 61-69

Kerr SJ (2011). Distribution and management of muskellunge in North America: An overview. Fisheries Policy Section, Biodiversity Branch. Ontario Ministry of Natural Resources. Peterborough, Ontario. 22 p. + appendices

Kerr SJ, Kirkpatrick A, Haxton TJ (2011). Characteristics of trophy-sized muskellunge (*Esox masquinongy*) angled from Ontario waters, 1917-2010. Fisheries Policy Section, Biodiversity Branch. Ontario Ministry of Natural Resources. Peterborough, Ontario. 7 p. + appendices.

LaPan SR, Schiavone A, Werner RG (1996). Spawning and post-spawning movements of the St. Lawrence River muskellunge (*Esox masquinongy*). In Managing muskies in the '90s. Workshop Proceedings [eds. Kerr, S. J. and C. H. Olver]. Ontario Ministry of Natural Resources, Southern Region Science and Technology Transfer Unit Workshop Proceedings WP-007. Pp. 73-82

Larson G, Schaetzl R (2001). Origin and evolution of the Great Lakes. Journal of Great Lakes Research 27: 518-546

Liskauskas AP (2007). Severn Sound muskellunge population assessment survey, 2007. Upper Great Lakes Management Unit, Ontario Ministry of Natural Resources. Unpublished technical report. 9pp.

Midwood JD, Chow-Fraser P (2012). Changes in aquatic vegetation and fish communities following 5 years of sustained low water levels in coastal marshes of eastern Georgian Bay, Lake Huron. Global Change Biology 18: 93-105

Murry BA, Farrell JM (2007). Quantification of native muskellunge nursery habitat: influence of body size, fish community composition, and vegetative structure. Environmental Biology of Fishes 79: 37-47

Rust AJ, Diana JS, Margenau TL, Edwards CJ (2002). Lake characteristics influencing spawning success of muskellunge in northern Wisconsin lakes. North American Journal of Fisheries Management 22: 834-841

Sellinger C, Stow C, Lamon E, Qian S (2008). Recent water level declines in the Lake Michigan−Huron system. Environmental Science & Technology 42: 367–373

US Fish and Wildlife Service (1981). Standards for the development of suitability index models. Ecology Service Manual 103, U.S. Fish and Wildlife Service, Division of Ecological Sciences, Washington, DC, USA

Wagner CP, Weber MJ, Wahl DH (2015). Structural complexity influences littoral coarse woody habitat selection by juvenile muskellunge. North American Journal of Fisheries Management 35: 14-19

Wahl DH (1995). Effect of habitat selection and behavior on vulnerability to predation of introduced fish. Canadian Journal of Fisheries and Aquatic Sciences 52: 2312-2319

Wahl DH, Stein RA (1988). Selective predation by three esocids: the role of prey behavior and morphology. Transaction of the American Fisheries Society 117: 142-151

Wahl DH, Stein RA (1989). Comparative vulnerability of three esocids to largemouth bass (*Micropterus salmoides*) predation. Canadian Journal of Fisheries and Aquatic Sciences 46: 2095-2103

Wilcox DA, Meeker JE (1991). Disturbance effects on aquatic vegetation in regulated and unregulated lakes in northern Minnesota. Canadian Journal of Botany 69: 1542–1551

Zorn SA, Margenau TL, Diana JS, Edwards CJ (1998). The influence of spawning habitat on natural reproduction of muskellunge in Wisconsin. Transactions of the American Fisheries Society 127: 995-1005

Chapter 1:

Thirty-year update: Changes in biological characteristics of degraded muskellunge nursery habitat in southern Georgian Bay, Lake Huron, Canada

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Leblanc, J.P., Weller, J.D., Chow-Fraser, P. 2014. Thirty-year update: Changes in biological characteristics of degraded muskellunge nursery habitat in southern Georgian Bay, Lake Huron, Canada. J. Great Lakes Res. 40, 870-878.

Abstract

Aquatic vegetation is a critical component of nursery habitat for young-of-the-year (YOY) muskellunge. The trophy status of the muskellunge fishery in southeastern Georgian Bay owes its reputation to the widespread distribution of aquatic vegetation in coastal marshes of this region. Unfortunately, wetland habitat has been in decline because of an unprecedented period of sustained low water levels since 1999. In this study, we strategically re-sampled 16 historic sites that supported YOY muskellunge in 1981. The sustained low water levels and increased shoreline modifications experienced by southeastern Georgian Bay may have contributed to the current disappearance of YOY muskellunge at those sites. These physical stressors appeared to have altered the habitat structure of the plant community and led to changes in fish communities, making them no longer suitable for YOY muskellunge. The precise mechanisms limiting survival to the YOY stage are unknown because spawning adults have been observed in the area in the spring of 2012 and 2013. These results corroborated previous sampling programs at the historic sites (2004-2005: n = 8 and 2007: n = 16) that employed other fishing gears and protocols as well as a supplemental YOY sampling in 2013 (n = 26 additional sites). If this muskellunge population is to remain self-sustaining, a complementary management strategy specifically developed for Georgian Bay is required. This should identify and ultimately protect suitable muskellunge breeding habitat by accounting for the unique geomorphology, current physical stressors affecting Georgian Bay, and the biological links between suitable spawning and nursery habitats.

Keywords: Muskellunge, nursery habitat, Georgian Bay, Lake Huron

Introduction

Currently, many native muskellunge (*Esox masquinongy*) populations are no longer self-sustaining (Dombeck et al. 1986; Rust et al. 2002), the primary reason for which appears to be degradation and alteration of spawning and nursery habitat (Dombeck et al. 1986; Farrell et al. 2007; Inskip 1986; Rust et al. 2002). Although the critical requirements of spawning habitat have been well defined (e.g., dissolved oxygen (DO) concentrations > 3.2 mg/L at the substrate water interface; Dombeck et al. 1984; Zorn et al. 1998), relatively little has been established for nursery habitat (Farrell et al. 2007; Kapuscinski and Farrell 2013; Kapuscinski et al. 2012; Murry and Farrell 2007), particularly for self-sustaining populations. Newly hatched muskellunge and young-of-the-year (YOY) are assumed to require aquatic vegetation for protection since they are vulnerable to predation by fish, birds and even predaceous insects (Johnson 1958; Wahl and Stein 1989). As such, muskellunge nursery habitat in coastal wetlands has been found in close proximity to areas where adults spawn (LaPan et al. 1996). These areas tend to have intermediate densities of aquatic plants including emergent, floating, and submersed aquatic taxa, which structure the upper water column (Craig and Black 1986; Murry and Farrell 2007; Werner et al. 1996) and that support suitable abundances of soft-rayed fusiform fish that YOY muskellunge prefer (Kapuscinski et al. 2012; Kapuscinski and Farrell 2013; Wahl and Stein 1988). Despite these generalizations, large differences in eco-regions exist within the Great Lakes with respect to geomorphology, ecological characteristics and wetland conditions (see Chow-Fraser and Albert 1999; Cvetkovic and

Chow-Fraser 2011), making it difficult to extrapolate from site to site in regard to specific habitat requirements for these early stages.

Since the mid-1990s, spawning habitats have been identified and monitored periodically throughout eastern and northern Georgian Bay (Liskauskas 2007), but detailed inventories of nursery habitats have only been conducted in 1981 and only in southeastern Georgian Bay in the Severn Sound region (Craig and Black 1986). Since 1999, water levels in the Bay have been extremely low (Sellinger et al. 2008) and in January 2013, they surpassed the record low level set in 1965. This period of sustained low water levels is unprecedented and has altered the habitat structure of many coastal wetlands in eastern Georgian Bay (Midwood and Chow-Fraser 2012). Since the unique geomorphology of these coastal marshes appears to limit the lakeward migration of aquatic vegetation (Mortsch 1998), Fracz and Chow-Fraser (2013) estimated that almost 25% of the wetland habitat available to fish have already been lost between the historical high and the current low water levels, and greater losses are anticipated with continued water level declines due to global climate change (see Fracz and Chow-Fraser 2013; Midwood and Chow-Fraser 2012; and Sellinger et al. 2008 for greater discussion). Such a magnitude of wetland loss and alteration is expected to have serious implications for the reproductive success of self-sustaining populations of muskellunge in Georgian Bay that use these wetlands as nursery habitat (Craig and Black 1986). Along with this change, large stretches of shoreline in southeastern Georgian Bay have also been modified for cottage and recreational development over the past 30 years, alterations that include shoreline hardening, vegetation removal and dredging.

The goals of this study are multi-fold. First, we carried out a field survey in 2012 to determine the current status of historic muskellunge nursery sites in Severn Sound, southeastern Georgian Bay, an area that has not been re-examined for over 20 years (Leslie and Timmins, 1994). Secondly, using information collected by Craig and Black (1986; see Figure 1.1) as reference conditions, we compared biotic characteristics between 1981 and 2012 to investigate whether the structural diversity of submerged aquatic (SAV) and emergent vegetation, an important determinant of the fish community (Kapuscinski and Farrell 2013; Murry and Farrell 2007), has changed. We speculate that declining water levels and shoreline modification are associated with altered habitat structure and have rendered the historic nursery habitats unsuitable for YOY muskellunge. Finally, we conducted an expanded survey to determine the location of nursery habitat for YOY muskellunge in the summer of 2013, by focusing on coastal wetlands associated with areas where adult muskellunge were found during the 2012 and 2013 spawning seasons. This is the first study conducted in Georgian Bay to investigate long-term changes in the habitat of early life stages of the muskellunge in Georgian Bay, and will reveal important insights on the potential effects of sustained low water levels on the habitat suitability of historic nursery habitat for this economically and ecologically important muskellunge trophy fishery.

Methods

Study Site

Our study sites occur in southeastern Georgian Bay, in the body of water known as Severn Sound (Figure 1.1). This region has shallow contours, and is relatively warm and productive compared to the rest of the bay which has deep, cold, oligotrophic waters (Bennett 1988; Weiler 1988). Similar to the eastern and northern shores of Georgian Bay, the northern portion of Severn Sound occurs on Precambrian Shield where coastal wetlands are found among rocky outcrops, islands, and in protected bays (deCatanzaro and Chow-Fraser 2011). Severn Sound began to experience nutrient enrichment by the mid-1980s that was attributed to agricultural and urban development within the watershed; this cultural eutrophication was sufficiently advanced that it was designated as an Area of Concern (AOC) by the International Joint Commission in 1987 and a Remedial Action Plan was enacted (Sherman 2002). It was delisted as an AOC in 2003, and although the symptoms of eutrophication have disappeared (Croft and Chow-Fraser 2007), water levels in the recent decade have remained extremely low and this may have exerted a different though equally adverse impact on the ecological integrity of the coastal wetlands in this region.

Historic Data

In 1981, Craig and Black (1986) surveyed the fish communities of 103 coastal wetlands in the Severn Sound region in an effort to identify muskellunge nursery habitats. Twenty of the 103 sampled coastal wetlands were found to support YOY muskellunge.

In this study, we will refer to these as "historic" sites and will consider them to have been suitable nursery habitat for muskellunge. The Ontario Ministry of Natural Resources (OMNR) provided field data from the 1981 technical report (Black and Craig 1982) that was used subsequently for their 1986 publication. Data from both documents will be used here to compare with data collected in 2012 (see below).

Fish Sampling

In 2012, we surveyed 16 of 20 historic sites sampled by Craig and Black (1986) using the same specifications of seine net (6.4 mm meshing x 15 m x 1.2 m) and same protocols they used (see Craig and Black 1986 for seining details); only 16 sites were included due to time constraints. Although only a single seine haul per site was used in 1981, we opted to use two seine hauls per site in both the June and July sampling (i.e., 4 seine hauls per site) to increase sampling rigor. The bottom of the seine net was chained to prevent vegetation from rolling the net, and a third person trailed the seine haul with a dipnet to catch or identify any fish that passed through the net. The sampling also took place to match the original 1981 dates for at least one of the four seining efforts; all seine hauls within wetlands were always separated by at least 100 m. Water temperature was taken at a depth of 50 cm at each site after each seine haul. In June and July of 2013, we conducted additional YOY sampling in coastal wetlands where adult muskellunge congregated during the spawning period in 2012 and 2013. This approach has been successful at locating muskellunge nursery habitat in other studies (LaPan et al. 1996; Leblanc pers. obs.) and was expected to yield best-bet locations of current nursery habitat for YOY in Severn Sound. The same net described previously was used in single hauls at

26 sites. The 2012 and 2013 Severn Sound seining technique was identical to that used in a northern Georgian Bay study in 2012 and 2013, which successfully caught YOY muskellunge in both June and July (JP. Leblanc unpubl. data). All fish caught in these surveys were identified to species, counted and then released in the water where they had been caught.

Aquatic Vegetation Survey

We examined the habitat structure and other characteristics of the historic nursery sites during the first week of August 2012. Due to time constraints, habitat features were characterized for only 14 of the 16 sites sampled for fish in 2012; none of the sites sampled in 2013 were surveyed for vegetation. In 1981, Craig and Black placed quadrats ($0.25 m^2$) at 2-m intervals along three transects that ran from the shore-water interface to the 1.0 m depth contour to survey the aquatic vegetation. In 1981, the average length of these transects was 23.8±2.1 m ($\bar{x}$±95% CI) but due to the drop in water level (from 176.7 m to 175.92 m) and the bathymetry of Severn Sound, the mean length of the 2012 transects was three times longer (71.4±18.6 m ($\bar{x}$±95% CI)). This made it impractical to sample every 2.0 m along the transect in 2012. Therefore, consistent with the protocol of Craig and Black (1986) we ensured that the three transects were separated by at least 10 m, and extended them perpendicular to shore to the 1.0 m depth contour. Placements of the quadrats were, however, separated by intervals greater than 2-m, but we ensured that there were at least 10 equally spaced quadrats along each transect. For smaller wetlands, the start of the three transects were equally spaced along the shore but converged to a central point of the wetland at 1.0 m depth. Transect lengths were consistent within a site, but varied among sites, depending on substrate slope.

Craig and Black (1986) estimated the percent cover of the dominant taxon of SAV and identified all emergent and floating vegetation to species where possible, and counted their stems within each quadrat. We followed this procedure except we used a standardized rake-sweep method (see Croft and Chow-Fraser 2009), where a garden rake was swept along the substrate-water interface within the quadrat boundaries and all the stems of SAV captured were identified and counted. This was required because high winds at the time of survey resulted in high sediment re-suspension that precluded a consistent visual estimation of SAV cover. We should note that clear water was normally observed throughout much of the season in 2012.

Shoreline Modification

Our approach was to compare the number of docks present during 1981 and 2012 to determine if human development had significantly modified the physical condition of the shoreline between the two time periods; however, we were unable to find aerial photos of these sites acquired in 1981 and 2012. The closest approximation of these two time periods were orthophotos taken in 1987 (Forest Resource Inventory aerial photos, OMNR) and IKONOS satellite image (1-m resolution) acquired in 2009. We imported both sets of images into Geographic Information System (ArcMap 10; ESRI Inc., Redlands CA, USA, 2011) and for each site-era we delineated the perimeter of the wetland and counted the number of docks along the shoreline for the 16 sites. We calculated the number of docks per shoreline length ($\# \cdot km^{-1}$) for each period and compared them statistically.

Statistical Analysis

All statistical analyses were conducted with the software package, STATISTICA 8.0 (StatSoft, Inc. 2007). We used a repeated measure statistical design to make comparisons between 1981 and 2012 data collected at the historic sites. Each site sampled (i.e. historic nursery wetland) was considered the sampling unit for both fish and habitat analyses. Thus, the data for each site from 2012 were matched with corresponding sites from 1981. When parametric tests were used, the data were transformed to satisfy parametric assumptions; however, if the data could not be normalized, then non-parametric equivalents were used. Log_{10} (n+1) transformations were used except for proportions, which were arcsine-square root transformed. The June 2013 fish community composition was only compared to the 1981 historic reference sites and not to the 2012 data. All data reported are in transformed units unless otherwise indicated.

Since we employed greater sampling effort in 2012 (4 samples per site) than in 1981 (one sample per site), one of the 2012 samples per site was randomly selected and used in the direct comparison between time periods. Frequency of occurrence (percentage of sites where a fish species was present), mean proportional abundance, fish species richness, and Shannon's diversity index scores were calculated for each site and compared to those calculated for historic data. Beta diversity index (β = gamma diversity – mean alpha diversity) was also calculated for each sampling period. Proportional abundances of all fish species that occurred in >65% of the sites were compared between time periods; those species occurring at <65% of the sites were first classified into functional guilds (see Table 1.1) and then grouped for comparison. Data collected in 2013 were treated in a similar manner and compared against data collected in 1981.

Emergent and floating vegetation were first classified into families. We standardized the data by dividing the stem counts for each family by total stem counts of all families (% total for each family). In order to make the 2012 data comparable to the 1981 data for SAV, we first had to convert the 2012 stem counts to an abundance category. Following the description of Craig and Black (1986) relative abundance ratings were calculated for each taxon within each site and their relative abundance ranks were compared to 1981 data. For all SAV taxa that occurred at >40% of the sites in 1981 and 2012, we compared median values of relative abundance ranks in the two time periods. To minimize potential Type-I errors, due to the large number of paired comparisons, a highly conservative Bonferroni correction of $\alpha = 0.005$ was used to test for significant differences between time periods. We also sorted SAV data according to two growth forms (i.e., "low growing" and "canopy growth" following Cvetkovic (2008)) and carried out a 2-factor repeated measures ANOVA (year * growth form as independent factors) to determine if there had been a significant change in habitat structure between 1981 and 2012 based on relative abundance ranks.

Craig and Black (1986) divided the nursery areas they sampled into four "depth zones" and provided a description of “typical muskellunge nursery habitat”. They arbitrarily divided transects into these zones but did not indicate the actual depth associated with the upper or lower limits of each zone. In order to compare the depths at each zone between 1981 and 2012, we estimated a substrate slope that would have been present in 1981 and used that to approximate the upper limit of each depth zone and then applied these to the 2012 data. The boundaries of the four zones were determined as follows: Zone 1: 0.0 to 0.10m; Zone 2: 0.11-0.53m, Zone 3: 0.54-0.90m and Zone 4: 0.91 to 1.0m. Using these estimated depth zones we directly compare the 1981 and 2012 stem counts of emergent and floating vegetation for each site after first performing a square root transformation. We then performed a two-factor repeated measures ANOVA (time * depth zones as independent factors) to determine if this vegetation type varied differentially among depth zones between time. For the 2012 data, we also determined the significant effect of depth zones and growth forms (i.e. low growing versus canopy) on stem densities of SAV using a two-factor ANOVA after first performing a $\log_{10}(n + 1)$ transformation. This analysis excluded depth zone 1 since no SAV was encountered there.

Results

Substantial changes in the fish community were noted between time periods; despite our intensive seining efforts in 2012, we found a complete absence of YOY muskellunge at all 16 historic nursery sites (Table 1.1; Figure. 1.2). There was a clear shift in the species composition of the fish community between years (Table 1.1): black crappie, smallmouth bass, and tadpole madtom (among others) that were common in 1981 were replaced with banded killifish, longear sunfish, and round goby in 2012 (i.e., ≥ 43 %). As a result of these substitutions, we did not find significant differences in species diversity between time periods (i.e., mean species richness and Shannon's Index scores; $p > 0.4$).

Of the three most numerically dominant species present in both time periods, the relative abundance of yellow perch increased significantly between 1981 and 2012 (mean difference ± SE: 0.233 ± 0.070; Paired t-test, $t_{15} = 3.330$, $p = 0.005$), while that for largemouth bass decreased significantly (mean difference ± SE: -0.356 ± 0.101; Paired t-test, $t_{15} = -3.537$, $p = 0.003$; Table 1.1). Although we did not detect any significant differences between time periods for pumpkinseeds (Paired t-test, $t_{15} = 0.423$, $p = 0.675$), the combined catch of pumpkinseeds and yellow perch accounted for >60% of all the fish caught in 2012, compared with only 39% in 1981 (Table 1.1). Thus, consistent with a decline in beta-diversity between 1981 ($\beta = 14.56$) and 2012 ($\beta = 11.12$), the fish community appeared less diverse in 2012, dominated by yellow perch and pumpkinseed. We also compared the less common species between time periods (see Table 1.1). The mean relative abundance of the "potential forage guild" for 1981 was 0.276 ± 0.07

($\bar{x}$±SE), which was not significantly different from the mean for 2012 of 0.390 ± 0.081(Paired t-test, t_{15} = 1.100, *p* = 0.289) (Table 1.1). Similarly, there was no significant difference between the mean proportional abundance of the "other species guild" 0.285 ± 0.077 ($\bar{x}$±SE) calculated for the 1981 data, and 0.153 ± 0.033 calculated for 2012 data (Paired t-test, t_{15} = -1.615, *p* = 0.127; Table 1.1).

Physical features of the historic nursery sites differed significantly between time periods. In addition to a significant difference in median transect length between time periods (28.0 m vs. 59.3 m; Wilcoxon Matched Pairs Test: z = 3.156, *p* = 0.004), the median value of docks per shoreline km associated with the 1987 aerial photos was significantly lower than that associated with the 2009 IKONOS satellite images (0.0 vs. 6.05 docks · km^{-1}; Wilcoxon Matched Pairs Test: z = 2.93, *p* = 0.003, n = 16). No significant differences in water temperature were detected between sampling periods (Wilcoxon Matched Pairs Test: *p* = 0.642); however, consistent with climate change predictions, water temperatures measured in 2012 showed greater variability (range: 17.4–30.5 °C) than those measured in 1981 (range: 21.0–28.0 °C).

Differences in the physical structure and taxonomic composition of the aquatic plant community were also evident. Average alpha richness of SAV was significantly lower in 1981 compared to 2012 ($\bar{x}$ difference ± SE: -3.714 ± 1.150, Paired-T_{13} = -3.229, *p* = 0.007), even though gamma richness did not differ between time periods (i.e., 17 species; Table 1.2). Due to differences in methods employed to survey the SAV community, (i.e. physically counting and identifying all SAV stems in 2012 vs. visual estimation of percent cover of SAV in 1981), we decided to only investigate differences between years with respect to the dominant SAV species present. We found relatively few differences on a species-by-species basis when relative abundance ranks were calculated for all of the common SAV species (encountered in >40% of the sites; Table 1.2). The only exceptions were *Myriophyllum spicatum* and *Potamogeton robbinsii* which were both more abundant in 2012 than in 1981 (Wilcoxon Matched Pairs Test: $p < 0.0025$; Table 1.2). Consequently, the relative abundance rank of pooled SAV growth forms was significantly greater in 2012 than in 1981 ($F_{1, 26} = 11.137$, $p = 0.003$; Figure 1.3), while low growth SAV had a significantly greater relative abundance rank than did canopy forms, when pooled within years ($F_{1, 26} = 51.216$, $p < 0.001$; Figure 1.3).

We wanted to know if mean stem densities for the two growth forms differed significantly among depth zones to describe present conditions of SAV at the historic sites (Figure 1.4). Within each depth zone, low-growing taxa were noted consistently more frequently than were canopy taxa (Figure 1.4). When pooled among depth zones, stem density of low-growing SAV was significantly greater than that of canopy SAV ($F_{1, 78} = 35.760$, $p < 0.001$). There was also a significant main effect of depth zone (SAV growth forms pooled; $F_{2, 78} = 11.921$, $p = 0.02$) with depth zone 2 having significantly lower stem densities than did depth zone 3 (Tukey HSD multiple comparison test; $p = 0.02$). The dominant canopy species in 2012 were *Elodea canadensis*, *Myriophyllum spicatum*, and *Vallisnerias americana*, which accounted for >40%, >24% and >14% of all the stems counted in 2012, respectively while the dominant taxa of low-growing forms were *Najas flexilis, Chara sp.,* and *Potamogeton robbinsii*, accounting for >85% of the stems counted for this growth form (see Table 1.2).

In 2012, we found fewer families of emergent and floating taxa per site than in 1981 ($\bar{x}$ difference ± SE: -3.928 ± 0.485, Paired-T_{13} = 8.089, $p < 0.0001$). Except for pipeworts (*Eriocaulaceae*), which was found more frequently in 2012 than in 1981, all other families were detected less frequently in 2012 than in 1981 (Table 1.3). Although we were unable to detect significant differences in percent composition of emergent and floating taxa at the family level, many families that had been present in 1981 were no longer present in 2012 (Table 1.3). We also compared stem densities of combined emergent and floating vegetation to determine significant differences between time periods and among depth zones. Although no significant interaction between time period and depth zone ($F_{3, 78} = 2.3246$, $p = 0.081$) was detected, differential patterns of emergent and floating vegetation stem densities within years and among depth zones were found based on Tukey HSD multiple comparison tests. Within respective years, stem counts near the shoreline were significantly greater than those measured at all other depth zones (Tukey HSD; $p < 0.001$; Figure 1.5); however, between years, stem densities in 2012 were always significantly lower than those in 1981 for all depth zones (Tukey-HSD; $p < 0.03$ in all cases; Figure 1.5). Whereas mean stem counts in 1981 were significantly higher in Zone 2 than in either Zone 3 or 4 ($p < 0.013$), we found no significant difference in stem densities of emergent and floating vegetation for depth zones 2, 3, or 4 in 2012 ($p > 0.191$; Figure 1.5). These data are consistent with the observation that the distribution of emergent and floating vegetation was less dense and more homogeneous in 2012 among all depth zones compared with those in 1981.

Twenty-six additional sites were sampled for YOY muskellunge in June 2013, in coastal wetlands where adult muskellunge had been caught during the 2012 and 2013 spawning period. Despite this increased effort, we did not find any YOY muskellunge in any coastal wetland. Although we found no significant differences in taxa richness between 1981 and 2013 ($t_{40} = 0.346$, $p = 0.731$), the beta diversity was slightly higher in 2013 ($\beta = 16.31$) than in 1981 ($\beta = 14.56$), and we found some differences in the species composition and community structure of the fish communities (Table 1.1). The proportional abundance of largemouth bass was significantly lower in 2013 ($\bar{x} \pm$ SE: 0.208 ± 0.041) than in 1981 ($\bar{x} \pm$ SE: 0.511 ± 0.094; $t_{40} = -3.380$, $p = 0.002$). By contrast, we found a higher proportion of fish that we grouped as "Other Species" (see Table 1.1) in 2013 (0.508 ± 0.055) compared with 1981 (0.285 ± 0.077; $t_{40} = 2.413$, $p = 0.02$; Table 1.1). This appeared to be driven by the presence of the invasive round goby. Since round goby had colonized Severn Sound only within the past decade, this species was absent in the 1981 samples, but it had been firmly established by 2013, accounting for approximately 60% of the catch. Once round gobies were excluded from the “Other Species” grouping, we no longer found a significant difference between time periods ($t_{40} = -0.1714$, $p = 0.865$).

Discussion

The current suitability of nursery habitats for YOY muskellunge in southeastern Georgian Bay is questionable. Despite the greater seining effort expended in 2012 compared with 1981, and an additional year (2013: 26 sites) targeting the "best-bet" nursery sites close to where adult muskellunge were found during the spawning season, we have not been able to find a single YOY. There have been significant changes in both the macrophyte and fish communities at the historic nursery sites, and at least some of these changes are related to the recent episode of sustained low water levels since 1999 (Midwood and Chow-Fraser 2012) and some are due to modifications of the shoreline from human activities over the past 3 decades (D. Weller, unpub. data). The plant community has changed with respect to species composition and habitat structure. We noted an increase in the relative abundance ranks of *M. spicatum* and *P. robbinsii* in 2012 and a less diverse community of emergent and floating vegetation, and hence a less diverse vertical structure. Similarly, we observed a significant change in the fish community, with a shift in species composition (e.g., establishment of round goby) and a loss in beta-diversity through time. Compared with 1981, we observed a significantly lower catch of largemouth bass but a significantly higher catch of yellow perch in 2012 at the historic nursery sites.

Since we only have data from two time periods, it is inappropriate to guess when the changes actually began. It is important to note that during the early 1990s, Leslie and Timmins (1994) found a few YOY muskellunge in southwestern Georgian Bay (i.e., in Sturgeon and Penetang Bays), which are located within an approximate 12 km radius from our furthest sites. By the following decade, however, Chow-Fraser (unpub. data) conducted electrofishing surveys and similar seining efforts in 2004, 2005 and 2007, and did not find any YOY muskellunge at 16 of the sites sampled by Craig and Black in 1981. In 2007, a shorter seine net (5.0 m x 1.0 m in 2007 versus 15.0 m x 1.2 m in 2012) with smaller mesh (4.0 mm in 2007 versus 6.4 mm in 2012) was hauled three times at each of 16 historic sites during June and July. In 2004 and 2005, day-time boat electrofishing surveys were used to sample eight of the historic sites opportunistically between mid-June and mid-August as part of a study to examine the effect of gear bias on sampling efficiency (see Cvetkovic et al. 2012). Because of these differences in methods, we were unable to make direct statistical comparisons with either the historic or 2012 data (Cvetkovic et al. 2012), but we can use these results to confirm that YOY muskellunge have not been present for at least the past decade. We are confident that if they had been present, the seining method we used in 2012 would have been able to catch YOY muskellunge in Severn Sound because we used this protocol successfully to sample YOY muskellunge in two embayments in northern Georgian Bay during 2012 (JP. Leblanc, unpub. data). These results confirm previous observations that the early life stages of muskellunge are highly sensitive to alterations of their breeding habitat (Dombeck et al. 1986; Farrell et al. 2007; Rust et al. 2002). This study is the first to show this same phenomenon in Georgian Bay, where the level of human activities is still relatively low compared to elsewhere in the Great Lakes.

Suitable muskellunge nursery habitat likely requires intermediate densities or cover of various macrophyte types (Cook and Solomon 1987; Craig and Black 1986;

Murry and Farrell 2007; Werner et al. 1996), sufficiently dense to provide cover from predation but not too dense to impede foraging activities (Crowder and Cooper 1982; Diehl and Eklöv 1995; Gotceitas and Colgan 1989). Since YOY preferentially use the upper portion of the water column (Murry and Farrell 2007; Werner et al. 1996), presence of canopy-forming SAV, floating and emergent vegetation are important structuring components of nursery habitat. Therefore, wetlands characterized by high densities of emergent vegetation (Craig and Black 1986; Murry and Farrell 2007) and canopy-forming SAV (Kapuscinski and Farrell 2013; Murry and Farrell 2007) should be considered high-quality nursery habitat, whereas wetlands dominated by low growth form SAV (e.g., macroalgae and *P. robbinsii*) with relatively low densities of canopy-forming SAV should be considered lower quality habitat (Kapuscinski and Farrell 2013). Direct comparisons of emergent and floating stem densities between 1981 and 2012 confirm that the historic nursery sites had become structurally homogeneous within the lower three depth zones. Furthermore, low-growing SAV taxa (primarily macroalgae), which are less suitable as nursery habitat than canopy forms, were consistently more abundant in all three depth zones. However, the mechanism(s) resulting in the altered macrophyte structure remains speculative. Interactions between low water levels, shoreline modification, and indirect physical processes such as increased ice-scour impacts from the shallower substrates, may act in tandem to facilitate currently observed macrophyte structure (i.e., diminished canopy vs. increased low SAV densities).

Differences in species composition and structure of the fish community likely followed changes in the macrophyte community at some point between 1981 and 2012

(Cvetkovic et al. 2010; Eadie and Keast 1984; Smokorowski and Pratt 2007; Weaver et al. 1997). Midwood and Chow-Fraser (2012) found a lag time of 5 years before both the plant and fish communities showed a significant response to sustained low water levels in eastern Georgian Bay. Therefore, it is likely that changes in the plant community did not facilitate a noticeable change in the fish community until the mid-2000s, at which point yellow perch began to increase at the expense of largemouth bass. This is consistent with the observation that largemouth bass prefer intermediate to high densities of aquatic vegetation (Scott and Crossman 1998) and Midwood and Chow-Fraser's (2012) finding that there was a general reduction in abundance of largemouth bass following a decline in amount of "fish habitat" in wetlands of eastern Georgian Bay as a result of sustained low water levels. Havens et al. (2005) recorded a similar negative effect of water-level decline on largemouth bass recruitment and abundance in Lake Okeechobee, Florida. The increased abundance of yellow perch can also be explained by the literature. We know that this species can thrive in many habitat types from macrophyte dominated areas (Bryan and Scarnecchia 1992; Fullerton and Lamberti 2006) to rocky habitats (Janssen and Luebke 2004), both of which are found at the historic sites. Past studies have also shown that habitats dominated by low-growing SAV, similar to what we currently see at the historic nursery sites, can lead to increased density of benthic macroinvertebrates (Hanson 1990), which tend to favor yellow perch (e.g., Dettmers et al. 2003; Graeb et al. 2004; Romare 2000).

It is interesting to note that the relative abundance of the preferred forage type for YOY muskellunge (i.e. soft-rayed fusiform species; Kapuscinski et al. 2012; Murry and

Farrell 2007) had not changed through time, even though some of the species had been replaced with ecological analogs (e.g., the reciprocal occurrence of bluntnose minnow in 1981 and banded killifish in 2012). Thus, it seems unlikely that availability of preferred forage was limiting muskellunge recruitment. Instead, we suggest that the relatively high numbers of round gobies and yellow perch are feeding on muskellunge larvae and eggs and thus limiting their recruitment (Fitzsimons 1990; Nichols et al. 2003; Riley and Marsden 2009; Steinhart et al. 2004). The negative association between yellow perch abundances and YOY muskellunge has been documented (Kapuscinski and Farrell 2013; Murry and Farrell 2007), and round gobies are known to be predators of eggs of many fish including other broadcast spawners (e.g., Lake Sturgeon (*Acipenser fulvescens*); Nichols et al. 2003). Nevertheless, this is pure speculation because the extent to which round gobies can limit muskellunge recruitment through egg depredation has not yet been studied (Kapuscinski et al. 2012). Given that muskellunge have a relatively low natural rate of recruitment (Scott and Crossman 1998; Zorn et al. 1998; Farrell and Werner 1999), continual exposure to increased egg and larval mortality could have dire consequences for the overall viability of the population (Nilsson 2006). That adults returned to the same areas during the spawning season in 2012 and 2013, areas which are close to the historic nursery sites, suggests that muskellunge exhibit spawning-site fidelity (Crossman 1990; Jennings et al. 2011; LaPan et al. 1996). If this is the case, then the sub-population in Severn Sound are inadvertently spawning in coastal wetlands that are no longer suitable habitat for YOY, and protecting these spawning habitats may do little to ensure the reproductive success of this trophy muskellunge fishery.

There is currently insufficient data to point to a decline in the adult muskellunge population in Georgian Bay (Kerr 2007); however, muskellunge populations in this region occur at low densities, and consist of genetically distinct sub-populations, including one from Seven Sound (Chris Wilson, OMNR, pers. comm.). Because muskellunge are long-lived and have slow growth, current monitoring programs (see Kerr 2007 and Liskauskas 2007) do not provide sufficient information to resolve statistically significant change in populations over time for a particular sub-region of Georgian Bay (Brosi and Biber 2009; Taylor and Gerrodette 1993). When we examined data from the muskellunge Volunteer Angler Diary Program (VADP; see Kerr 2007 and OMNR website: http://www.mnr.gov.on.ca) specifically for Severn Sound between 1995 and 2010, angler effort appeared to have been constant through time, while angler catch-per-unit-effort (CPUE; measured as the number of muskellunge angled per rod hour) showed a negative, albeit not statistically significant relationship with time (OMNR unpubl. data). This divergent pattern between angler effort and CPUE with time also casts doubt on the presumption based on VADP indices that the current muskellunge population is self-sustaining (Kerr 2007; Mosindy and Duffy 2007).

Despite the strong recommendations by Craig and Black (1986) that the breeding habitats in Severn Sound be protected from human development, and the demonstrated association between shoreline modifications and muskellunge reproductive dysfunction elsewhere (Dombeck et al. 1986; Rust et al. 2002), the density of docks and development of marinas were permitted to increase along the shoreline between 1981 and 2012. This demonstrates clearly that we cannot rely on current planning regulations to protect critical fish habitat for this self-reproducing population in Georgian Bay, and there is urgency to educate local planning units on the tremendous value of coastal wetlands in this region (Brazner and Beals 1997; Jude and Pappas 1992; Wei et al. 2004).

We suggest that the observed change in macrophyte structure, in addition to shoreline modifications, may have been responsible for the disappearance of the YOY muskellunge. Thus, in addition to restricting the harvest of adults, an additional management strategy must include more stringent protective measures of both critically important spawning *and* nursery habitat. Novel tools that can efficiently and effectively identify suitable muskellunge spawning and nursery habitat must be developed specifically for Georgian Bay (e.g. Habitat Suitability Index model; Cook and Solomon 1987). Our study shows that in southeastern Georgian Bay, suitable muskellunge nursery habitat may be very limited; therefore, more detailed information regarding specific nursery habitat requirements for muskellunge, the processes that structure them, as well as linkages between spawning and nursery habitat must be elucidated (Farrell et al. 2007). If the southeastern Georgian Bay muskellunge population is to persist, complementary management strategies are needed, with greater emphasis on habitat protection.

Acknowledgments

We wish to thank Arunas Liskauskas (OMNR) for his assistance sampling adult muskellunge at historic nursery sites, as well as Dr. Jon Midwood, Christopher Biberhofer, Julia Rutledge, Jim Hutchings and Jim Herod for their assistance with data collection. We are indebted to Brenda and David Flowers as well as Ralph and Caroline Grose for offering their home and cottage, respectively to us while we were sampling in Severn Sound. As well we are grateful to the Ontario Ministry of Natural Resources for their logistical support and to two anonymous reviewers for their insightful comments and suggestions. This project was funded in part by a research grant from the Sierra Club Canada Foundation, the Ontario Ministry of Natural Resources through the Canada-Ontario Agreement, and grants from the Great Lakes Basin Conservancy, Muskies Canada Inc., and the Georgian Bay Musky Association.

References

Bennett, B.E., 1988. On the physical limnology of Georgian Bay. Hydrobiologia. 163, 21-34.

Black, R., Craig, R., 1982. Muskellunge (*Esox masquinogy*) nursery habitat studies in Severn Sound of Georgian Bay June 1982. Lake Huron Fisheries Assessment Unit. HU. 19.

Brazner, J.C., Beals, E.W. 1997. Patterns in fish assemblages from coastal wetland and beach habitats in Green Bay, Lake Michigan: a multivariate analysis of abiotic and biotic forcing factors. Can. J. Fish. Aquat. Sci. 54, 1743-1761.

Brosi, B.J., Biber, E.G. 2009. Statistical inference, Type II error, and decision making under the US Endangered Species Act. Front. Ecol. Environ. 7, 487-494.

Bryan, M.D., Scarnecchia, D.L. 1992. Species richness, composition, and abundance of fish larvae and juveniles inhabiting natural and developed shoreline of a glacial Iowa lake. Environ Biol. Fish. 35, 329-341.

Chow-Fraser, P., Albert, D., 1999. Identification of eco-reaches of Great Lakes coastal wetlands that have high biodiversity values. Discussion paper for SOLEC ’98. Env. Canada-USEPA Pub.

Cook, M.F., Solomon, R.C., 1987. Habitat suitability index models: muskellunge. U.S. Fish and Wildlife Service Biol. Rep. 82 (10.148). 33 pp. retrieved from http://www.nwrc.usgs.gov/wdb/pub/hsi/hsi-148.pdf

Craig, R.E., Black, R.M., 1986. Nursery Habitat of Muskellunge in Southern Georgian Bay, Lake Huron, Canada. American Fisheries Society Special Publication 15. Pp. 79–86, *in* Hall.

Croft, M.V., Chow-Fraser, P, 2007. Use and Development of the Wetland Macrophyte Index to Detect Water Quality Impairment in Fish Habitat of Great Lakes Coastal Marshes. J. Great Lakes Res. 33, 172-197.

Croft, M.V., Chow-Fraser, P., 2009. Non-random sampling and its role in habitat conservation: a comparison of three wetland macrophyte sampling protocols. Biodivers. Conserv. 18, 2283-2306.

Crossman, E.J., 1990. Reproductive Homing in Muskellunge, *Esox masquinongy*. Can. J. Fish. Aquat. Sci. 47, 1803-1812.

Crowder, L.B. Cooper, W.E., 1982. Habitat structural complexity and the interaction between bluegills and their prey. Ecology. 63, 1802-1813.

Cvetkovic, M., 2008. Factors affecting macrophyte and fish distribution in coastal wetlands of Georgian Bay. Master's Thesis. McMaster University, Hamilton, Ontario.

Cvetkovic, M., Chow-Fraser, P., 2011. Use of ecological indicators to assess the quality of Great Lakes coastal wetlands. Ecol. Indic. 11, 1609-1622.

Cvetkovic, M., Kostuk, K., Chow-Fraser, P., 2012. Gear-Type Influences of Fish Catch and a Wetland Fish Index in Georgian Bay Wetlands. N. Am. J. Fish. Manage. 32, 313-324.

Cvetkovic, M., Wei, A., Chow-Fraser, P., 2010. Relative importance of macrophyte community versus water quality variables for predicting fish assemblages in coastal wetlands of the Laurentian Great Lakes. J. Great Lakes Res. 36, 64-73.

deCatanzaro, R., Chow-Fraser, P., 2011. Effects of landscape variables and season on reference water chemistry of coastal marshes in eastern Georgian Bay. Can. J. Fish. Aquat. Sci. 68, 1009-1023.

Dettmers, J.M., Raffenberg, M.J., Weis, A.K., 2003. Exploring zooplankton changes in Southern Lake Michigan: Implications for yellow perch recruitment. J. Great Lakes Res. 29, 355-364.

Diehl, S., Eklöv, P., 1995. Effects of piscivore-mediated habitat use on resources, diet, and growth of perch. Ecology. 76, 1712-1726.

Dombeck, M.P., Menzel, B.W., Hinz, P. N., 1984. Muskellunge Spawning Habitat and Reproductive Success. Trans. Am. Fish. Soc. 113, 205–216.

Dombeck, M.P., Menzel, B.W., Hinz, P.N., 1986. Natural Muskellunge Reproduction in Midwestern Lakes. American Fisheries Society Special Publication 15. Pp. 122–134, *in* Hall.

Eadie, J.McA., Keast, A., 1984. Resource heterogeneity and fish species diversity in lakes. Can. J. Zool. 62, 1689-1695.

Farrell, J.M., Werner, R.G., 1999. Distribution, abundance, and survival of Age-0 muskellunge in Upper St. Lawrence River nursery bays. N. Am. J. Fish. Manage. 19, 309-320.

Farrell, J.M., Klindt, R.M., Casselman, J.M., LaPan, S.R., Werner, R.G., Schiavone, A., 2007. Development, implementation, and evaluation of an international muskellunge management strategy for the upper St Lawrence River. Environ Biol. Fish. 79, 111-123.

Fitzsimons, J.D, 1990. Yellow perch predation on lake trout egg in Keuka Lake, New York. J. Great Lakes Res. 16, 130-132.

Fracz, A., Chow-Fraser, P., 2013. Impacts of declining water levels on the quantity of fish habitat in coastal wetlands of eastern Georgian Bay, Lake Huron. Hydrobiologia. 705, 151-169.

Fullerton, A.H., Lamberti, G.A., 2006. A comparison of habitat use and habitat-specific feeding efficiency by Eurasian ruffe (*Gymnocephalus cernuus*) and yellow perch (*Perca flavescens*). Ecol. Freshw. Fish. 15, 1-9.

Gotceitas, V., Colgan, P., 1989. Predator foraging success and habitat complexity: quantitative test of the threshold hypothesis. Oecologia. 80, 158-166.

Graeb, B.D.S., Dettmers, J.M., Wahl, D.H., Caceres, C.E., 2004. Fish size and prey availability affect growth, survival, prey selection, and foraging behavior of larval yellow perch. Trans. Am. Fish. Soc. 133, 504-514.

Hanson, J.M., 1990. Macroinvertebrate size-distributions of two contrasting freshwater macrophyte communities. Freshwater Biol. 24, 481-491.

Havens, K.E., Fox, D., Gornak, S., Hanlon, C., 2005. Aquatic vegetation and largemouth bass population response to water-level variations in Lake Okeechobee, Florida (USA). Hydrobiologia. 539, 225-237.

Inskip, P.D., 1986. Negative associations between abundances of muskellunge and northern pike: evidence and possible explanations. American Fisheries Society Special Publication 15. Pp. 135–150, *in* Hall.

Janssen, J., Luebke, M.A., 2004. Preference for rocky habitat by Age-0 yellow perch and alewives. J. Great Lakes Res. 30, 93-99.

Jennings, M.J., Hatzenbeler, G.R., Kampa. J.M., 2011. Spring capture site fidelity of adult muskellunge in inland lakes. N. Am. J. Fish. Manage. 31, 461-467.

Johnson, L.D., 1958. Pond culture of muskellunge in Wisconsin. Wisc. Cons. Dept. Tech. Bull. 17. D-J Proj F-10-R. 54 pp.

Jude, D.J., Pappas, J., 1992. Fish utilization of Great Lakes coastal wetlands. J. Great Lakes Res. 18, 651-672.

Kapuscinski, K.L., Farrell, J.M., 2013. Habitat factors influencing fish assemblage at muskellunge nursery sites. J. Great Lakes Res. doi.org/10.1016/j.jglr.2012.11.007

Kapuscinski, K.L., Farrell, J.M., Murry, B.A., 2012. Feeding Strategies and Diets of Young-of-the-Year Muskellunge from Two Large River Ecosystems. N. Am. J. Fish. Manage. 32, 635-647.

Kerr, S.J., 2007. Characteristics of Ontario muskellunge (*Esox* masquinogy) fisheries based on volunteer angler diary information. Environ Biol. Fish. 79, 61-69.

LaPan, S.R., Schiavone, A., Werner, R.G., 1996. Spawning and Post-Spawning Movements of the St. Lawrence River Muskellunge (*Esox masquinongy*). In Managing muskies in the '90s. Workshop Proceedings [eds. Kerr, S. J. and C.

H. Olver]. Ontario Ministry of Natural Resources, Southern Region Science and Technology Transfer Unit Workshop Proceedings WP-007. Pp. 73 - 82.

Leslie, J.K., Timmins, C.A., 1994. Ecology of young-of-the-year fishes in Severn Sound, Lake Huron. Can. J. Zool. 72, 1887-1897.

Liskauskas, A.P., 2007. Severn Sound muskellunge population assessment survey, 2007. Upper Great Lakes Management Unit, Ontario Ministry of Natural Resources. Unpublished technical report. 9pp.

Midwood, J.D., Chow-Fraser, P., 2012. Changes in aquatic vegetation and fish communities following 5 years of sustained low water levels in coastal marshes of eastern Georgian Bay, Lake Huron. Global Change Biol. 18, 93-105.

Mortsch, L.D., 1998. Assessing the impact of climate change on the Great Lakes shoreline wetlands. Clim. Change. 40, 391-416.

Mosindy, T.E., Duffy, M.J., 2007. The use of angler diary surveys to evaluate long-term changes in muskellunge populations on Lake of the Woods, Ontario. Environ Biol. Fish. 79, 71-83.

Murry, B.A., Farrell, J.M., 2007. Quantification of native muskellunge nursery habitat: influence of body size, fish community composition, and vegetative structure. Environ Biol. Fish. 79, 37-47.

Nichols, S. J., Kennedy, G., Crawford, E., Allen, J., French III, J., Black, G., Blouin, M. Hickey, J., Chernyak, S., Hass, R., Thomas, M., 2003. Assessment of Lake

Sturgeon (*Acipenser fluvescens*) spawning efforts in the lower St. Clair River, Michigan. J. Great Lakes Res. 29, 383-391.

Nilsson, J., 2006. Predation of northern pike (*Esox lucius* L.) eggs: a possible cause of regionally poor recruitment in the Baltic Sea. Hydrobiologia. 553, 161-169.

Riley, J.W., Marsden, J.E., 2009. Predation on emergent lake trout fry in Lake Champlain. J. Great Lakes Res. 35, 175-181.

Romare, P., 2000. Growth of larval and juvenile perch: importance of dies and fish density. J. Fish Biol. 56, 876-889.

Rust, A. J., Diana, J.S., Margenau, T.L., Edwards, C.J., 2002. Lake Characteristics Influencing Spawning Success of Muskellunge in Northern Wisconsin Lakes. N. Am. J. Fish. Manage. 22, 834-841.

Scott, W.B., Crossman, E.J., 1998. Freshwater fishes of Canada. Galt House Publications Ltd. Oakville, Ontario, Canada.

Sellinger, C.E., Stow, C.A., Lamon, E.C., Qian, S.S., 2008. Recent water level declines in the Lake Michigan-Huron system. Environ. Sci. & Technol. 42, 367-373.

Sherman, R.K., 2002. Severn sound remedial action plan stage 3 report: the status of restoration and delisting of Severn Sound as an area of concern. Environment Canada and Ontario Ministry of the Environment. http://www.severnsound.ca/SSRATSStage3TextOnly.pdf. Accessed 24 Aug 07.

Smokorowski, K.E., Pratt, T.C., 2007. Effect of a change in physical structure and cover on fish and fish habitat in freshwater ecosystems – a review and meta-analysis. Environ. Rev. 15, 15-41.

StatSoft, Inc. (2007). STATISTICA (data analysis software system), version 8.0. www.statsoft.com.

Steinhart, G.B., Marschall, E.A., Stein, R.A., 2004. Round Goby predation on smallmouth bass offspring in nests during simulated catch-and-release angling. Trans. Am. Fish. Soc. 133, 121-131.

Taylor, B.L., Gerrodette, T., 1993. The Uses of Statistical Power in Conservation Biology: The Vaquita and Northern Spotted Owl. Conserv. Biol. 7, 489-500.

Wahl, D.H., Stein, R.A., 1988. Selective Predation by Three Esocids: The Role of Prey Behavior and Morphology. Trans. Am. Fish. Soc. 117, 142-151.

Wahl, D.H., Stein, R.A., 1989. Comparative Vulnerability of Three Esocids to Largemouth Bass (*Micropterus salmoides*) predation. Can. J. Fish. Aquat. Sci. 46, 2095-2103.

Weaver, M.J., Magnuson, J.J., Clayton, M.K., 1997. Distribution of littoral fishes in structurally complex macrophytes. Can. J. Fish. Aquat. Sci. 54, 2277-2289.

Wei, A., Chow-Fraser, P., Albert, D., 2004. Influence of shoreline features on fish distribution in the Laurentian Great Lakes. Can. J. Fish. Aquat. Sci. 61, 1113-1123.

Weiler, R.R., 1988. Chemical limnology of Georgian Bay and the North Channel between 1974 and 1980. Hydrobiologia. 163, 77-83.

Werner, R.G., Klindt, R., Jonckheere, B., 1996. Vegetative characteristics of muskellunge (*Esox masquinongy*) spawning and nursery habitat in the 1000 Islands section of the St. Lawrence River. Great Lakes Res. Rev. 2, 29-35.

Zorn, S.A., Margenau, T.L., Diana, J.S., Edwards, C.J., 1998. The Influence of Spawning Habitat on Natural Reproduction of Muskellunge in Wisconsin. Trans. Am. Fish. Soc. 127, 995-1005.

Table 1.1

Frequency of occurrence (%) and mean (±S.E.) relative abundance of fish sampled at 16 coastal wetlands in southeastern Georgian Bay (1981 and 2012; see Fig. 1) and the 2013 (n = 26) sampling of best-bet nursery habitat locations. Data for 1981 were obtained from Black and Craig (1982). Mean alpha species richness and Shannon Diversity index scores did not differ significantly between years ($p = 0.476$ and 0.958, respectively). Species presented alphabetically by common name within ecological guild group membership such that species occurring at >65% of sites sampled all years were considered "Standalone species". Species occurring at <65% of sites were classified as "Potential forage" for YOY muskellunge if body type could be described as soft-rayed and fusiform (Murry and Farrell, 2007; Kapuscinski et al., 2012) while all other species were classified as "Other species". Untransformed data displayed for presentation purposes.

Ecological guild	Common name	Scientific name	Frequency of occurrence (%)			Relative abundance		
			1981	2012	2013	1981	2012	2013
N/A	Muskellunge	*Esox masquinongy*	100	0	0	0.030 ± 0.007	0	0
Standalone species	Largemouth bass	*Micropterus salmoides*	75	69	69	0.297 ± 0.065	0.034 ± 0.088	0.077 ± 0.023
	Pumpkinseed	*Lepomis gibbosus*	88	88	88	0.258 ± 0.062	0.291 ± 0.063	0.366 ± 0.049
	Yellow perch	*Perca flavescens*	88	94	85	0.151 ± 0.034	0.341 ± 0.052	0.157 ± 0.035
Potential forage	Banded killifish	*Fundulus diaphanus*	0	50	27	0	0.027 ± 0.018	0.014 ± 0.089
	Blackchin shiner	*Notropis heterodon*	25	25	23	0.040 ± 0.045	0.048 ± 0.026	0.038 ± 0.031
	Blacknose shiner	*Notropis heterolepis*	0	0	15	0	0	0.013 ± 0.007
	Bluntnose minnow	*Pimephales notatus*	44	25	31	0.058 ± 0.028	0.033 ± 0.022	0.015 ± 0.007
	Brook silverside	*Labidesthes sicculus*	13	38	38	0.021 ± 0.019	0.055 ± 0.033	0.018 ± 0.008
	Central mudminnow	*Umbra limi*	<13	0	4	No data	0	0.001 ± 0.001
	Golden shiner	*Notemigonus crysoleucas*	<13	6	8	No data	0.003 ± 0.003	0.003 ± 0.003
	Iowa darter	*Etheostoma exile*	<13	6	8	No data	0.002 ± 0.002	<0.0001
	Johnny darter	*Etheostoma nigrum*	13	6	15	0.009 ± 0.006	0.001 ± 0.001	0.001 ± 0.001
	Logperch	*Percina caprodes*	<13	19	12	No data	0.022 ± 0.021	0.005 ± 0.004
	Spotfin shiner	*Cyprinella spiloptera*	0	25	19	0	0.010 ± 0.007	0.002 ± 0.002
	Spottail shiner	*Notropis hudsonius*	0	0	4	0	0	0.002 ± 0.002
Other species	Black crappie	*Pomoxis nigromaculatus*	44	0	0	0.014 ± 0.007	0	0
	Bowfin	*Amia calva*	<13	0	0	No data	0	0
	Brown bullhead	*Ameiurus nebulosus*	<13	25	4	No data	0.020 ± 0.012	<0.0001
	Longear sunfish	*Lepomis megalotis*	0	44	73	0	0.092 ± 0.035	0.100 ± 0.024
	Longnose gar	*Lepisosteus osseus*	<13	6	0	No data	0.007 ± 0.007	0
	Mottled sculpin	*Cottus bairdii*	<13	0	4	No data	0	<0.0001
	Rock bass	*Ambloplites rupestris*	<13	13	12	No data	0.002 ± 0.001	0.002 ± 0.002
	Round goby	*Neogobius melanostomus*	0	50	77	0	0.010 ± 0.004	0.165 ± 0.038
	Smallmouth bass	*Micropterus dolomieu*	<13	0	4	No data	0	0.001 ± 0.001
	Tadpole madtom	*Noturus gyrinus*	<13	0	19	No data	0	0.003 ± 0.002

Table 1.2. Frequency of occurrence (Freq occur; %) and mean relative abundance (Rel Abund) with 95% Confidence Interval (CI) relative abundance of SAV sampled in 1981 and 2012. Common taxa are those occurring in > 40% of the samples. A conservative Bonferroni correction of α = 0.005 was used to test differences between median values between time periods. Untransformed data displayed for presentation purposes.

	1981			**2012**		
SAV Taxa	Freq Occur	Rel Abund[d]	CI	Freq Occur	Rel Abund[d]	CI
Slender water nymph (*Najas flexilis*)[a]	92.9	6.21	1.07	100	6.00	0.91
Chara spp. (*Chara sp.*)[a]	85.7	4.50	1.56	92.9	5.71	1.07
Variable pondweed (*Potamogeton gramineus*)[b]	85.7	3.50	1.26	64.3	1.93	1.12
Water celery (*Vallisneria americana*)[b]	57.1	2.57	1.53	100	3.43	0.90
Common waterweed (*Elodea canadensis*)[b]	42.9	1.50	1.15	92.9	2.57	1.17
Coontail (*Ceratophyllum demersum*)[b]	42.9	0.57	0.44	71.4	0.71	0.27
Clasping-leaved pondweed (*Potamogeton richardsonii*)[b]	64.3	1.14	0.78	50.0	0.50	0.30
Milfoil sp. [b, c] †	42.9	0.43	0.30	100	2.64	1.12
Fern-leaf pondweed (*Potamegeton robbinsii*)[a] †	28.6	0.29	0.27	100	3.14	1.34
Flat-stemmed pondweed (*Potamogeton zosteriformis*)[b]	35.7	0.64	0.66	64.3	1.29	0.77

† Indicates median values are significantly different between time periods ($p < 0.0025$) based on a Wilcoxon Matched Pairs Test.

[a] Low growing SAV taxa [b]Canopy SAV taxa [c]Data for 1981 were not identified to species whereas 2012 data consisted only of (*Myriophyllum spicatum)* [d]In decreasing mean relative abundance, those taxa occurring in <43% of sites in 1981 were: arrowhead spp. (*Sagittaria spp.*), pipewort (*Eriocaulon aquaticum*), bladderwort spp. (*Utricularia spp.*), Beck's water marigold (*Bidens beckii*), quillwort (*Isoetes spp.)*, pondweed spp. (*Potamogeton spp.*), and large-leaved pondweed (*Potamogeton amplifolius*)

[e] In decreasing mean relative abundance, those taxa in the "Other" category in 2012 were: quillwort (*Isoetes spp.*), curly-leaf pondweed (*Potamogeton crispus*), Beck's water marigold, freshwater sponges, slender pondweed (*Potamogeton pusillus*), sago pondweed (*Stuckenia pectinatus*) and large-leaved pondweed (*Potamogeton amplifolius*).

Table 1.3. Comparison of frequency of occurrence, and percent composition with 95% Confidence Interval (CI) of families of emergent + floating vegetation sampled in 1981 and 2012. Data correspond to means for 16 sites. Overall family richness was significantly lower in 2012 (3.57 ± 0.562) than in 1981 (7.50 ± 0.416) (Paired t-test, $t_{14} = 8.089$, $p < 0.0001$).

Emergent and floating plant families	Frequency occurrence		% composition		±95% Confidence interval	
	1981	2012	1981	2012	1981	2012
Grasses (*Poaceae*)	100	21	7	5	4.4	9.7
Arrowheads (*Alismataceae*)	100	<20	10	<3	12.1	--
Sedges (*Cyperaceae*)	93	86	54	42	13.8	20.3
Pickerelweed (*Pontederiaceae*)	79	21	9	4	4.9	5.6
Water lilies (*Numphaeaceae*)	79	50	7	13	4.6	13.0
Pondweeds (*Potamogetonaceae*)	79	43	5	3	3.8	3.7
Rushes (*Juncaceae*)	71	--	4	--	3.3	--
Burreeds (*Sparganiaceae*)	64	<20	2	<3	2.3	--
Pipewort (*Eriocaulaceae*)	--	64	--	17	--	15.4
Cattails (*Typhaceae*)	<20	29	<2	4	--	5.0
Others	71[a]	21[b]	3	3	2.4	6.2

[a] In decreasing frequency of occurrence are 7 families: irises (*Iridaceae*), cattails (*Typhaceae*), pipeworts (*Eriocaulaceae*), horsetails (*Equisetaceae*), arums (*Araceae*), parsley (*Umbelliferae*) and smartweeds (*Polygonaceae*).

[b] In decreasing frequency of occurrence are 2 families: burreeds (*Sparganiaceae*) and arrowhead (*Alismataceae*).

Figure 1.1. Map of study area in southeastern Georgian Bay (inset shows location of Georgian Bay within the Laurentian Great Lakes). Triangles identify locations of 16 sites (corresponding to those sampled by Craig and Black, 1986) sampled in 2012, while open circles show locations of 26 additional sites sampled in 2013 (see Methods).

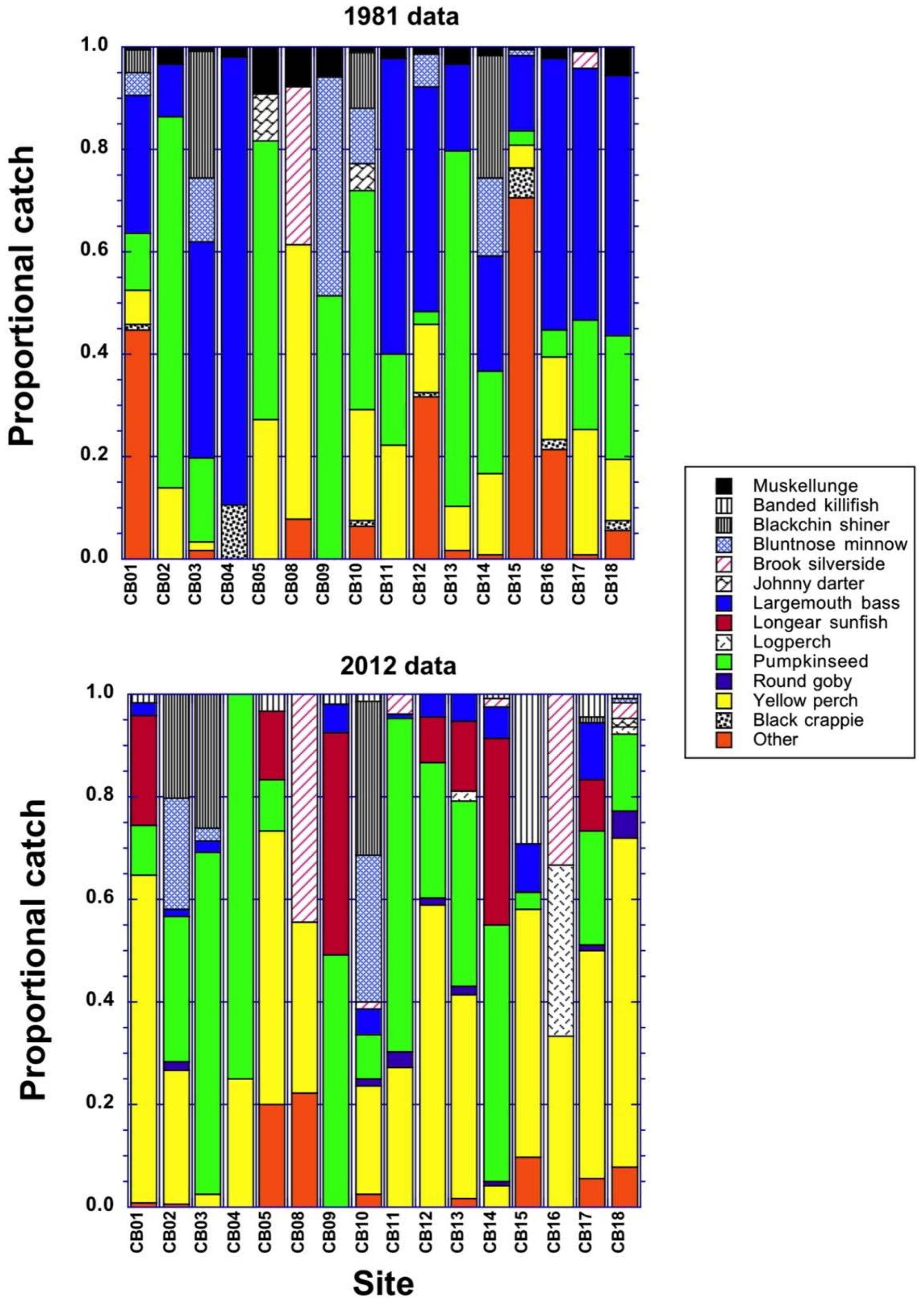


Figure 1.2. Comparison of proportional abundance of fish caught in the 1981 and 2012 surveys. Untransformed data displayed for presentation purposes.

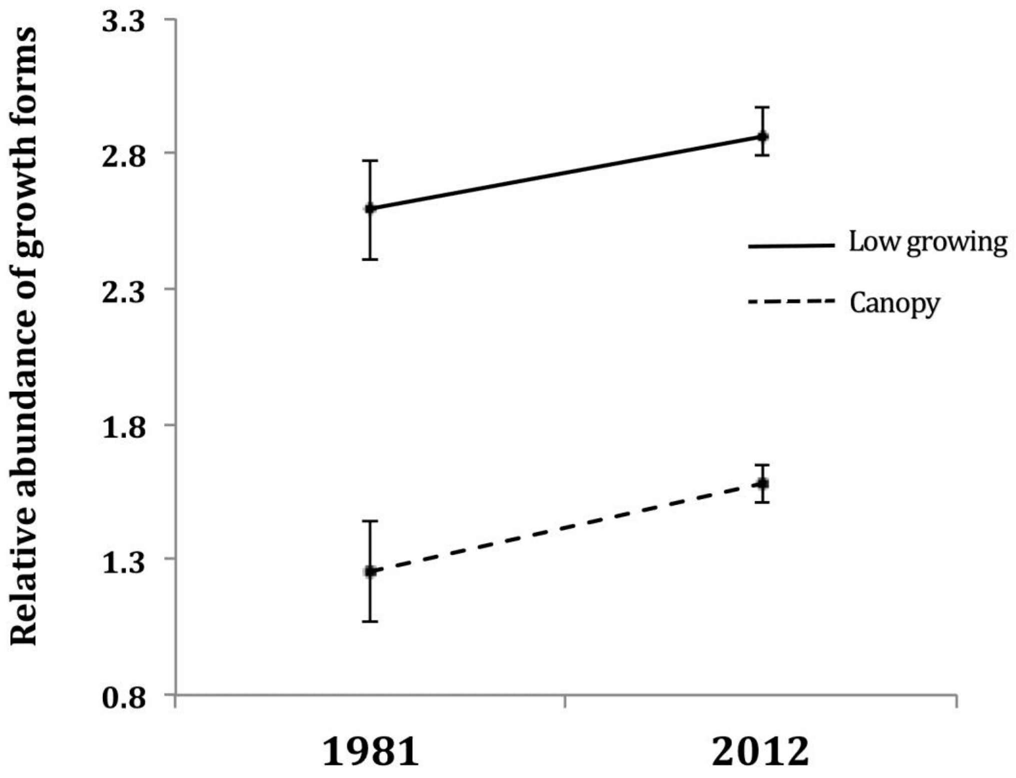


Figure 1.3. Comparison of mean (± S.E.) relative abundance ratings of low growing and canopy growth forms surveyed in 1981 and 2012. Based on a 2-factor repeated measures ANOVA, no significant interaction was detected (p = 0.880) indicating that relative abundance ratings of SAV growth forms followed similar patterns between years. However, significant main effects of year ($F_{1, 26}$ = 11.137, p = 0.003) and SAV growth from ($F_{1, 26}$ = 51.216, p < 0.001) were detected.

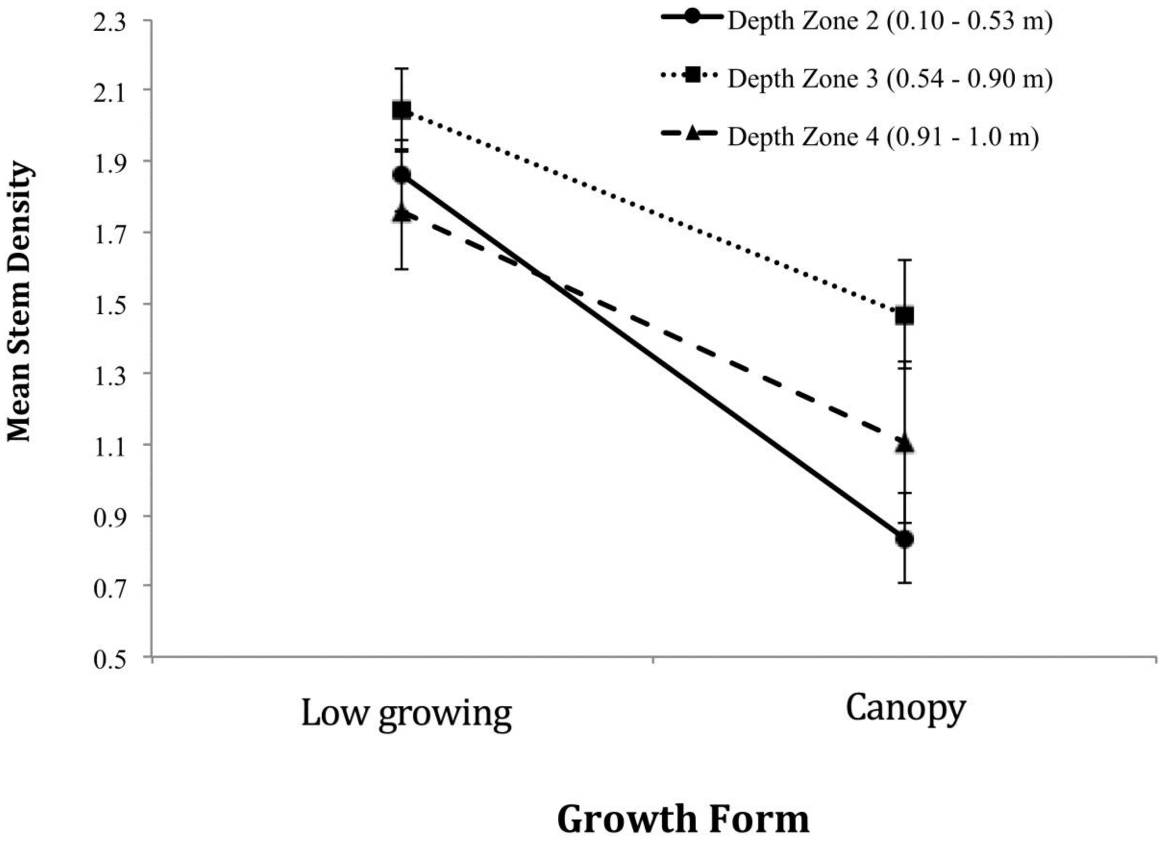


Figure 1.4. Comparison of mean stem density ($\log_{10}$ (n+1)) of SAV for two growth forms sampled in 2012. Data are plotted separately for each depth zone (2 to 4 inclusive). Two-factor ANOVA indicated no significant interaction between growth form and Depth Zone ($F_{2,\,78}$ = 1.191, *p* = 0.309). Stem densities of canopy plants were consistently lower than those of low-growing forms irrespective of depth zone ($F_{1,\,78}$ = 35.760, *p* < 0.001). When data was pooled by depth zone a significant main effect was noted ($F_{1,\,78}$ = 3.927, *p* = 0.02) with depth zone 2 having significantly lower SAV stem densities than only depth zone 3 (Tukey HSD, *p* = 0.02).

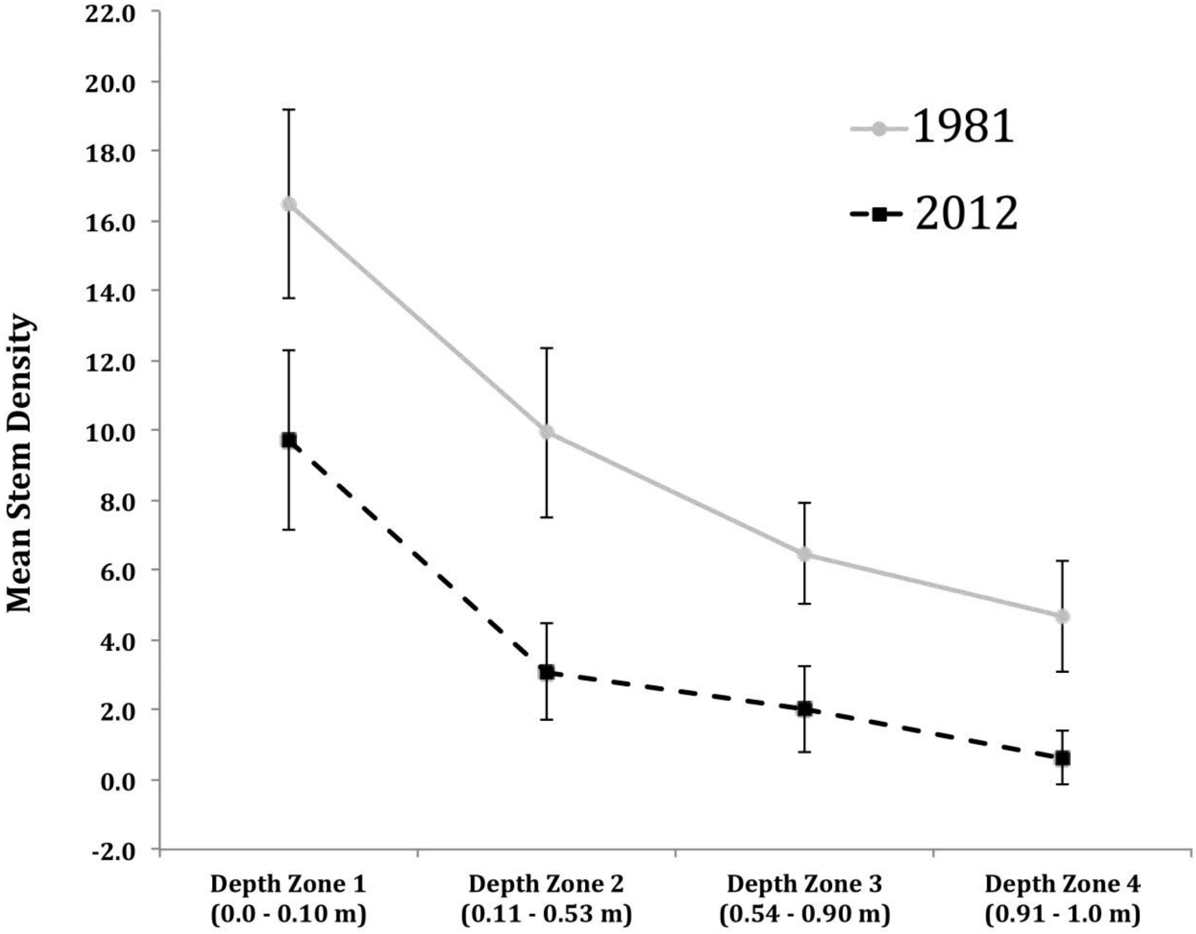


Figure 1.5. Comparison of mean (± 95% CI) stem densities (square root transformed) of emergent and floating vegetation measured at four depth zones in 1981 and 2012. There was no significant interaction between depth zone and time period (2-factor repeated measures; $F_{3, 78} = 2.3246$, $p = 0.0813$); mean densities calculated in 2012 were all uniformly lower than those in 1981 (Tukey-HSD multiple comparison tests; $p < 0.05$).

Chapter 2:

Similarities in fish communities between muskellunge nursery sites from two adjoining embayments in northern Georgian Bay, Lake Huron

For submission: Leblanc JP, Weller JD, Chow-Fraser P (2015, CH2). Similarities in fish communities between muskellunge nursery sites from two adjoining embayments in northern Georgian Bay, Lake Huron

Abstract

As an apex species, adult muskellunge (*Esox masquinongy*) exert a strong influence on the species composition of the fish community in near-shore ecosystems. Less is known about young-of-the-year (YOY) and their associations with coastal wetland fish taxa in nursery areas, especially in understudied areas of the Great Lakes such as Georgian Bay. We collected fish community data during July 2012 and 2013 in northern Georgian Bay to determine if aspects of fish community in which YOY muskellunge are present (YOY-Musky sites) differ significantly from those in which YOY are absent (No-Musky sites). In total, 94 wetland units were seined in two embayments of northern Georgian Bay. Sixteen were YOY-Musky sites, 11 sites contained YOY northern pike (*E. lucius*) and three of these sites had both esocids in the same seine haul. In both embayments, YOY-Musky sites had higher species diversity, higher relative abundances of preferred forage species (e.g. *Cyprinidae* spp.), and lower relative abundances of yellow perch (*Perca flavescens*) than No-Musky sites. We attribute the absence of YOY muskellunge in wetlands where yellow perch are abundant to high rates of muskellunge egg depredation. We hypothesize that the fish community is an important feature of the nursery habitat for YOY muskellunge, and should be used to develop models to identify suitable nursery habitat in Georgian Bay.

Keywords: YOY muskellunge, nursery habitat, fish community, yellow perch, Georgian Bay, suitability

Introduction

Georgian Bay, Lake Huron, supports Ontario's largest Great Lakes muskellunge (*Esox masquinongy*) fishery (Kerr et al. 2011). The Ontario Ministry of Natural Resources and Forestry (OMNRF) manages these naturally reproducing populations primarily by protecting breeding adults (only individuals > 137 cm can be harvested in Georgian Bay), while muskellunge anglers have adopted a voluntary catch-and-release philosophy (Kerr 2007). In addition, the OMNRF advocates protection of breeding habitats because alterations to spawning habitats have been linked to failed natural recruitment elsewhere (Dombeck et al. 1986; Rust et al. 2002). As yet, there is no recommendation for protection of nursery habitat, even though a spatial linkage between spawning and nursery habitat is believed (LaPan et al. 1996; Weller et al. 2015). The primary reason for this is likely because young-of-the-year (YOY) muskellunge are elusive and characteristics of suitable nursery habitat have not yet been explicitly documented for Georgian Bay.

The species composition of the fish community associated with the wetland should play an important role in determining the suitability of that habitat for YOY muskellunge (Wahl 1999; Murry and Farrell 2007; Kapuscinski and Farrell 2014). For example, suitable habitat must have ample prey items, including relatively high numbers of preferred prey; secondly, it should have a low number of egg or larval predators since YOY muskellunge are thought to stay close to spawning grounds (LaPan et al. 1996; Weller et al. 2015). In studies of the lower Great Lakes (St. Lawrence and Niagara Rivers; see Table 2.1), and inland lakes, preferred prey of muskellunge have included soft-rayed fusiform taxa (e.g. fathead minnows (*Pimephales promelas*) and gizzard shad (*Dorosoma cepedianum*) in Wahl and Stein 1988; banded killifish (*Fundulus diaphanus*) and *Cyprinidae* spp. in Kapuscinski et al. 2012) whereas non-preferred prey have included laterally compressed and spiny species (e.g. *Lepomis* spp.; Wahl and Stein 1988; Szendrey and Wahl 1996). Predators of the YOY have included largemouth bass (*Micropterus salmoides*; Wahl and Stein 1989) while yellow perch (*Perca flavescens*) are assumed to be predators of muskellunge eggs and larvae (Murry and Farrell 2007; Leblanc et al. 2014).

Though data from the Lower Lakes exist, it is inappropriate to extrapolate directly from these studies to wetlands of Georgian Bay without proper validation. First, coastal marshes of the St. Lawrence River and those in northern and eastern Georgian Bay are located in different eco-regions (Eastern Temperate Forests vs Northern Forests, respectively; CEC 1997) that have distinctive land-use patterns, vegetation and climates that can influence the distribution of fish taxa (Jennings et al. 1999; Seilheimer and Chow-Fraser 2006; Smokorowski and Pratt 2007; Trebitz et al. 2009; Cvetkovic et al. 2010) irrespective of the presence of muskellunge. Secondly, because of the unique geomorphology of eastern and northern Georgian Bay, most of the coastal marsh units are small and lacustrine (< 2 ha; Midwood et al. 2012) compared to the larger riverine marshes that dominate the upper St. Lawrence River (Ball et al. 2003). Therefore, it is prudent to conduct a proper study in Georgian Bay to guide management of this important muskellunge fishery.

Within Georgian Bay, there exists only a single study, dating back to 1981 that describes wetland conditions of nursery habitat in southeastern Georgian Bay (Craig and Black 1986). Leblanc et al. (2014) found that current nursery conditions have changed substantially over the past 30 years and attributed an absence of YOY muskellunge to these changes. One of the largest and most dramatic changes has been the unprecedented and sustained low water levels experienced in Georgian Bay since 1999 (Sellinger et al. 2008), which have been associated with negative effects on both the quality and quantity of habitat in coastal marshes for both plants and fish communities (Mortsch 1998; Midwood and Chow-Fraser 2012; Fracz and Chow-Fraser 2013). Undoubtedly, this new hydrological regime will be associated with changes in wetland habitat, but the extent to which this will influence the type of fish assemblage remains a matter of speculation.

In this study, we investigate how species composition of the fish community differs between sites that support YOY muskellunge and those that do not. We conducted this study using data collected in two embayments of northern Georgian Bay where there is minimal human disturbance, in order to eliminate any confounding effects of human disturbance through shoreline modifications (e.g., Dombeck et al. 1986; Leblanc et al. 2014). Results should allow identification of key aspects of the fish community that are important determinants towards habitat suitability for YOY muskellunge in Georgian Bay, and ultimately help develop a site-specific habitat suitability index (HSI) to complement current management strategies for muskellunge in Georgian Bay.

Methods

Description of Study Sites

The study sites in northern Georgian Bay have been given aliases, to honour the request of local cottagers, who wish to prevent over-exploitation of the muskellunge fishery. The larger of the two embayments, Eager Bay, is hydrologically connected to northern Georgian Bay, while a narrow channel connects Plant Lake to Eager Bay (see Figure 2.1). Both sites have relatively similar maximum depths but differ in surface area and limnological characteristics (see Table 2.2); Plant Lake is smaller, warmer, and more dystrophic (with lower pH and conductivity). Human development in both sites is very low, with only a small number of summer residents (e.g., 0.3 docks $\cdot$ km^{-1}), many of which are affiliated with Georgian Bay conservation groups. Based on the water-quality characteristics (i.e. Water Quality Index; Chow-Fraser 2006), Cvetkovic and Chow-Fraser (2011) ranked wetlands in this region of northern Georgian Bay to be "excellent" and in reference condition.

Field sampling

The same protocol used to survey for YOY muskellunge in southeastern Georgian Bay and previously described by Leblanc et al. (2014) was used in both northern Georgian Bay embayments. This involved drawing a single, standard seine net (15 x 1.2 m, 6.4 mm mesh) through each coastal wetland to survey the fish community during July of 2012 and 2013. All fish species caught were identified to lowest taxonomic level (see Table 2.3 for all Latin names), counted, and a subset measured for total length (TL; to the nearest mm). Wetland units were operationally defined in the field as either bay or fringing wetlands that had a continuous band of emergent vegetation near shore and submersed aquatic vegetation between shore and the 1.0 m contour. Fringing wetland units were further distinguished by natural barriers (e.g., rock faces or points) that bisected the band of emergent vegetation. Mean size of all wetland units was approximately 1.1 ha (S.E. = 0.17).

In July of 2013, we used an YSI 6600 sonde to measure water-chemistry parameters (i.e., conductivity, water temperature, pH, and dissolved oxygen) at 0.5 m depth at study sites. Turbidity was measured in triplicate at each site with a Hach Portable Turbidimeter with water collected at the same depth measured by the YSI 6600. This was done at 6 sites where YOY muskellunge had been caught (YOY-Musky) and 6 where no YOY muskellunge had been caught (No-Musky) that were randomly chosen.

During May 2014, we positioned GoPro^{TM} cameras over platforms that were baited with muskellunge eggs to determine the likelihood of which fish species are limiting early-life survivorship of muskellunge. The platforms were submerged in 1.0 m of water at historic muskellunge nursery sites in Severn Sound. These sites were selected because adult muskellunge had been observed to congregate there during the spawning season between 2012 and 2014 (Leblanc et al. 2014). An arbitrary number of muskellunge eggs were distributed on one platform, in the field of view of the GoPro^{TM} camera, and filmed continuously for approximately 80 minutes (i.e., the battery life of the GoPro^{TM} camera), while another platform was used as a control (with no eggs) and also filmed. This was repeated 6 times at different locations. The footage was reviewed and all fish observed over the platforms (baited and un-baited) that were eating muskellunge eggs were identified. The behaviour of muskellunge egg predators was assessed by determining the amount of time it took potential predators to find the baited platforms, an estimate of average number of fish observed over the baited platform, and amount of time spent over the platform. The rate at which muskellunge eggs could be preyed on was determined by the foraging behaviour of fish, which was defined as an attack or strike at the baited platform. The actual rate at which muskellunge eggs were depredated could not be assessed quantitatively, because the number of eggs on the platform at the start and end of the footage could not be reliably estimated. Thus, the total number of strikes by all fish observed at the platform was counted and divided by the average number of fish observed over the platform during multiple 2-minutes intervals. This was then converted into an estimate of the number of strikes per fish per minute to estimate the potential rate of muskellunge egg depredation.

Statistical Analysis

We compared frequency of occurrence (Freq occ; %) and the relative abundance (Rel AB) of the residual fish community between YOY-Musky and No-Musky sites. Frequency of occurrence was calculated as the percentage of wetland units in which a species was caught, and the residual proportional abundance was calculated after excluding YOY muskellunge. Taxa that were found in more than 40% of sites in Plant Lake and Eager Bay (combined YOY-Musky and No-Musky sites) and that were considered unsuitable prey (e.g., *Lepomis* spp.; Wahl and Stein 1988; Szendrey and Wahl 1996) or egg/larval predators (e.g., basses and yellow perch; Wahl and Stein 1989;

Murry and Farrell 2007) were analyzed individually (Table 2.3). Other fish taxa that may influence habitat suitability for YOY were classified into 3 functional guilds and grouped for analysis (i.e., Cyprinids, Other Fusiform, Other Species; Wahl 1999; Kapuscinski et al. 2012) (Table 2.3).

For all statistical analyses, one seine haul per wetland was considered the sampling unit and all analyses were conducted with SATISTICA 8.0 (StatSoft, Inc. 2007). We first investigated patterns among fish taxa and guilds between embayments (Plant Lake vs Eager Bay) and site-type (YOY-Musky vs No-Musky) with a factorial multivariate analysis of variances (MANOVA; study site * site-type as factors). Residual proportional abundance data were used in the analyses after arcsine-square root transformation, and unless otherwise stated, these are reported in transformed units. Significant interactions between embayments and site-type could be interpreted as evidence that fish distribution patterns associated with YOY-Musky sites is dependent on the embayment of origin. Significant univariate results between site-type and study sites were determined based on $\alpha = 0.05$.

General metrics of the diversity of fish species were investigated with independent factorial ANOVAs (study site * site-type as factors) on residual species richness and Shannon diversity index, respectively. Residual species richness accounts for inflated species richness from the presence of YOY muskellunge. Thus, residual species richness was total species richness at YOY muskellunge sites excluding any YOY muskellunge. Shannon diversity index was estimated from residual proportional abundances. Residual species richness and Shannon diversity did not require data transformation.

Results

Between 2012 and 2013, 94 sites were seined for fish in July in northern Georgian Bay. Twenty YOY muskellunge were caught at 16 wetland units (YOY-Musky sites); and 12 YOY northern pike (*Esox lucius*) were caught at 11 wetland units (Figure 2.1). Three coastal wetlands were found to be sympatric with both YOY muskellunge and northern pike caught in the same seine haul. The remaining 67 wetland units did not yield YOY esocids (No-Musky sites).

The total lengths (TL) of YOY muskellunge caught in July ranged from 79 mm to 140 mm over the two years. There were significant differences in TL between years; YOY muskellunge caught in July of 2012 were significantly longer ($\bar{x}$ ± SE: 120.8 ± 4.74 mm TL) than those from July of 2013 ($\bar{x}$ ± SE: 102.4 ± 6.29 mm TL; $F_{1, 12} = 5.243$, $p = 0.04$; original units presented). Similarly, largemouth bass caught in 2012 were significantly longer ($\bar{x}$ ± SE: 62.3 ± 5.28 mm TL) than those from 2013 ($\bar{x}$ ± SE: 54.3 ± 4.91 mm TL; Mann-Whitney U test, $p = 0.004$). This difference appears to reflect a three week earlier spawning season in 2012 compared with 2013 (JP Leblanc, pers. obs.); consequently, July water temperature measured at 0.5 m depth was significantly warmer in 2012 ($\bar{x}$ ± SE: 25.6 ± 0.19 °C) than in 2013 ($\bar{x}$ ± SE: 25.0 ± 0.25 °C; $F_{1, 74} = 6.61$, $p = 0.04$). Comparable patterns in TL between years (i.e., 2012 being slightly larger) were observed for most other species, although differences were not significant ($p > 0.05$). The only exception was for yellow perch, which were significantly shorter in 2012 ($\bar{x}$ ± SE: 72.8 ± 3.33 mm TL) than in 2013 ($\bar{x}$ ± SE: 81.0 ± 3.44 mm TL; Mann-Whitney U test, *p*

= 0.02). In general, majority of fish caught were YOY or yearlings except for Cyprinids and Other Fusiform spp., which were all adults. We found no significant differences between years with respect to species composition ($p > 0.05$), and therefore, pooled the fish community data to continue analyses.

Study Site Effects, Water Chemistry & Fish Community Composition

There were statistically significant differences in water chemistry parameters between Eager Bay and Plant Lake (Figure 2.2). Plant Lake had significantly lower pH, conductivity, dissolved oxygen and significantly higher water temperatures compared with Eager Bay (main-effect ANOVA; $p < 0.02$, in all cases). Therefore, although both embayments are oligotrophic, Plant Lake is dystrophic (i.e., tan coloured water) and has a greater influence from the watershed, whereas Eager Bay is more influenced by the alkaline water of Georgian Bay; however, within embayments, no significant differences between site-types existed for any of the water-chemistry variables (Tukey-HSD, $p > 0.05$, in all cases; Figure 2.2).

There were other significant differences between embayments with respect to the fish communities when comparisons of the 6 standalone fish species and 3 guilds were assessed (Wilks $\lambda = 0.534$, $F_{8, 72} = 6.813$, $p < 0.001$). When data were pooled by water body, Plant Lake had significantly higher proportional abundances of smallmouth bass ($F_{1, 79} = 5.959$, $p = 0.017$; Table 2.3) and a tendency for higher proportional abundances of Cyprinids ($F_{1, 79} = 3.197$, $p = 0.07$; Table 2.3). In contrast, Eager Bay had significantly higher proportional abundances of yellow perch ($F_{1, 79} = 8.240$, $p = 0.005$; Table 2.3) and marginally higher proportional abundances of pumpkinseeds ($F_{1, 79} = 3.867$, $p = 0.053$; Table 2.3).

There was no significant interaction between water body and site-type (YOY-Musky vs No-Musky sites; factorial MANOVA (Wilks $\lambda = 0.902$, $F_{8, 72} = 0.858$, $p = 0.566$); however, Tukey-HSD multiple comparison tests showed that patterns in the relative abundance of yellow perch differed between site-type within embayments. There were significantly lower abundances of yellow perch at YOY-Musky sites than at No-Musky sites in Eager Bay (Tukey-HSD: $p < 0.05$; Figure 2.3). Similarly, the relative abundance of yellow perch within Plant Lake was marginally lower in YOY-Musky than in No-Musky sites (Figure 2.3).

Combined data from both embayments showed a significant difference in fish groups between YOY-Musky and No-Musky sites (Wilks $\lambda = 0.697$, $F_{8, 72} = 3.427$, $p = 0.001$). Muskellunge nursery sites were associated with significantly higher residual species richness (9.13±0.515 vs 7.52±0.318 for YOY-Musky and No-Musky sites, respectively; $F_{1, 79} = 6.397$, $p = 0.013$) and Shannon diversity (1.72±0.082 vs 1.46±0.049 for YOY-Musky vs No-Musky sites, respectively; $F_{1, 79} = 6.779$, $p = 0.011$). We also found significantly more Cyprinids in the YOY-Musky sites ($\bar{x}$ ± S.E., 0.488 ± 0.050; $F_{1, 79} = 5.51$, $p = 0.02$) than in the No-Musky sites ($\bar{x}$ ± S.E., 0.338 ±0.035; Table 2.3; Figure 2.3). Thus, YOY-Musky sites appeared to have lower relative abundances of yellow perch but higher abundances of Cyprinid species, and overall greater species diversity compared with No-Musky sites. No significant differences were noted for the any of the other fish taxa or functional guilds with respect to site type ($p > 0.05$; Table 2.3; Table 2.4).

Potential Muskellunge Egg Predators:

Five of the 6 baited platforms demonstrated muskellunge egg depredation by fish. In total, 8 fish species were identified at the baited muskellunge egg platforms in May 2014. Of the species observed, yellow perch was always the first to find the baited platforms, generally in less than 20 minutes ($\bar{x}$ ± S.E.: 17.8 ± 4.02 minutes) from when the platform was positioned in the water, and was often the sole species depredating muskellunge eggs (Figure 2.4). Other species observed depredating muskellunge eggs included a total of two round goby (*Neogobius melanostomus*) and four bluntnose minnow; however, they remained over the baited platform for less than 10 minutes. In contrast, once yellow perch found the baited platforms they consistently remained over the platform for the duration of the recording (approximately 80 minutes). Approximately 6 yellow perch ($\bar{x}$ ± S.E.: 5.7 ± 0.43) were observed over the baited platform at any given time during the course of the recording; however, as many as 15 could be counted within the field of view of the camera. The feeding rate of yellow perch also appeared relatively prolific, and yellow perch would attempt to strike the baited platform at a mean rate of 4.9 (S.E. = 0.90) strikes per individual per minute. The rate at which yellow perch would strike the baited platform showed a highly significant negative relationship with time since the platform was first detected (Pearson Correlation = -0.867, $p < 0.0001$; Figure 2.5). However, the mean number of yellow perch over the baited platform remained consistent with time (Pearson Correlation 0.273 $p = 0.219$; Figure 2.5), and yellow perch appeared to spend more time scanning the platform for the few remaining muskellunge eggs that were embedded in the platform. It should be noted that during the 5 recordings that showed muskellunge egg depredation, the number of eggs on the platform were reduced substantially to only a few eggs that fish could not access. None of the other species observed over the baited platforms (i.e., adult northern pike, bowfin; *Amia calva*, brown bullhead; *Ameiurus nebulosus*; pumpkinseed; rock bass) appeared to eat any muskellunge eggs, but we cannot ascertain whether or not they were potential larval predators. No fish were seen at any of the un-baited platforms.

Discussion

We found consistent patterns in the residual fish communities at muskellunge nursery sites within the two embayments of northern Georgian Bay. First, YOY-Musky sites in both embayments had lower relative abundances of yellow perch. Secondly, they had higher relative abundance of Cyprinid species and thirdly, overall species diversity (both richness and Shannon scores) were higher. This was in spite of different limnological conditions and differences in fish assemblages between the study sites. Our findings are in general agreement with those hypothesized to foster YOY muskellunge survival (Wahl and Stein 1989; Murry and Farrell 2007; Kapuscinski et al. 2012) and consistent with the general ecological framework of Wahl (1999).

Some differences between our results and those reported for wetlands in the lower Great Lakes that should be noted. In contrast to sites in the St. Lawrence River (Murry and Farrell 2007; Kapuscinski and Farrell 2014), sunfish were the dominant taxon caught with YOY muskellunge in Georgian Bay. Although bluegills and pumpkinseeds have been considered sub-optimal forage for YOY muskellunge (Wahl and Stein 1988), they were found in large numbers throughout Georgian Bay coastal wetlands, and accounted for approximately 40 % of the fish community (Cvetkovic et al. 2012). We do not know if YOY muskellunge consume pumpkinseeds or bluegills in Georgian Bay, but the high abundance of these sunfish does not differ between site types in this study. The literature has also indicated that *Micropterus* spp. (Wahl and Stein 1989; Szendrey and Wahl 1996) and rock bass (Murry and Farrell 2007) are predators of YOY muskellunge. In this study, however, the TL of these fish were on average only half that of YOY muskellunge caught in July; therefore, gape limitations precluded muskellunge as prey at the time of sampling. All of the bass combined accounted for only 16 % of the fish community caught with YOY muskellunge, and there were no consistent differences in relative abundances between YOY-Musky and No-Musky sites. Nevertheless, it is possible that at earlier stages of muskellunge development (e.g., larvae and smaller YOYs), both *Micropterus* spp. and rock bass could have been a source of larval mortality (Wahl and Stein 1989; Szendrey and Wahl 1996; Murry and Farrell 2007).

We found no significant differences between site-types for any of the water-chemistry variables, and this suggests to us that water chemistry is not a discriminating factor with respect to habitat suitability for YOY muskellunge within Georgian Bay. We caution against interpreting this as evidence that water quality is unimportant (Cook and Solomon 1987); a more appropriate interpretation is that all embayments in Georgian Bay have excellent water quality (Cvetkovic and Chow-Fraser 2011) and that the quality of water in Georgian Bay should not be considered limiting towards habitat suitability for early life stages of esocids.

Although July water temperatures were significantly warmer in 2012 than 2013, water temperatures were below the critical thermal maxima (32.8 °C; Bonin and Spotila 1978) and were within the temperature range (between 22.5 and 27.5 °C) that appears to promote the highest physiological benefits for YOY muskellunge (Bevelhimer et al. 1985; Clapp and Wahl 1996). Thus, the current thermal regime in northern Georgian Bay does not appear to be limiting the suitability of nursery habitat. If, however, water temperatures continue to rise in the Great Lakes, as predicted from global climate change scenarios (Dobiesz and Lester 2009; Trumpickas et al. 2009), YOY muskellunge may experience symptoms of thermal stress at temperatures exceeding 27.5 °C for extended periods of time (Bevelhimer et al. 1985; Clapp and Wahl 1996). Therefore, water temperatures should be monitored in the early-life habitats of muskellunge, and this information should be included as a criterion of habitat suitability along with changes in water level.

YOY muskellunge survival and recruitment is expected to depend on limited abundances of early-life predators (Wahl and Stein 1989). Although yellow perch is an important prey for adult muskellunge (Scott and Crossman 1998; Bozek et al. 1999), they can hamper the recruitment of muskellunge by competing with and preying on their early-life stages (Walters and Kitchell 2001). We have shown that yellow perch are potentially prolific muskellunge egg predators in Georgian Bay, and therefore, the relatively high abundance of yellow perch at No-Musky sites could be limiting muskellunge recruitment through increased egg and larvae mortality (Fitzsimons 1990; Nilsson 2006; Riley and Mardsen 2009). These differences in relative abundance of yellow perch (i.e., lower at YOY-Musky and higher at No-Musky sites) are consistent with Leblanc et al.'s (2014) observations that wetlands with YOY-Musky were associated with low number of yellow perch 30 years ago, but that these same wetlands no longer support YOY muskellunge, and are now associated with relatively high numbers of yellow perch. The observed high rate of egg depredation by yellow perch in this study may explain the antagonistic relationship between yellow perch and YOY muskellunge in other studies of the lower Great Lakes (Murry and Farrell 2007; Kapuscinski and Farrell 2014).

Fish species that are soft-rayed with fusiform morphology (e.g., *Cyprinidae* spp.) are considered preferred forage for YOY muskellunge (Wahl and Stein 1988; Kapuscinski et al. 2012). Suitable abundances of preferred forage should help YOY muskellunge grow quickly and attain a size that allows them to escape predation by gape-limited piscivores (Wahl and Stein 1989; Szendrey and Wahl 1996). We interpret the higher relative abundances of Cyprinid species at muskellunge nursery sites in northern Georgian Bay to indicate greater availability of preferred prey for the YOY. The greater fish species diversity at nursery sites may also provide alternative prey to predators of YOY muskellunge (Wahl 1999). Since fish species diversity is often related to habitat structure and complexity (Eadie and Keast 1984), this overall higher diversity may be an indirect effect of more suitable macrophyte community (Warfte and Barmuta 2004; Murry and Farrell 2007; Wagner et al. 2015) for these ambush predators.

Management Implications

Effective fishery management requires identification of factors that limit or promote the survival of target species (Rosenfeld and Hatfield 2006). We have identified unique metrics of the fish community that could be used to predict habitat suitability of nursery sites. These metrics, together with those associated with habitat features and site geomorphology could be combined to produce a habitat suitability index (HSI) that can be used to identify nursery habitats for YOY muskellunge in Georgian Bay. The HSI must be built on robust ecologically-meaningful relationships that can be applied broadly across northern and eastern Georgian Bay. Given that there have been predicted and observed changes in coastal wetland fish and macrophyte communities throughout

Georgian Bay (King et al. 1999; Casselman 2002, Midwood and Chow-Fraser 2012), development of such an HSI is very timely so that managers can identify and protect these high-quality nursery habitats for the trophy muskellunge fishery.

Acknowledgments

We wish to thank Christopher Biberhofer, members of the Chow-Fraser lab and field technicians for their assistance with data collection. We are indebted to Harvey and Lorna Meirke, Jerry Burke, and Pitfields General Store for providing lodging and boats while we were sampling in northern Georgian Bay. We are also grateful to the OMNRF for their logistical support. This project was funded in part by a research grant from the Sierra Club Canada Foundation, the Ontario Ministry of Natural Resources and Forestry through the Canada-Ontario Agreement, and grants from the Great Lakes Basin Conservancy, Muskies Canada Inc., and the Georgian Bay Musky Association.

References

Ball H, Jalava J, King T, Maynard L, Potter B, Pulfer T (2003). The Ontario Great Lakes Coastal Wetland Atlas: A Summary of Information (1983-1997). Environment Canada, Canadian Wildlife Service

Bebelhimer MS, Stein RA, Carline RF (1985). Assessing significance of physiological differences among three esocids with a bioenergetics model. Canadian Journal of Fisheries and Aquatic Sciences 42: 57-69

Bonin JD, Potila JR (1978). Temperature tolerance of larval muskellunge (*Esox masquinongy* Mitchill) and F_1 hybrids reared under hatchery conditions. Comparative Biochemistry and Physiology A, Comparative Physiology 59: 245-248

Bozek MA, Burri TM, Frie RV (1999). Diets of muskellunge in northern Wisconsin Lakes. North American Journal of Fisheries Management 19: 258-270

Casselman JM (2002). Effects of temperature, global extremes, and climate change on year-class production of warmwater, coolwater, and coldwater fishes in the Great Lakes basin. American Fisheries Society Symposium 32: 39-60

CEC (Commission for Environmental Cooperation; Montréal, Québec). & Secretariat. (1997). Ecological regions of North America: toward a common perspective. The Commission

Chow-Fraser P (2006). Development of the wetland water quality index for assessing the quality of Great Lakes coastal wetlands. In: Simon, T.P., Steward, P.M.

(Eds.), Coastal Wetlands of the Laurentian Great Lakes: Health, Habitat, and Indicators. Indiana Biological Survey, Bloomington, Indiana, pp. 137-166

Clapp DF, Wahl DH (1996). Comparison of food consumption, growth, and metabolism among muskellunge: An investigation of population differentiation. Transaction of the American Fisheries Society 125: 402-410

Cook MF, Solomon RC (1987). Habitat suitability index models: muskellunge. U.S. Fish and Wildlife Service Biol. Rep. 82 (10.148). 33 pp. retrieved from http://www.nwrc.usgs.gov/wdb/pub/hsi/hsi-148.pdf

Craig RE, Black RM (1986). Nursery habitat of muskellunge in southern Georgian Bay, Lake Huron, Canada. American Fisheries Society Special Publication 15. Pp. 79–86, *in* Hall

Cvetkovic M, Chow-Fraser P (2011). Use of ecological indicators to assess the quality of Great Lakes coastal wetlands. Ecological Indicators 11:1609-1622

Cvetkovic M, Kostuk K, Chow-Fraser P (2012). Gear-type influences on fish catch and a wetland fish index in Georgian Bay wetlands. North American Journal of Fisheries Management 32: 313-324

Cvetkovic M, Wei A, Chow-Fraser P (2010). Relative importance of macrophyte community versus water quality variables for predicting fish assemblages in coastal wetlands of the Laurentian Great Lakes. Journal of Great Lakes Research 36: 64-73

Dobiesz NE, Lester NP (2009) Changes in mid-summer water temperature and clarity across the Great Lakes between 1968 and 2002. Journal of Great Lakes Research 35: 371-384

Dombeck MP, Menzel BW, Hinz PN (1986). Natural muskellunge reproduction in Midwestern lakes. American Fisheries Society Special Publication 15. Pp. 122–134, *in* Hall

Eadie JM, Keast A (1984). Resource heterogeneity and fish species diversity in lakes. Canadian Journal of Zoology 62: 1689-1695

Fitzsimons JD (1990). Yellow perch predation on lake trout egg in Keuka Lake, New York. Journal of Great Lakes Research 16: 130-132

Fracz A, Chow-Fraser P (2013). Impacts of declining water levels on the quantity of fish habitat in coastal wetlands of eastern Georgian Bay, Lake Huron. Hydrobiologia 705: 151-169

Jennings MJ, Bozek MA, Hatzenbeler GR, Emmons EE, Staggs MD (1999). Cumulative effects of incremental shoreline habitat modification on fish assemblages in north temperate lakes. North American Journal of Fisheries Management 19: 18-27

Kapuscinski KL, Farrell JM (2014). Habitat factors influencing fish assemblage at muskellunge nursery sites. Journal of Great Lakes Research 40: 135-147

Kapuscinski KL, Farrell JM, Murry BA (2012). Feeding strategies and diets of young-of-the-year muskellunge from two large river ecosystems. North American Journal of Fisheries Management 32: 635-647

Kerr SJ (2007). Characteristics of Ontario muskellunge (*Esox masquinongy*) fisheries based on volunteer angler diary information. Environmental Biology of Fishes 79: 61-69

Kerr SJ, Kirkpatrick A, Haxton TJ (2011). Characteristics of trophy-sized muskellunge (*Esox masquinongy*) angled from Ontario waters, 1917-2010. Fisheries Policy Section, Biodiversity Branch. Ontario Ministry of Natural Resources. Peterborough, Ontario. 7 p. + appendices

King JR, Shuter BJ, Zimmerman AP (1999). Empirical links between thermal habitat, fish growth, and climate change. Transactions of the American Fisheries Society 128: 656-665

LaPan SR, Schiavone A, Werner RG (1996). Spawning and post-spawning movements of the St. Lawrence River muskellunge (*Esox masquinongy*). In Managing muskies in the '90s. Workshop Proceedings [eds. Kerr, S. J. and C. H. Olver]. Ontario Ministry of Natural Resources, Southern Region Science and Technology Transfer Unit Workshop Proceedings WP-007. Pp. 73 - 82

Leblanc JP, Weller JD, Chow-Fraser P (2014). Thirty-year update: changes in biological characteristics of degraded muskellunge nursery habitat in southern Georgian Bay, Lake Huron, Canada. Journal of Great Lakes Research 40: 870-878

Midwood JD, Chow-Fraser P (2012). Changes in aquatic vegetation and fish communities following 5 years of sustained low water levels in coastal marshes of eastern Georgian Bay, Lake Huron. Global Change Biology 18: 93-105

Midwood JD, Rokitnicki-Wojcik D, Chow-Fraser P (2012). Development of an inventory of coastal wetlands for eastern Georgian Bay, Lake Huron. International Scholarly Research Network (ISRN Ecology) 2012: 1-13

Mortsch LD (1998). Assessing the impact of climate change on the Great Lakes shoreline wetlands. Climatic Change 40: 391-416

Murry BA, Farrell JM (2007). Quantification of native muskellunge nursery habitat: influence of body size, fish community composition, and vegetative structure. Environmental Biology of Fishes 79: 37-47

Nilsson J (2006). Predation of northern pike (*Esox lucius* L.) eggs: a possible cause of regionally poor recruitment in the Baltic Sea. Hydrobiologia 553: 161-169

Riley JW, Marsden JE (2009). Predation on emergent lake trout fry in Lake Champlain. Journal of Great Lakes Research 35: 175-181

Rosenfeld JS, Hatfield T (2006). Information needs for assessing critical habitat of freshwater fish. Canadian Journal of Fisheries and Aquatic Sciences 63: 683-698

Rust A J, Diana JS, Margenau TL, Edwards CJ (2002). Lake characteristics influencing spawning success of muskellunge in northern Wisconsin Lakes. North American Journal of Fisheries Management 22: 834-841

Scott WB, Crossman EJ (1998). Freshwater fishes of Canada. Galt House Publications Ltd. Oakville, Ontario, Canada

Seilheimer TS, Chow-Fraser P (2006). Development and use of the wetland fish index to assess the quality of coastal wetlands in the Laurentian Great Lakes. Canadian Journal of Fisheries and Aquatic Sciences 63: 354-366

Sellinger CE, Stow CA, Lamon EC, Qian SS (2008). Recent water level declines in the Lake Michigan-Huron system. Environmental Science and Technology 42: 367-373

Smokorowski KE, Pratt TC (2007). Effect of a change in physical structure and cover on fish and fish habitat in freshwater ecosystems – a review and meta-analysis. Environmental Reviews 15: 15-41

StatSoft, Inc. (2007). STATISTICA (data analysis software system), version 8.0. www.statsoft.com

Szendrey TA, Wahl DH (1996). Size-specific survival and growth of stocked muskellunge: effects of predation and prey availability. North American Journal of Fisheries Management 16: 395-402

Trebitz AS, Brazner JC, Danz NP, Pearson MS, Peterson GS, Tanner DK, Taylor DL, West CW, Hollenhorst TP (2009). Geographic, anthropogenic, and habitat influences on Great Lakes coastal wetland fish assemblages. Canadian Journal of Fisheries and Aquatic Sciences 66: 1328-1342

Trumpickas J, Shutter BJ, Minns CK (2009). Forecasting impacts of climate change on Great Lakes surface water temperatures. Journal of Great lakes Research 35: 454-463

Wagner CP, Weber MJ, Wahl DH (2015). Structural complexity influences littoral coarse woody habitat selection by juvenile muskellunge. North American Journal of Fisheries Management 35: 14-19

Wahl DH (1999). An ecological context for evaluating the factors influencing muskellunge stocking success. North American Journal of Fisheries Management 19: 238-248

Wahl DH, Stein RA (1988). Selective predation by three esocids: the role of prey behavior and morphology. Transactions of the American Fisheries Society 117: 142-151

Wahl DH, Stein RA (1989). Comparative vulnerability of three esocids to largemouth bass (*Micropterus salmoides*) predation. Canadian Journal of Fisheries and Aquatic Sciences 46: 2095-2103

Walters C, Kitchell JF (2001). Cultivation/depensation effects on juvenile survival and recruitment: implications for the theory of fishing. Canadian Journal of Fisheries and Aquatic Sciences 58: 39-50

Warfte DM, Barmuta LA (2004). Habitat structural complexity mediates the foraging success of multiple predator species. Oecologia 141: 171-178

Weller JD, Leblanc JP, Liskauskas A, Chow-Fraser P (2015). Spawning-site fidelity in sub-populations of muskellunge in Georgian Bay: Implications of habitat loss. Transactions of the American Fisheries Society (in submission)

Table 2.1. Comparison of fish communities associated with YOY muskellunge in published studies. CYP=Family Cyprinidae; PER=Family Percidae[a]; CEN=Family Centrarchidae[b]; SUN=Bluegills and/or pumpkinseeds; FRY= fish < 30 mm total length; BDK=Banded Killifish; DAR=Darters.

			Taxonomic Group						
Authors	**Method used**	**Location of study**	CYP	PER	CEN	SUN	FRY	BDK	DAR
Craig & Black (1986)	Mean proportional abundance in seine surveys during June &July	Southeastern Georgian Bay	0.117	0.136 (YP only)	**0.321** (LMB only)	0.176	-	-	-
Murry & Farrell (2007)	Mean proportional abundance in seine surveys	Up. St. Lawrence R.							
		During July	**0.227**	0.017	0.072	0.058	**0.527**	-	-
		During August	0.071	0.293	0.087	0.111	**0.364**	-	-
Kapuscinski et al. (2012)	Weight of stomach contents in YOY muskellunge	St. Lawrence R.	Rank 2	-	-	-	-	**Rank 1**	Rank 3
		Upper Niagara R.	**Rank 1**	-	-	-	-	Rank 2	Rank 3
Kapuscinski & Farrell (2014)	% total catch of family caught in mid-July and early August at muskellunge nursery sites	Buffalo Harbour	20-45	~10	**40-60**	-	-	-	-
		Up. Niagara R.	**>65**	<10	10-20	-	-	-	-
		Up. St. Lawrence R.	**5-75**	5-30	10-60	-	-	-	-
This study	Mean proportional abundance in seine surveys during July	Eager Bay	0.186	0.159	0.068	**0.482**	< 0.05	< 0.05	< 0.05
		Plant Lake	**0.333**	0.109	0.093	**0.316**	< 0.05	< 0.05	< 0.05

[a] In Craig and Black (1986), Murry and Farrell (2007) and this study, Percidae included only yellow perch; in Kapuscinski and Farrell (2014) it included 5 species.

[b] For Craig and Black (1986), Centrarchidae included only largemouth bass (LMB). In Murry and Farrell (2007) and this study, Centrarchidae included both largemouth and smallmouth bass, while in Kapuscinski and Farrell (2014), 6 species were included in the Centrarchidae taxonomic group.

Table 2.2. Comparison of lake morphology and means (±SE) of limnological variables measured in Eager Bay and Plant Lake. Means for Plant Lake and Eager Bay are for 6 sites. All limnological variables were measured at 0.5 m depth with an YSI 6600 sonde during July 2013 between 11:00 am and 1:00 pm.

Variable	**Plant Lake**	**Eager Bay**
Maximum Depth (m)	**28**	**21**
Surface Area (km^2)	**4**	**15**
pH	**6.97** (0.03)	**7.75** (0.08)
Conductivity µS/cm	**68.2** (0.17)	**98.3** (10.46)
Temperature (°C)	**23.1** (0.11)	**22.0** (0.39)
Dissolved Oxygen (mg/L)	**6.6** (0.18)	**8.2** (0.17)
Turbidity (NTU)	**2.3** (0.10)	**2.14** (0.19)

Table 2.3. Frequency of occurrence (Freq. Occ; %) and mean (SE) proportional abundances (untransformed data) of fish taxa grouped according to four conditions: YOY-Musky sites, No-Musky sites, all sites in Eager Bay and all sites in Plant Lake. There were no significant differences in mean (± SE) abundance of fish caught per seine haul between the YOY-Musky and No-Musky sites (**123.7**±41.2 vs **109.2** ± 20.1; $t_{81} = 0.316$, $p = 0.753$).

Fish Group	Common Name (Latin Name)	YOY-Muskellunge		No-Musky		Eager Bay		Plant Lake	
		Freq. Occ.	**Mean (SE)**	**Freq. Occ.**	**Mean (SE)**	**Freq. Occ.**	**Mean (SE)**	**Freq. Occ.**	**Mean (SE)**
Standalone Taxa	Yellow perch † (*Perca flavescens*)	100	**0.140** (0.022)	94.0	**0.192** (0.018)	97.3	**0.249** (0.024)	93.5	**0.128** (0.016)
	Pumpkinseed (*Lepomis gibbosus*)	100	**0.301** (0.046)	91.0	**0.246** (0.021)	97.3	**0.302** (0.030)	89.1	**0.220** (0.024)
	Bluegill (*Lepomis macrochirus)*	93.8	**0.119** (0.021)	77.6	**0.170** (0.025)	70.3	**0.091** (0.019)	89.1	**0.216** (0.032)
	Largemouth bass (*Micropterus salmoides*)	93.8	**0.045** (0.007)	74.6	**0.047** (0.005)	86.5	**0.048** (0.005)	71.7	**0.045** (0.007)
	Rock bass (*Ambloplites rupestris*)	75.0	**0.079** (0.020)	59.7	**0.058** (0.011)	56.8	**0.046** (0.013)	67.4	**0.075** (0.013)
	Smallmouth bass † (*Micropterus dolomieu*)	50.0	**0.033** (0.016)	55.2	**0.035** (0.010)	35.1	**0.019** (0.007)	69.6	**0.048** (0.014)
Cyprinids ^{E}	Bluntnose minnow (*Pimephales notatus*)	87.5	**0.162** (0.043)	65.7	**0.105** (0.022)	62.2	**0.075** (0.022)	76.1	**0.149** (0.030)
	Common shiner (*Luxilus cornutus*)	50.0	**0.023** (0.011)	31.3	**0.041** (0.011)	37.8	**0.043** (0.014)	32.6	**0.033** (0.011)
	Cyprinid spp.	31.3	**0.022** (0.012)	13.4	**0.004** (0.001)	16.2	**0.005** (0.002)	17.4	**0.009** (0.004)
	Blackchin shiner (*Notropis heterodon*)	25.0	**0.030** (0.024)	16.4	**0.009** (0.005)	24.3	**0.019** (0.011)	13.0	**0.008** (0.006)
	Blacknose shiner (*Notropis heterolepis*)	18.8	**0.004** (0.002)	7.5	**0.002** (0.001)	8.1	**0.002** (0.001)	10.9	**0.002** (0.001)
	Golden shiner (*Notemigonus crysoleucas*)	6.3	**0.001** (0.001)	6.0	**0.001** (0.001)	2.7	**0.001** (0.001)	8.7	**0.001** (0.001)

Table 2.3 Continued

Other Fusiform	Johnny darter (*Etheostoma nigrum*)	37.5	**0.011** (0.006)	43.3	**0.029** (0.009)	43.2	**0.034** (0.016)	41.3	**0.020** (0.006)
	Alewife (*Alosa pseudoharenus*)	18.8	**0.003** (0.002)	14.9	**0.028** (0.013)	18.9	**0.029** (0.018)	13.0	**0.018** (0.013)
	Brook silverside (*Labidesthes sicculus*)	18.8	**0.003** (0.002)	13.4	**0.005** (0.003)	10.8	**0.007** (0.005)	17.4	**0.003** (0.001)
	Banded killifish (*Fundulus diaphanus*)	6.3	**0.004** (0.004)	6.0	**0.001** (0.001)	8.1	**0.002** (0.001)	4.3	**0.002** (0.001)
	White sucker (*Catostomus commersonii*)	6.3	**< 0.001** (<0.001)	9.0	**0.002** (0.001)	16.2	**0.004** (0.002)	2.2	**0.001** (0.001)
	Iowa darter (*Etheostoma exile*)	0	**0**	6.0	**0.002** (0.001)	5.4	**0.001** (0.001)	4.3	**0.002** (0.001)
	Logperch (*Percina caprodes*)	0	**0**	4.5	**0.002** (0.001)	8.1	**0.003** (0.002)	0	**0**
Other Species	Bullhead spp. (*Ameiurus spp.*)	37.5	**0.009** (0.004)	28.4	**0.013** (0.005)	40.5	**0.016** (0.005)	21.7	**0.010** (0.006)
	Black crappie (*Pomoxis nigromaculatus*)	25.0	**0.007** (0.004)	11.9	**0.003** (0.001)	13.5	**0.004** (0.002)	15.2	**0.004** (0.002)
	Lepomis spp.	12.5	**0.003** (0.002)	9.0	**0.003** (0.002)	2.7	**0.001** (0.001)	15.2	**0.004** (0.002)
	Longnose gar (*Lepisosteus osseus*)	6.3	**0.001** (0.001)	6.0	**0.001** (0.001)	5.4	**0.001** (0.001)	6.5	**0.001** (0.001)
	Northern pike (*Esox lucius*; TL > 200 mm)	0	**0**	7.5	**0.001** (0.001)	2.7	**< 0.001** (<0.001)	8.7	**0.002** (0.001)

† Indicates significant differences between Eager Bay and Plant Lake ($p < 0.05$).
^{E} Indicates significant differences between YOY-Muskellunge and No-Musky sites ($p < 0.05$).
^{R} YOY esocids were excluded in calculations; they were used to identify nursery sites for muskellunge, pike or both.

Table 2.4. Frequency of occurrence (F. Occ; %), mean (±S.E.) proportional abundance (R. AB), and mean (±S.E.) number of fish taxa caught per seine haul (Caught; No. Site $^{-1}$) for data sorted according to four conditions: YOY-Musky sites, No-Musky sites, all sites in Eager Bay and all sites in Plant Lake.

	YOY-Musky Eager Bay (n = 10)			**YOY-Musky Plant Lake (n = 6)**			**No-Musky Eager Bay (n = 27)**			**No-Musky Plant Lake (n = 40)**		
Taxon	**F. Occ.**	**Mean (S.E.) R. AB**	**Mean (S.E.) Caught**	**F. Occ.**	**Mean (S.E.) R. AB**	**Mean (S.E.) Caught**	**F. Occ.**	**Mean (S.E.) R. AB**	**Mean (S.E.) Caught**	**F. Occ.**	**Mean (S.E.) R. AB**	**Mean (S.E.) Caught**
Muskellunge	100	**0.013** (0.002)	**1.1** (0.10)	100	**0.019** (0.009)	**1.3** (0.21)	0	**0**	**0**	0	**0**	**0**
Pumpkinseed	100	**0.360** (0.064)	**42.7** (13.15)	100	**0.192** (0.030)	**35.8** (14.95)	96.3	**0.278** (0.033)	**23.8** (4.24)	87.5	**0.224** (0.027)	**25.3** (8.53)
Yellow perch	100	**0.157** (0.029)	**14.7** (2.42)	100	**0.106** (0.028)	**11.8** (4.01)	96.3	**0.282** (0.028)	**26.2** (4.43)	92.5	**0.131** (0.018)	**8.9** (1.30)
Largemouth bass	100	**0.056** (0.008)	**5.5** (0.90)	83.3	**0.025** (0.010)	**2.5** (1.34)	81.5	**0.044** (0.007)	**3.9** (0.64)	70	**0.048** (0.007)	**4.4** (0.91)
Bluegill	90	**0.116** (0.030)	**14.5** (5.37)	100	**0.118** (0.026)	**19.8** (8.86)	63	**0.081** (0.024)	**8.6** (3.85)	87.5	**0.230** (0.036)	**50.9** (31.62)
Bluntnose minnow	90	**0.116** (0.043)	**12.5** (5.09)	83.3	**0.234** (0.086)	**48.0** (27.91)	51.9	**0.060** (0.025)	**5.9** (4.23)	75	**0.136** (0.032)	**11.3** (3.36)
Rock bass	80	**0.071** (0.018)	**6.3** (1.58)	66.7	**0.091** (0.047)	**15.2** (7.44)	48.1	**0.036** (0.017)	**3.5** (1.37)	67.5	**0.073** (0.014)	**7.3** (1.70)
Common shiner	50	**0.014** (0.008)	**1.4** (0.73)	50	**0.037** (0.025)	**7.7** (6.00)	33.3	**0.054** (0.019)	**8.6** (3.48)	30	**0.033** (0.012)	**2.8** (1.00)
Bullhead spp.	40	**0.012** (0.006)	**1.2** (0.55)	33.3	**0.004** (0.003)	**0.5** (0.34)	40.7	**0.017** (0.007)	**1.9** (0.80)	20	**0.011** (0.006)	**0.7** (0.33)
Blackchin shiner	30	**0.044** (0.038)	**2.9** (2.06)	16.7	**0.005** (0.005)	**0.5** (0.50)	22.2	**0.009** (0.005)	**1.1** (0.62)	12.5	**0.009** (0.007)	**0.6** (0.38)
Johnny darter	30	**0.004** (0.002)	**0.3** (0.15)	50	**0.022** (0.015)	**1.5** (0.72)	48.1	**0.045** (0.021)	**1.3** (0.42)	40	**0.019** (0.006)	**1.0** (0.28)

Table 2.4 Continued

Smallmouth bass	30	**0.011** (0.007)	**0.8** (0.47)	83.3	**0.066** (0.037)	**4.7** (2.06)	37	**0.021** (0.009)	**0.7** (0.22)	67.5	**0.045** (0.015)	**1.2** (0.21)
Alewife	20	**0.005** (0.004)	**0.3** (0.21)	16.7	**0.001** (0.001)	**0.2** (0.17)	18.5	**0.038** (0.025)	**8.9** (7.92)	12.5	**0.020** (0.015)	**0.8** (0.58)
Black crappie	20	**0.007** (0.006)	**0.4** (0.31)	33.3	**0.005** (0.005)	**0.7** (0.49)	11.1	**0.002** (0.002)	**0.2** (0.15)	12.5	**0.004** (0.002)	**0.3** (0.15)
Cyprinid spp.	20	**0.007** (0.005)	**0.7** (0.52)	50	**0.044** (0.028)	**3.3** (2.42)	14.8	**0.004** (0.002)	**0.6** (0.39)	12.5	**0.004** (0.002)	**0.3** (0.12)
Blacknose shiner	10	**0.002** (0.002)	**0.1** (0.10)	33.3	**0.007** (0.005)	**1.5** (1.31)	7.4	**0.002** (0.001)	**0.6** (0.44)	7.5	**0.002** (0.001)	**0.08** (0.04)
Brook silverside	10	**0.001** (0.001)	**0.2** (0.20)	33.3	**0.005** (0.004)	**0.3** (0.21)	11.1	**0.008** (0.006)	**0.7** (0.53)	15	**0.003** (0.001)	**0.30** (0.13)
Longnose gar	10	**0.001** (0.001)	**0.1** (0.10)	0	**0**	**0**	3.7	**0.001** (0.001)	**0.04** (0.04)	7.5	**0.001** (0.001)	**0.08** (0.04)
White sucker	10	**0.001** (0.001)	**0.20** (0.20)	0	**0**	**0**	18.5	**0.005** (0.003)	**0.6** (0.42)	2.5	**0.001** (0.001)	**0.03** (0.03)
YOY Northern pike	10	**0.001** (0.001)	**0.1** (0.10)	16.7	**<0.001** (<0.001)	**0.2** (0.17)	0	**0**	**0**	0	**0**	**0**
Banded killifish	0	**0**	**0**	16.7	**0.010** (0.010)	**0.3** (0.33)	11.1	**0.003** (0.002)	**0.1** (0.06)	2.5	**<0.001** (<0.001)	**0.03** (0.03)
Golden shiner	0	**0**	**0**	16.7	**0.002** (0.002)	**0.2** (0.17)	3.7	**0.001** (0.001)	**0.04** (0.04)	7.5	**0.001** (0.001)	**0.1** (0.06)
Iowa darter	0	**0**	**0**	0	**0**	**0**	7.4	**0.002** (0.002)	**0.1** (0.08)	5	**0.002** (0.002)	**0.1** (0.08)
Lepomis spp.	0	**0**	**0**	33.3	**0.007** (0.006)	**0.8** (0.65)	3.7	**0.002** (0.002)	**0.2** (0.15)	12.5	**0.004** (0.002)	**0.5** (0.31)
Logperch	0	**0**	**0**	0	**0**	**0**	11.1	**0.004** (0.003)	**0.2** (0.12)	0	**0**	**0**
N. pike (TL>200 mm)	0	**0**	**0**	0	**0**	**0**	3.7	**0.001** (0.001)	**0.04** (0.04)	10	**0.002** (0.001)	**0.1** (0.06)

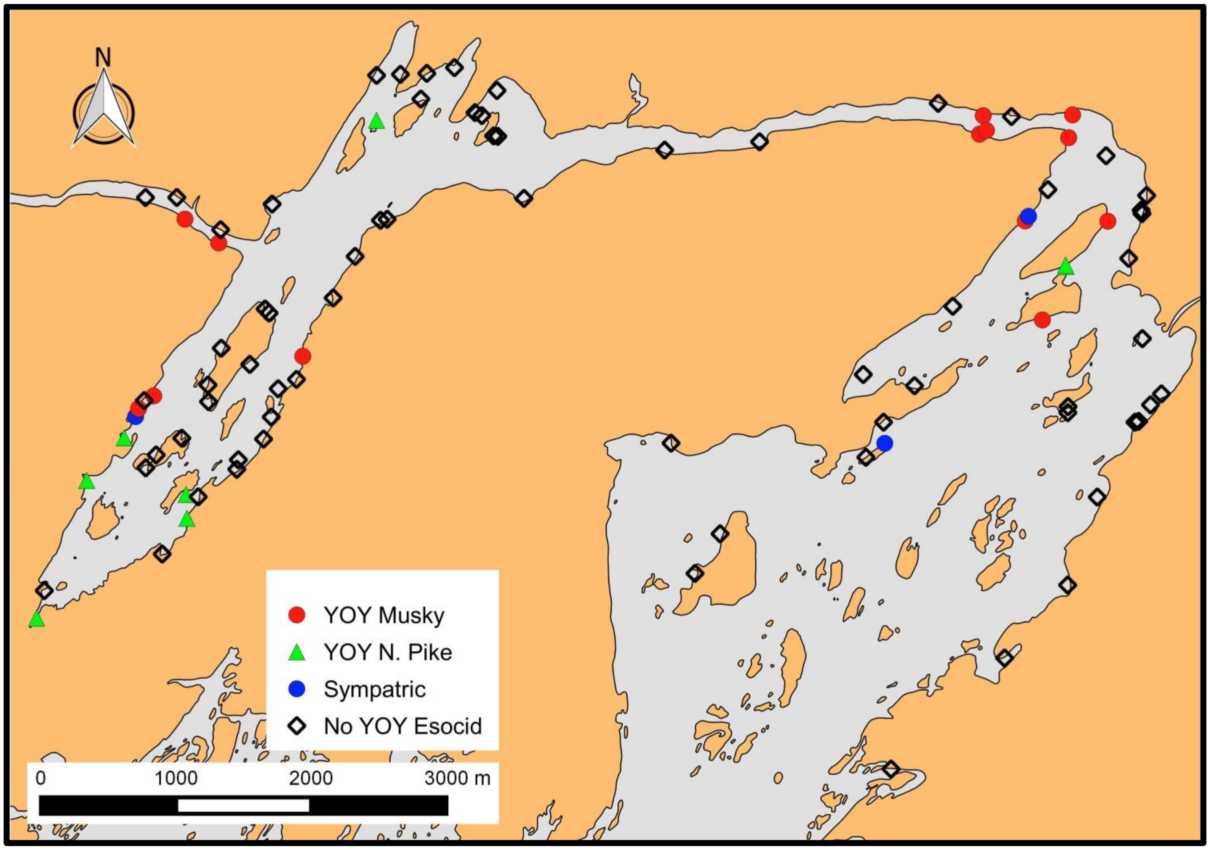


Figure 2.1. Map showing locations surveyed for esocids in Plant Lake (left embayment) and Eager Bay (right embayment) during July of 2012 and 2013. Sites where YOY muskellunge were found (YOY Musky; solid red circles) are differentiated from those where YOY northern pike were found (YOY N. Pike; solid green triangles). Sites where YOY muskellunge and northern pike were caught in the same seine haul (sympatric; solid blue circle) are shown. Sites that had been surveyed but that did not have any esocids are indicated by open diamonds (n = 67)

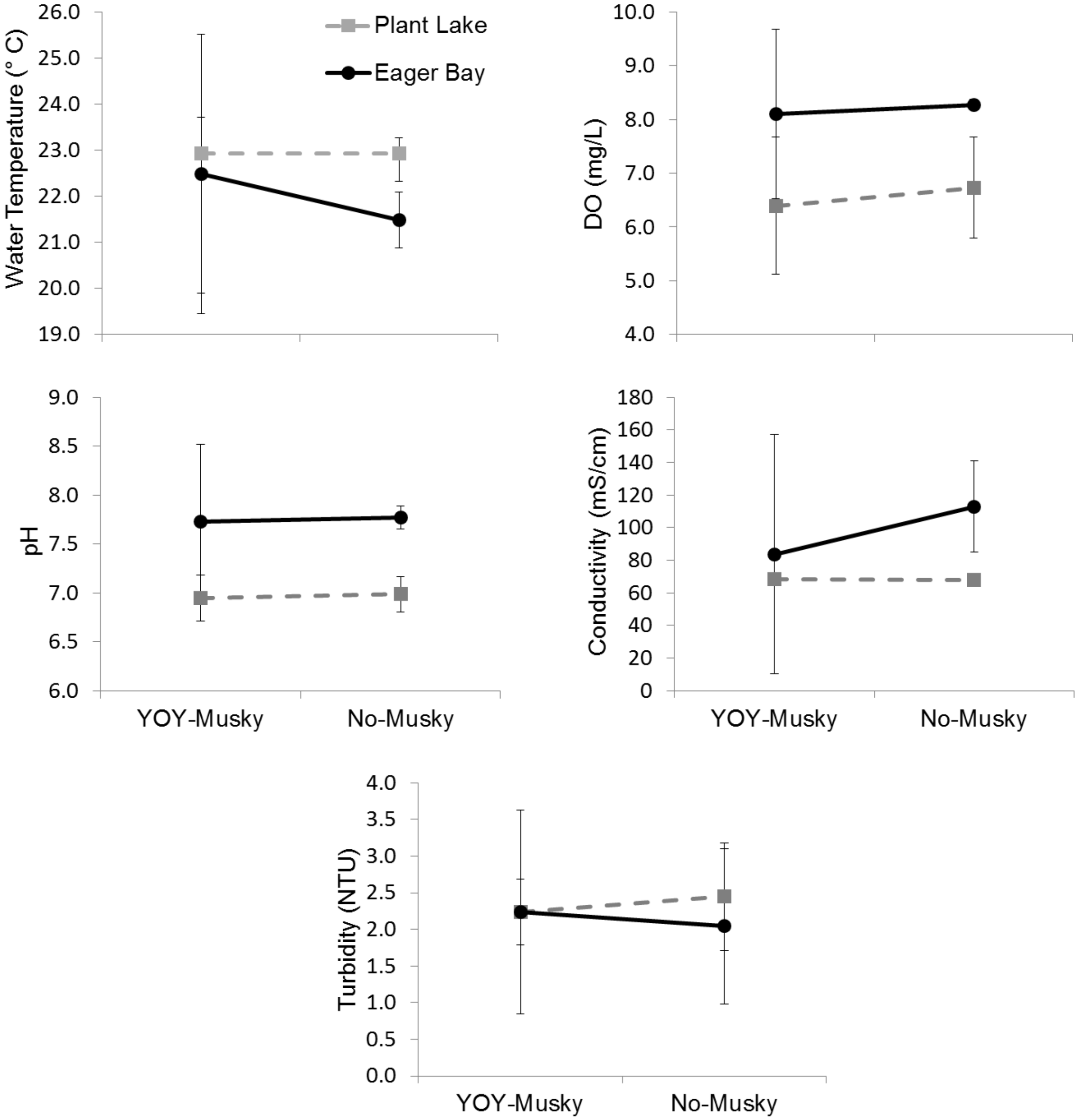


Figure 2.2. Comparison of mean (± 95% CI) water temperature, pH, dissolved oxygen (DO), conductivity, and turbidity values measured at 0.5 m depth at sampling stations in Eager Bay and Plant Lake. No differences between the YOY-Musky (n = 6) and No-Musky sites (n = 6) were detected for any of the parameters when data were separately analyzed by site (Tukey-HSD, $p > 0.05$; two-way ANOVAs), but there were significant main effect differences between water bodies for water temperature ($F_{1,8} = 8.450$, $p = 0.020$), DO ($F_{1,8} = 39.136$, $p = 0.0002$), pH ($F_{1,8} = 62.350$, $p < 0.0001$) and conductivity ($F_{1,8} = 10.957$, $p = 0.011$).

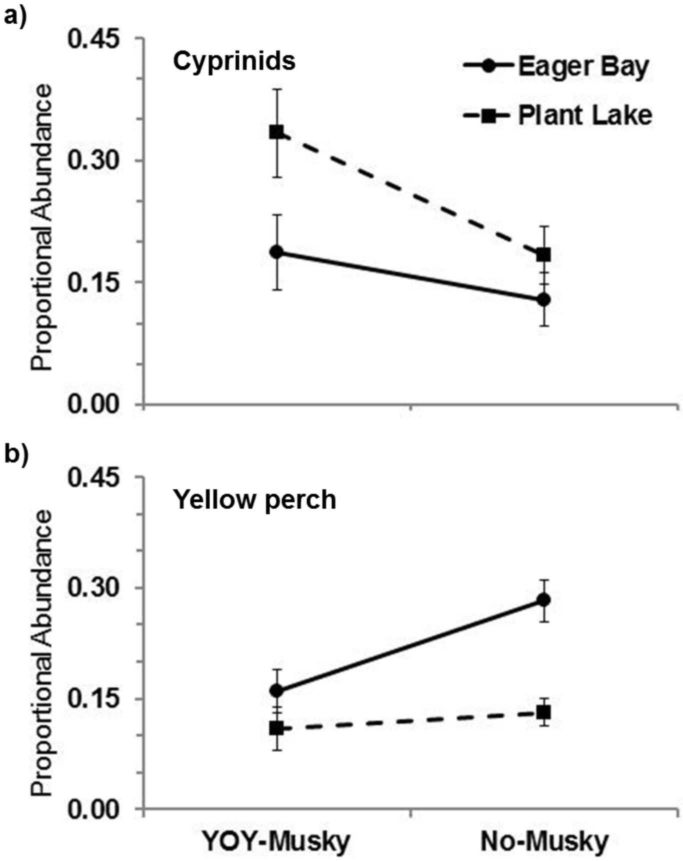


Figure 2.3. Mean±SE of proportional abundances of a) Cyprinids and b) Yellow perch found in different site types (i.e. YOY-Musky and No-Musky sites). Significant differences between site types were found when data for Plant Lake and Eager Bay were pooled by taxon (Cyprinids: $F_{1,79} = 5.51$, $p = 0.02$; Yellow perch: $F_{1,79} = 8.240$, $p = 0.005$). Mean relative abundance of Yellow perch at YOY-musky sites in both embayments were statistically similar (Tukey-HSD; $p > 0.05$) but were higher in Eager Bay ($p < 0.05$) at No-Musky sites.

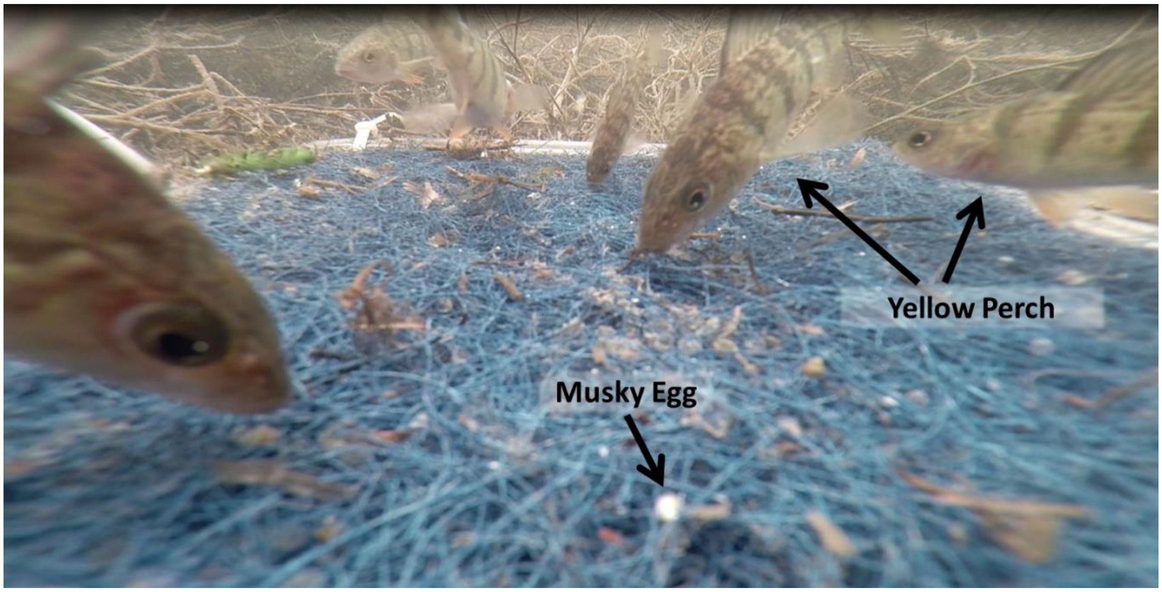


Figure 2.4. An image from an 80-minute footage taken with the GoPro^{TM} camera, showing a platform baited with muskellunge eggs at a historic nursery site in Severn Sound. Yellow perch was the primary species eating muskellunge eggs in this footage. Other species that ate muskellunge eggs included bluntnose minnow and round goby but at lower frequencies. No fish were observed at un-baited platforms.

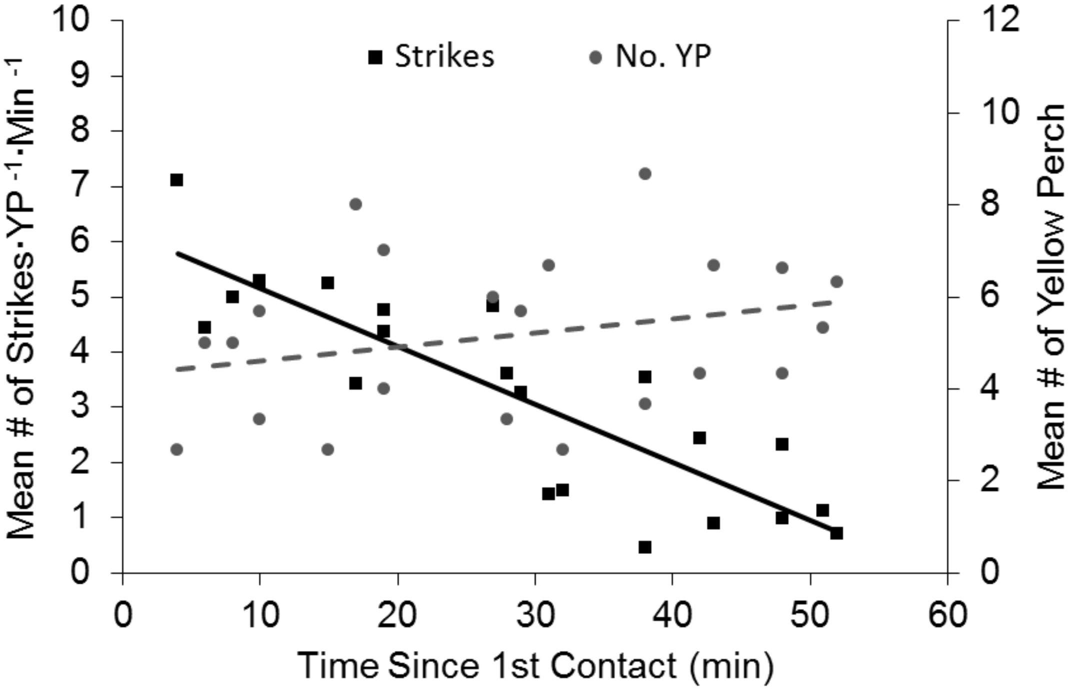


Figure 2.5. Mean number of strikes per yellow perch (YP) per minute (Strikes: black squares) and mean number of yellow perch (No. YP: grey circles) over baited platforms as a function of time since platform was first detected. A significant negative relationship (solid black line) was found between the rate at which yellow perch would strike the baited platform and time since the platform was first detected (Pearson Correlation = -0.867, $p < 0.0001$). In contrast, there was no significant relationship between number of yellow perch over the platform and amount of time after the platform was first detected (Pearson Correlation 0.273 $p = 0.219$; dashed grey line).

Chapter 3:

Nearshore ecosystem features predict suitability of muskellunge nursery habitats in Georgian Bay, Lake Huron

For submission: Leblanc JP, Chow-Fraser P (2015, CH3). Nearshore ecosystem features predict suitability of muskellunge nursery habitats in Georgian Bay, Lake Huron

Abstract

We conducted a two-year study to determine the habitat characteristics of young-of-the-year (YOY) muskellunge (*Esox masquinongy*) in coastal wetlands of northern Georgian Bay. During August of 2012 and 2013, we sampled 55 wetland-units (depths 0.5-1.0 m), 16 of which contained at least one YOY from July seining. Habitat variables that were significantly different between sites where YOY muskellunge were found (YOY-Musky sites) and those where they were absent (No-Musky sites) included higher densities and greater diversity of submersed aquatic vegetation (SAV) in the upper water-column (i.e., Canopy SAV), a smaller contribution of substrate-covering SAV, and steeper substrate slopes (Wilks $\lambda = 0.672$, $F_{4, 50} = 6.106$, $p<0.001$). When we combined these habitat variables with metrics of the fish community (i.e., higher residual species richness, lower relative abundances of yellow perch (*Perca flavescens*), and higher relative abundances of Cyprinid species in YOY-Musky sites), we were able to correctly classify 87.5% of the YOY-Musky and 89.7% of the No-Musky sites with a Discriminant Function Analysis (Wilks $\lambda = 0.575$, $F_{7, 47} = 4.955$, $p<0.001$). Variation in characteristics of the macrophyte community (e.g., densities of substrate-covering SAV and Diversity of Canopy SAV) were directly related to site bathymetry ($r^2 \geq 0.11$, $p \leq 0.01$). The habitat features we identified are consistent with those hypothesized to allow YOY muskellunge to hide from predators and forage efficiently for prey and thus increase their chance for survival. These seven ecosystem characteristics should be useful predictors of suitable habitat for YOY muskellunge in Georgian Bay.

Keywords: Muskellunge, nursery habitat, bathymetry, predation refuge, macrophyte, Georgian Bay

Introduction

A primary requirement for the management of self-sustaining fish populations is identifying and protecting the most limiting habitat for the species (Rosenfeld and Hatfield 2006). For the ecologically and economically valuable muskellunge (*Esox masquinongy*) in the Great Lakes, early-life habitats are considered more limiting than those used by later-life stages (Cook and Solomon 1987; Kapuscinski et al. 2014). This is because the early-life of esocids are sensitive to the condition of their coastal wetland habitats (Casselman and Lewis 1996; Murry and Farrell 2007), and alterations to these early-life habitats have been linked to failed natural recruitment in muskellunge (Dombeck et al. 1986; Rust et al. 2002; Leblanc et al. 2014). Thus, identifying and protecting wetlands used by muskellunge for spawning and nursery habitats should be a management priority (Farrell et al. 2007; Kapuscinski and Farrell 2014; Kapuscinski et al. 2014).

There is widespread acceptance that young-of-the-year (YOY) muskellunge prefer to occupy the upper water column in their wetland habitat (Wahl and Stein 1989; Wahl 1995) within relatively shallow water (< 1.5 m depths; Craig and Black 1986; Farrell and Werner 1999). The water column itself is generally described as being structurally complex, with macrophytes that grow to the water's surface and that occur at intermediate densities or cover (Craig and Black 1986; Murry and Farrell 2007). This type of environment is assumed to provide sufficient protection from predators (Murry and Farrell 2007; Kapuscinski and Farrell 2014; Wagner et al. 2015), while allowing YOY ambush opportunities to successfully prey on their preferred forage (i.e., soft-rayed fusiform fish; Kapuscinski et al. 2012). From an ecological perspective, suitability of nursery habitat for muskellunge is therefore a balancing of predation risks and foraging opportunities within the same habitat structure (Wahl 1999).

Within the Great Lakes context, no other population of muskellunge is as unique as those in Georgian Bay. First, the trophy-calibre muskellunge found here are among the largest in Ontario (Casselman et al. 1999). Secondly, the fishery consists of sub-populations along the eastern and northern shores of Georgian Bay that are genetically distinct (Kapuscinski et al. 2013; Chris Wilson, pers. comm., Ontario Ministry of Natural Resources and Forestry, Peterborough, ON). These genetically distinct sub-populations are likely maintained through the muskellunge’s affinity to the same spawning and nursery areas year-after-year (Weller et al. 2015).

Unfortunately, more than a decade of unprecedented low water levels in Lake Huron may have altered muskellunge nursery habitats sufficiently to make them no longer suitable for YOY in some wetlands of southeastern Georgian Bay (Leblanc et al. 2014). Low water levels have already decreased heterogeneity of the plant community and a concomitant decrease in the species richness of fish communities in wetlands of eastern Georgian Bay (Midwood and Chow-Fraser 2012), and further declines could severely restrict access of fish to coastal wetlands in the same region (Fracz and Chow-Fraser 2013). Given that the Great Lakes may be entering a novel hydrologic regime with even more extreme low water levels (Sellinger et al. 2008), there is an urgent need to develop tools to identify and protect suitable habitat for YOY muskellunge in Georgian Bay.

Characteristics related to the suitability of muskellunge nursery habitat have been published for wetlands located in the lower Great Lakes (Murry and Farrell 2007; Kapuscinski and Farrell 2014), but it may be inappropriate to extrapolate these results directly to wetlands of eastern Georgian Bay without field validation. This is because wetlands of eastern and northern Georgian Bay have unique site geomorphologies compared with those in the lower Great Lakes and connecting channels (DeCatanzaro and Chow-Fraser 2010) that result in differences in the macrophyte and fish communities (Seilheimer and Chow-Fraser 2007; Croft and Chow-Fraser 2009). It is therefore important to develop a set of characteristics that are relevant to sites within Georgian Bay, rather than simply adopting results from published studies developed for sites elsewhere in the Great Lakes basin.

The objectives of this study are to identify and quantify wetland characteristics that can be used to define suitability of muskellunge nursery habitat specifically in Georgian Bay. We make the explicit assumption that all coastal wetland habitats are available for use by YOY muskellunge, but that some sites are more suitable than others and that we are able to identify the features that make them used preferentially. We test the transferability of the factors identified as important in the literature to determine if they are equally applicable to Georgian Bay. These include: stem densities of Submersed Aquatic Vegetation (SAV) that blanket the substrate (i.e., substrate-covering SAV), densities of SAV that grow throughout the water column (i.e., Canopy SAV; Murry and Farrell 2007), the stem density ratio of substrate-covering**:**Canopy SAV, the diversity of Canopy SAV (indicated by proportional abundance of *Vallisneria americana*), the density of macro-algae (e.g., *Chara* spp.; Craig and Black 1986; Murry and Farrell 2007), the density of floating and emergent vegetation, and the slope of the substrate (Table 3.1).

This study was conducted in remote regions of northern Georgian Bay, where coastal wetlands exist in reference conditions, with little human disturbance (Cvetkovic and Chow-Fraser 2011; Leblanc et al. 2015, CH2). Results will advance the ability to assess the current status of critical habitat throughout eastern and northern Georgian Bay and to predict how the suitability of these habitats will change in response to different water-level scenarios for this trophy-calibre muskellunge fishery.

Methods

Habitat sampling

During the month of August in 2012 and 2013, habitat assessments were made at coastal wetlands where YOY muskellunge were collected by seine (i.e., YOY-Musky, n = 16) and 39 randomly selected No-Musky sites (sites where YOY muskellunge were not caught). These sites had been identified in July of respective years (see Leblanc et al. 2015, CH2 for study site description; Figure 3.1). Assessments of coastal wetland habitat followed the sampling protocol described previously by Leblanc et al. (2014); however, depending on transect length, quadrats (0.25 m^2) were positioned at equal intervals of a minimum of 2.0 m.

We only consider habitat to be suitable at depths > 0.5 m since majority of the YOY muskellunge caught (i.e., 19 of 20 individuals) occurred at depths greater than 0.5 m. Therefore, prior to statistical analyses, we estimated a mean value from all quadrats sampled at depths > 0.5 m to 1.0 m for each site (approximately 12 quadrats). These habitat variables consisted of macrophyte and bathymetric features that reflect some aspect of the structure in the water column or that had been identified as being an important feature of muskellunge nursery habitat elsewhere (Table 3.1). For example, submersed aquatic vegetation (SAV) was classified as either substrate-covering SAV (Sub SAV) or Canopy structuring SAV (Can SAV) to represent the contribution of various forms of SAV in the water column (Leblanc et al. 2014; Table 3.1). We also identified SAV to the lowest taxonomic level, and determined if stem counts were significantly different between site-types (i.e. YOY-Musky and No-Musky sites; Mann-Whitney U test) for all those taxa that occurred at > 33 % of our sampling sites. Similarly, we compared between site-types with respect to species richness and Shannon Diversity Index of Can SAV.

Habitat features that differentiate between site-types

We used SATISTICA 8.0 (StatSoft, Inc. 2007) for statistical analyses, and univariate results from a Multivariate Analysis of Variance (MANOVA) of the habitat variables (Table 3.1) were used to identify specific habitat characteristics that differed between site-types. Variables that differed significantly ($\alpha = 0.05$) were assumed to contribute predictive power towards discriminating between the YOY-Musky and No-Musky sites, and were used in a subsequent discriminant function analysis (DFA). Prior to analyses, all variables were transformed to satisfy parametric and multivariate assumptions (Table 3.1). Although some of the variables used in the DFA were weakly correlated ($r < 0.4$), tolerance values indicated a lack of variable redundancy (Tolerance values > 0.77; Quinn and Keough 2006). The contribution and ecological interpretation of the variables selected to discriminate between site-types was inferred from standardized coefficients and factor structure correlations of the DFA canonical axis (Quinn and Keough 2006).

Ecosystem-based features that differentiate between site-types

We combined habitat variables that described aspects of the water-column structure (listed above) with metrics of the fish community (i.e., proportional abundance of yellow perch (*Perca flavescens*) and Cyprinid species, and residual fish species richness; Table 3.1; Leblanc et al. 2015, CH2) in a DFA. All of the initial transformations of the variables (Table 3.1) satisfied parametric and multivariate assumptions, and tolerance values indicated a lack of variable redundancy (Tolerance > 0.72). As in the first DFA, contribution and ecological interpretation of the selected variables to discriminate between site-types was inferred from the standardized coefficients and factor structure correlations of the DFA canonical axis (Quinn and Keough 2006).

The small sample size used to discriminate between site-types precluded the use of holdout data for validation purposes. Thus, performances of the DFAs were assessed based on the classification of cases from the DFA, the false-negative rate and Cohen's Kappa. Cohen's Kappa is a model assessment metric that includes chance when inferring model agreement and is considered a more robust assessment of model performance than is the classification of cases alone (Fielding and Bell 1997). Landis and Koch (1977) interpreted Kappa values (K) < 0.40 to have fair to poor model agreement; values between 0.61 and 0.8 were considered to have substantial model agreement; while K-values > 0.81 were considered almost perfect predictive models. Although arbitrary, the proposed interpretation of Cohen's Kappa is considered relevant towards ecological model performance (Manel et al. 2001). Owing to the general scarcity of nursery habitat (e.g., Craig and Black 1986; Leblanc et al. 2015, CH2), we want to be conservative when evaluating the suitability of wetlands for YOY muskellunge, and therefore we want to minimize the false-negative rate (i.e., classifying YOY-Musky sites as No-Musky sites).

Thus, despite high overall model accuracy, the false-negative rate was used to indicate the potential conservation value of the DFA models.

Results

MANOVA

We found overall significant differences in habitat features between YOY-Musky and No-Musky sites (one-way MANOVA; Wilks' $\lambda = 0.568$, $F_{7, 47} = 5.010$, $p < 0.001$; Figure 3.2). When we tested each variable individually, we found that YOY-Musky sites had significantly higher overall densities of Can SAV ($F_{1, 53} = 4.529$, $p = 0.038$; Figure 3.2a), which included higher densities of Can SAV species *Potamogeton richardsonii*, *Elodea canadensis*, and *Ceratophyllum demersum* (Table 3.2). This corresponded with significantly higher Shannon diversity index of Can SAV at the YOY-Musky sites (mean ± SE: 1.15 ± 0.10) compared with the No-Musky sites (mean ± SE: 0.81 ± 0.06; $t_{53} = 2.752$, $p = 0.005$), but no significant differences in species richness of Can SAV (mean ± SE: YOY-Musky = 6.04 ± 0.23; No-Musky = 6.51 ± 0.32; $t_{53} = 0.807$, $p = 0.423$). Conversely, the proportional abundance of *V. americana* was significantly lower in YOY-Musky sites ($F_{1, 53} = 10.032$, $p = 0.003$; Figure 3.2b).

There were no differences in substrate slope between site-type for data observed from shore to the 0.5 m contour (Tukey HSD, $p > 0.05$); however, beyond 0.5 m, slopes associated with YOY-Musky sites were significantly steeper than those for No-Musky sites ($F_{1, 53} = 11.430$, $p = 0.001$; Figure 3.2c). Some variation in the composition of the macrophyte community appeared to be weakly, though significantly related to the steepness of the substrate slopes; densities of Sub SAV ($R^2 = 0.214$, $p < 0.001$; Figure 3.3), ratio of Sub SAV:Can SAV ($R^2 = 0.160$, $p = 0.003$; Figure 3.3), and proportional abundance of *V. americana* ($R^2 = 0.109$, $p = 0.015$; Figure 3.3) all varied negatively with slope. In contrast, no relationship existed between substrate slope and density of Can SAV (p = 0.466); however, Shannon Diversity Index of the Can SAV was positively related with substrate slope (R^2 = 0.114, p = 0.013; Figure 3.3).

Differences between site-types were predominately associated with the canopy SAV community; we found no significant differences with respect to floating and emergent vegetation taxa ($F_{1, 53}$ = 0.166, p = 0.685), densities of Sub SAV ($F_{1, 53}$ = 2.876, p = 0.096), or densities of marcoalgae SAV ($F_{1, 53}$ = 1.565, p = 0.216). However, the ratio of Sub SAV**:**Can SAV stem densities was lower in YOY-Musky sites than in No-Musky sites ($F_{1, 53}$ = 10.931, p = 0.002; Figure 3.2d), where YOY-Musky sites had, on average, twice as many stems of Can SAV than Sub SAV stems (Figure 3.2d). We also found that median stem densities of *Chara* spp. were significantly lower at YOY-Musky sites than in No-Musky sites (Mann-Whitney U test, $p < 0.05$; Table 3.2).

Discriminating site-types with habitat variables only

Four of the seven habitat variables were found to differ significantly between the site-types (Figure 3.2). These included stem densities of Canopy SAV, proportional abundance of *V. americana*, the ratio of Sub SAV**:**Can SAV stem density, and substrate slope, that are all related to structural features of the upper water-column in the wetland. These variables were therefore used in the DFA to discriminate between site-types. We found a significant model that had an overall accuracy of 85.5% (Wilks' λ = 0.672, $F_{4, 50}$ = 6.106, p = 0.0004; Table 3.3). The classification matrix indicated that 12 of 16 of the YOY-Musky sites (75.0%) and 35 of 39 (89.7%) of the No-Musky sites were correctly classified. Although this model was associated with a Cohen's Kappa value of 0.650 (indicating substantial model agreement), the false-negative rate was unacceptably high for conservation purposes (25%).

The canonical axis corresponds to a habitat gradient reflecting structure and complexity of the upper water column in the wetland (Table 3.3). YOY-Musky sites (canonical axis centroid mean ± 95% CI: 1.07 ± 0.502) were characterized by a denser and more diverse macrophyte community, and were associated with higher densities of Can SAV, lower relative abundance of *V. americana* and steeper substrate slopes (Table 3.3). In contrast, the No-Musky sites (centroid mean ± 95% CI: -0.44 ± 0.321) were associated with high densities of vegetation that occupy the lower water column, limited diversity of Can SAV and shallow substrate slopes (Table 3.3), indicating a less diverse plant structure in the upper water column. Each variable had a strong contribution towards the discriminating function of the model (Table 3.3).

Discriminating site types with ecosystem variables

To improve discriminating power, we added three metrics of the fish community to the four habitat variables and re-ran the DFA. The resultant 7-variable model was highly significant (Wilks $\lambda = 0.575$, $F_{7, 47} = 4.955$, $p < 0.001$; Table 3.4) and improved the overall accuracy of the classification (87.5% accuracy; 14 of 16 YOY-Musky sites correctly classified) but more importantly reduced the false-negative rate to 12.5% (Figure 3.4). The Cohen's Kappa increased to 0.745, indicating substantial model agreement. As in the previous case, the standardized coefficients and factor structure matrix yielded similar information (Table 3.4). Densities of Can SAV and steeper substrate slope were positively related with YOY-Musky sites while the proportional abundance of *V. americana* and the SAV ratio variable were negatively related (Table 3.4). YOY-Musky sites were positively associated with metrics related to habitat complexity in the upper water-column (e.g., Can SAV density and diversity, substrate slope and residual fish species richness) and a fish community with higher relative abundances of their preferred forage (e.g., Cyprinid species), and lower relative abundance of early-life predators (i.e., yellow perch).

We also examined how the combination of different variables affected the false-negative rate of the DFA, which allowed us to make inferences about the power of particular variables to discriminate between site-types (Table 3.5). Regardless of the combination of variables used, the model with the lowest false-negative rate included all 7 variables, and the next best model included all variables except the proportional abundance of yellow perch (Table 3.5). When only metrics of the fish community were used, only 4 of the 16 YOY-Musky sites were correctly classified; however, the majority of the top performing models included variables related to the habitat and fish community (Table 3.5). Specifically, substrate slope and residual fish species richness were consistently found among the top models, and on their own, correctly identified 11 of the 16 YOY-Musky sites (Table 3.5). It is worth noting that the two YOY-Musky sites misclassified by the 7 variable DFA were located very close to where YOY northern pike were found (Figure 3.4), and that one of these sites was never identified as a YOY-Musky site by any of the models tested (i.e., site 16; Table 3.5). Furthermore, nearly all of the false-positive cases stemming from the 7-variable model were associated with sites adjacent to YOY nursery sites or where adult muskellunge had been caught during the spawning season (Figure 3.4).

Discussion

In Georgian Bay, the wetland units where YOY muskellunge were found had distinctive ecosystem characteristics that allowed these sites to be statistically discriminated from other wetland units. Suitable nursery habitat was more likely to have a steeper substrate slope that allowed for a more diverse community of submersed aquatic vegetation that created a more structurally complex canopy in the upper water column during an extended period of sustained low water levels (Sellinger et al. 2008). This in turn should allow YOY muskellunge to both hide from predators and to forage effectively. These conditions are consistent with those described by Craig and Black (1986) in coastal wetlands of southeastern Georgian Bay some 30 years ago, when YOY muskellunge were still common; on the other hand, the conditions that described the No-Musky sites are consistent with those same sites sampled by Leblanc et al. (2014) in 2012 when they failed to find any YOY. These consistencies attest to the spatial and temporal transferability of the DFA in predicting results for habitats that are hundreds of kilometers apart in Georgian Bay, and being applied to data collected over 30 years earlier.

The association between some macrophyte communities and substrate slope has been noted by Duarte and Kalff (1986) when they examined littoral zones of lakes. Our coastal wetlands that had steeper substrate slopes tended to support a more diverse community of Canopy SAV, while shallower substrate slopes promoted higher densities of low-growing substrate-covering SAV, as well as higher relative abundances of *V. americana*. The exact mechanism that allows for these growth forms to dominate in shallow or steep slopes is not known but may be related to different tolerances of disturbances that are bathymetrically dependent (e.g., increased wave action at shallow slopes; Titus and Adams 1979; Angradi et al. 2013). Nevertheless, identification of slope as a key feature makes it possible for habitats to be screened for suitability with appropriate information about the site bathymetry and lake levels.

Two key differences between muskellunge nursery habitats from Severn Sound and northern Georgian Bay are wetland bathymetries observed pre- and post-low water levels and degree of shoreline modification. Basin bathymetry in northern Georgian Bay retained a substrate slope that was steep even after water levels declined by almost a meter after 1998 (D. Weller, unpubl. data), whereas those in Severn Sound became much shallower (Leblanc et al. 2014). Thus, muskellunge nursery habitats in northern Georgian Bay were likely buffered from the effects of sustained low water levels observed in Severn Sound (Leblanc et al. 2014). This has substantial management implications because muskellunge exhibit site fidelity to breeding habitat (Crossman 1990; LaPan et al. 1996; Jennings et al. 2011; Weller et al. 2015), and will continue to use the same wetlands to spawn even though the sites have been altered and have limited recruitment potential (Leblanc et al. 2014). Additionally, comparable slopes (~ 3 – 6 °) to those observed here, were noted at muskellunge spawning locations in lakes outside of the Great Lakes Basin (i.e., northern Wisconsin Lakes; Nohner and Diana 2015). Thus, substrate slope appears to be an important determinant of suitable habitat for muskellunge early-life stages in lacustrine systems (Nohner and Diana 2015), including Georgian Bay, and have predictive properties towards macrophyte community composition and structure. Second, the degree of shoreline modification in northern Georgian Bay has remained comparable with those observed in southeastern Georgian Bay when YOY muskellunge were first found 30 years ago (Leblanc et al. 2014). This appears to further highlight the importance of limiting the amount of shoreline modification at coastal wetlands used by muskellunge during their early-life in Georgian Bay (Craig and Black 1986; Leblanc et al. 2014).

Our results differ somewhat from those of previous studies conducted in the St. Lawrence River (Werner et al. 1996; Murry and Farrell 2007). The YOY muskellunge in northern Georgian Bay appeared to avoid sites where *V. americana* dominated (i.e., approx. 75 % of SAV community). Instead, they tended to frequent areas with higher densities of Canopy SAV such as *P. richardsonii*, *E. canadensis*, and *C. demersum*. Unlike *V. americana*, which has limited horizontal branching, these other SAV species have leaves or leaflets that branch horizontally from their vertical stems, and thus contribute to habitat complexity in the water column and offer potential refuge from predation to the YOY (Gotceitas and Colgan 1989: Warfte and Barmuta 2004). Our observations differ from those of Murry and Farrell (2007), who found that YOY muskellunge in the St. Lawrence River were often sampled in dense patches of primarily *V. americana*. These differences illustrate the difficulty in generalizing about the suitability of plant taxa for YOY muskellunge. Instead, it may be more appropriate to focus on the pattern of habitat complexity associated with a particular macrophyte community, regardless of the taxonomic composition (Savino and Stein 1982; Werner et al. 1983: Warfte and Barmuta 2004).

The suitability of muskellunge nursery habitat appeared best defined by characteristics that described the composition of the fish and habitat communities in the wetland. Consistent with the proposed ecological framework of Wahl (1999), greater habitat complexity of the upper water column alone appeared insufficient to predict the survival potential of early life-stages. There must also be adequate densities of suitable prey and a limited number of egg predators (Murry and Farrell 2007; Kapuscinski et al. 2012; Leblanc et al. 2015, CH2). By accounting for the composition of the fish community, the 7-variable DFA improved the overall accuracy of the classification and reduced the false negative rate.

The literature indicates that the composition of wetland fish communities is closely related to the associated plant communities (Brazner and Beals 1997; Smokorowski and Pratt 2007; Cvetkovic et al. 2010; Midwood and Chow-Fraser 2012). Thus, differences in fish communities between YOY-Musky and No-Musky sites appeared to follow patterns in habitat complexity observed at both sites. Wetlands with low structural complexity in their macrophyte community may promote increased densities and availability of benthic macro-invertebrates (Hanson 1990: Cobb and Watzin 1998) and this condition appears to favour the abundance of yellow perch (Schaeffer et al. 2000). Thus, the lower relative abundance of yellow perch at muskellunge nursery sites may also be related to greater macrophyte diversity and complexity (Leblanc et al. 2014; Leblanc et al. 2015, CH2). Additionally, highly complex habitats are likely to support a greater number of fish species (Tonn and Magnuson 1982; Eadie and Keast 1984), including the YOY muskellunge that need to hide within the canopy to ambush their prey and avoid being detected by larger piscivores (Savino and Stein 1989; Wagner et al. 2015).

The performance of the DFA improved when all 7 variables were used to discriminate between site-types but inclusion of this large number of variables could lead to over-fitting. However, we feel that these variables are complementary rather than redundant, as they describe different components of the structure in the nearshore habitat. Further investigation should be conducted to identify a more parsimonious model that incorporates fewer but more integrative metrics of plant complexity in the upper water column.

Despite the potential for model over-fitting with the 7-variable DFA, nearly all of the false-positive cases were adjacent to locations where YOY muskellunge were eventually found or where we had observed adult muskellunge during the spawning season. This suggests that the site was in fact suitable for YOY, but that we failed to confirm its true status because of pseudo-absences during the July seining (LaPan et al. 1996). The two YOY-Musky sites that were misclassified as No-Musky sites were located near habitat that had been identified as northern pike nurseries. Early-life habitats for these conspecifics are very similar, and are differentiated by only slight differences in substrate slope, with northern pike occupying sites that are shallower (e.g., shallow emergent habitats; Cooper et al. 2008) than those used by muskellunge (Farrell 2001; Cooper et al. 2008). Our false-negative cases may therefore reflect habitat with slopes at the extreme end of preference for YOY muskellunge (JP Leblanc, pers. obs.), in other words, habitat that may not be as good in quality as those with higher slope. The binary nature of the DFA means that habitat can only be classified as either suitable or not suitable even though in reality, there is probably a range in suitability as a result of the quality of the habitat.

Since we had no *a priori* information which of the wetlands had been used by YOY muskellunge, we decided to sample as widely as possible in both embayments and this meant we only had time and resources to conduct a single seine haul per wetland unit. This may have compromised the accuracy of the presence-absence models and we have to accept that some wetland units where YOY muskellunge had not been caught may in fact have been used by YOY. This error would undoubtedly have influenced the performance of the DFA, but we do not have sufficient data to determine how many of our presumed absences were actually pseudo-absences. Nevertheless, we know that when we re-sampled two wetland units in 2013, a single seine was required to confirm the presence of YOY in one wetland (1.2 ha), whereas three seines were required to confirm the other (1.5 ha). Thus, in some instances greater sampling effort was necessary to reduce pseudo-absences and ensure replicability (i.e., consistently catching YOY at identified nursery sites) with our seining protocol.

As part of a separate study in 2013, adult muskellunge were monitored by radio-tracking during the spawning period to identify potential early-life habitats (JP Leblanc, unpubl. data). When sites identified as likely early-life habitats were seined in July, a single seine was needed to catch YOY muskellunge at 4 of 5 wetland units. Although pseudo-absences from our sampling protocol is a possibility, the frequency of pseudo-absences from the seining appeared limited when used in the relatively small wetland units ($\bar{x}$ ± S.E.: 1.1 ± 0.17 ha; Leblanc and Chow-Fraser 2015, CH2) within the target area. Future studies should ascertain the minimum effort required to accurately sample a site for presence/absence in Georgian Bay or estimate abundances of YOY muskellunge (e.g., Farrell and Werner 1999; Murry and Farrell 2007).

Management Implications

Our results provide the first quantifiable definition of suitable muskellunge nursery habitat in Georgian Bay, in a region that is generally accepted as being in reference condition. This information can assist managers to identify and protect high-quality habitats for YOY muskellunge, as well as provide guidance for restoring/rehabilitating sites that have been degraded by human activities. Some habitat identified as suitable by our model may not be occupied by muskellunge if it is not located close to spawning sites. This is an important consideration because of the muskellunge's demonstrated site fidelity as discussed earlier. Therefore, the proper way to use our results is to first target wetlands located near known spawning sites and then screen them for suitability based on site bathymetry. This should also allow researchers to predict how suitability of coastal marshes may change with respect to nursery habitat under different water-level scenarios in Georgian Bay.

Although our definition of suitable muskellunge nurseries was developed during an unprecedented period of sustained low water levels, we believe that it can be applied to higher or lower water levels that have been predicted by various global circulation models and emission scenarios (e.g. Mortsch & Quinn 1996; Lofgren et al. 2002; Angel and

Kunkel 2010**;** Hanrahan et al. 2010). Any forecast of water-level change can be incorporated to determine the suitability of particular sites as long as there is information on shoreline slope. For instance, nearshore bathymetries that retain a slope of moderate steepness (e.g., between 3 and 7 °) would likely buffer wetlands from adverse effects of high or low water levels (e.g., northern Georgian Bay). The moderately sloped wetlands should provide a more consistent depth zone for the macrophyte community to colonize as water levels fluctuate. By comparison, excessively shallow locations (e.g. southeastern Georgian Bay) may lead to changes in habitat suitability as the macrophyte community has to migrate a long distance to colonize at the appropriate depth zone.

Although the 7-variable DFA model has not yet been validated with an independent field dataset, the associated Cohen's Kappa value indicates relatively strong model performance. All variables included are grounded in sound ecological principles, and are consistent with hypotheses that have been tested by researchers in other regions of the Great Lakes (Murry and Farrell 2007; Kapuscinski and Farrell 2014). We are also encouraged that patterns from the model was transferable from northern Georgian Bay to southeastern Georgian Bay, and appeared able to explain results of a study conducted 30 years earlier, when water levels were higher. Therefore, we are confident that the relationships we have identified in this study will advance management objectives to sustain the naturally reproducing muskellunge fishery in Georgian Bay.

Acknowledgements

We wish to thank Dan Weller, Chris Biberhofer and members of the Chow-Fraser lab and field technicians for their assistance with data collection between 2012 and 2014. We are indebted to Harvey and Lorna Meirke, Jerry Burke, and Pitfields General Store for providing lodging and boats while we were sampling in northern Georgian Bay. We are also grateful to the Ontario Ministry of Natural Resources and Forestry for their logistical support. This project was funded in part by a research grant from the Sierra Club Canada Foundation, the Ontario Ministry of Natural Resources through the Canada-Ontario Agreement, the Ontario Graduate Scholarship Fund, The Dr. Ed. Crossman Scholarship Fund from Muskies Canada Inc., grants from the Great Lakes Basin Conservancy, and charitable contributions from the Georgian Bay Musky Association.

References

Angel JR, Kunkel KE (2010). The response of Great Lakes water levels to future climate scenarios with an emphasis on Lake Michigan-Huron. Journal of Great Lakes Research 36: 51-58

Angradi TR, Person MS, Bolgrien DW, Bellinger BJ, Starry MA, Reschke C (2013). Predicting submerged aquatic vegetation cover and occurrence in a Lake Superior estuary. Journal of Great Lakes Research 39: 536-546

Brazner JC, Beals EW (1997). Patterns in fish assemblages from coastal wetland and beach habitats in Green Bay, Lake Michigan: a multivariate analysis of abiotic and biotic forcing factors. Canadian Journal of Fisheries and Aquatic Sciences 54: 1743-1761

Casselman JM, Lewis A (1996). Habitat requirements of northern pike (*Esox lucius*). Canadian Journal of Fisheries and Aquatic Sciences 53: 161-174

Casselman JM, Robinson CJ, Crossman EJ (1999). Growth and ultimate length of muskellunge from Ontario water bodies. North American Journal of Fisheries Management 19: 271-290

Cobb SE, Watzin MC (1998). Trophic interactions between yellow perch (*Perca flavescens*) and their benthic prey in a littoral zone community. Canadian Journal of Fisheries and Aquatic Sciences 55: 28-36

Cook MF, Solomon RC (1987). Habitat suitability index models: muskellunge. U.S. Fish and Wildlife Service Biol. Rep. 82 (10.148). 33 pp. retrieved from http://www.nwrc.usgs.gov/wdb/pub/hsi/hsi-148.pdf

Cooper JE, Mead JV, Farrell JM, Werner RG (2008). Potential effects of spawning habitat changes on the segregation of northern pike (*Esox lucius*) and muskellunge (*E. masquinongy*) in the Upper St. Lawrence River Hydrobiologia 601: 41-53

Craig RE, Black RM (1986). Nursery habitat of muskellunge in southern Georgian Bay, Lake Huron, Canada. American Fisheries Society Special Publication 15. Pp. 79–86, *in* Hall

Croft MV, Chow-Fraser P (2009). Non-random sampling and its role in habitat conservation: a comparison of three wetland macrophyte sampling protocols. Biodiversity and Conservation 18: 2283-2306

Crossman EJ (1990). Reproductive homing in muskellunge, *Esox masquinongy*. Canadian Journal of Fisheries and Aquatic Sciences 47: 1803-1812

Cvetkovic M, Chow-Fraser P (2011). Use of ecological indicators to assess the quality of Great Lakes coastal wetlands. Ecological Indicators 11: 1609–1622

Cvetkovic M, Wei A, Chow-Fraser P (2010). Relative importance of macrophyte community versus water quality variables for predicting fish assemblages in coastal wetlands of the Laurentian Great Lakes. Journal of Great Lakes Research 36: 64-73

DeCatanzaro R, Chow-Fraser P (2010). Relationship of road density and marsh condition to turtle assemblage characteristics in the Laurentian Great Lakes. Journal of Great Lakes Research 36: 357-365

Dombeck MP, Menzel BW, Hinz PN (1986). Natural muskellunge reproduction in Midwestern Lakes. American Fisheries Society Special Publication 15. Pp. 122–134, *in* Hall

Duarte CM, Kalff J (1986). Littoral slope as a predictor of maximum biomass of submerged macrophyte communities. Limnology and Oceanography 31: 1072-1080

Eadie JM, Keast A (1984). Resource heterogeneity and fish species diversity in lakes. Canadian Journal of Zoology 62: 1689-1695

Farrell JM (2001). Reproductive success of sympatric northern pike and muskellunge in an Upp.er St. Lawrence River bay. Transactions of the American Fisheries Society 130: 796-808

Farrell JM, Klindt RM, Casselman JM, LaPan SR, Werner RG, Schiavone A (2007). Development, implementation, and evaluation of an international muskellunge management strategy for the upper St Lawrence River. Environmental Biology of Fishes 79: 111-123

Farrell JM, Werner RG (1999). Distribution, abundance, and survival of Age-0 muskellunge in Upper St. Lawrence River nursery bays. North American Journal of Fisheries Management 19: 309-320

Fielding AH, Bell JF (1997). A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation. 24: 38-49

Fracz A, Chow-Fraser P (2013). Impacts of declining water levels on the quantity of fish habitat in coastal wetlands of eastern Georgian Bay, Lake Huron. Hydrobiologia. 705: 151-169

Gotceitas V, Colgan P (1989). Predator foraging success and habitat complexity: quantitative test of the threshold hypothesis. Oecologia 80: 158-166

Hanarahan JL, Kravtsov SV, Roebber PJ (2010). Connecting past and present climate variability to water levels of Lakes Michigan and Huron. Geophysical Research Letters 37: L01701

Hanson JM (1990). Macroinvertebrate size-distributions of two contrasting freshwater macrophyte communities. Freshwater Biology 24: 481-491

Jennings MJ, Hatzenbeler GR, Kampa JM (2011). Spring capture site fidelity of adult muskellunge in inland lakes. North American Journal of Fisheries Management 31: 461-467

Kapuscinski KL, Farrell JM (2014). Habitat factors influencing fish assemblage at muskellunge nursery sites. Journal of Great Lakes Research 40: 135-147

Kapuscinski KL, Farrell JM, Murry BA (2012). Feeding strategies and diets of young-of-the-year muskellunge from two large river ecosystems. North American Journal of Fisheries Management 32: 635-647

Kapuscinski KL, Farrell JM, Wilkinson MA (2014). Trends in muskellunge population and fishery characteristic in Buffalo Harbor (Lake Erie) and the Niagara River. Journal of Great Lakes Research 40: 125-134

Kapuscinski KL, Sloss BL, Farrell JM (2013). Genetic population structure of muskellunge in the Great Lakes. Transactions of the American Fisheries Society 142: 1075-1089

Keddy P, Reznicek A (1986) Great Lakes vegetation dynamics: the role of fluctuating water levels and buried seeds. Journal of Great Lakes Research 12: 25–36

Landis JR, Koch GG (1977). The measurement of observer agreement for categorical Data. Biometrics 33: 159-174

LaPan SR, Schiavone A, Werner RG (1996). Spawning and post-spawning movements of the St. Lawrence River muskellunge (*Esox masquinongy*). In Managing muskies in the '90s. Workshop Proceedings [eds. Kerr, S. J. and C. H. Olver]. Ontario Ministry of Natural Resources, Southern Region Science and Technology Transfer Unit Workshop Proceedings WP-007. Pp. 73 - 82

Leblanc JP, Weller JD, Chow-Fraser P (2014). Thirty-year update: changes in biological characteristics of degraded muskellunge nursery habitat in southern Georgian Bay, Lake Huron, Canada. Journal of Great Lakes Research 40: 870-878

Leblanc JP, Weller JD, Chow-Fraser P (2015, CH2). Similarities in fish communities between muskellunge nursery sites from two adjoining embayments in northern Georgian Bay, Lake Huron (Chapter 2)

Lofgren BM, Quinn FH, Clites AH, Assel RA, Eberhardt AJ, Luukkonen CL (2002). Evaluation of potential impacts of Great Lakes water resources based on climate scenarios of two GCMs. Journal of Great Lakes Research 28: 537-554

Manel S, Williams HC, Ormerod SJ (2001). Evaluating presence-absence models in ecology: the need to account for prevalence. Journal of applied Ecology 38: 921-931

Midwood JD, Chow-Fraser P (2012). Changes in aquatic vegetation and fish communities following 5 years of sustained low water levels in coastal marshes of eastern Georgian Bay, Lake Huron. Global Change Biology 18: 93-105

Mortsch LD, Quinn FH (1996). Climate change scenarios for Great Lakes Basin ecosystem studies. Limnology and Oceanography 41: 903-911

Murry BA, Farrell JM (2007). Quantification of native muskellunge nursery habitat: influence of body size, fish community composition, and vegetative structure. Environmental Biology of Fishes 79: 37-47

Nohner JK, Diana JS (2015). Muskellunge spawning site selection in northern Wisconsin lakes and a GIS-based predictive habitat model. North American Journal of Fisheries Management 35: 141-157

Quinn GP, Keough MJ (2006). Experimental Design and Data Analysis for Biologists. Cambridge University Press

Rosenfeld JS, Hatfield T (2006). Information needs for assessing critical habitat of freshwater fish. Canadian Journal of Fisheries and Aquatic Sciences 63: 683-698

Rust AJ, Diana JS, Margenau TL, Edwards CJ (2002). Lake characteristics influencing spawning success of muskellunge in northern Wisconsin lakes. North American Journal of Fisheries Management 22: 834-841

Savino JF, Stein RA (1982). Predator-prey interactions between largemouth bass and bluegills as influenced by simulated submersed vegetation. Transactions of the American Fisheries Society 111: 255-266

Savino JF, Stein RA (1989). Behavioural interactions between fish predators and their prey: effects of plant density. Animal Behaviour 37: 311-321

Schaeffer JS, Diana JS, Haas RC (2000). Effects of long-term Changes in the benthic community on yellow perch in Saginaw Bay, Lake Huron. Journal of Great Lakes Research 26: 340-351

Seilheimer TS, Chow-Fraser P (2007). Application of the wetland fish index to northern Great Lakes marshes with emphasis on Georgian Bay coastal wetlands. Journal of Great Lakes Research 33: 154-171

Sellinger CE, Stow CA, Lamon EC, Qian SS (2008). Recent water level declines in the Lake Michigan-Huron system. Environmental Science and Technology 42: 367-373

Smokorowski KE, Pratt TC (2007). Effect of a change in physical structure and cover on fish and fish habitat in freshwater ecosystems – a review and meta-analysis. Environmental Reviews 15: 15-41

StatSoft, Inc. (2007). STATISTICA (data analysis software system), version 8.0. www.statsoft.com

Titus JE, Adams MS (1979). Comparative carbohydrate storage and utilization patterns in the submersed marcophytes, *Myriophyllum spicatus* and *Vallisneria Americana*. American Midland Naturalist 102: 263-272

Tonn WM, Magnuson JJ (1982). Patterns in the species composition and richness of fish assemblages in northern Wisconsin lakes. Ecology 63: 1149-1166

Wagner CP, Weber MJ, Wahl DH (2015). Structural complexity influences littoral coarse woody habitat selection by juvenile muskellunge. North American Journal of Fisheries Management 35: 14-19

Wahl DH (1995). Effect of habitat selection and behavior on vulnerability to predation of introduced fish. Canadian Journal of Fisheries and Aquatic Sciences 52: 2312-2319

Wahl DH (1999). An ecological context for evaluating the factors influencing muskellunge stocking success. North American Journal of Fisheries Management 19: 238-248

Wahl DH, Stein RA (1989). Comparative vulnerability of three esocids to largemouth bass (*Micropterus salmoides*) predation. Canadian Journal of Fisheries and Aquatic Sciences 46: 2095-2103

Warfte DM, Barmuta LA (2004). Habitat structural complexity mediates the foraging success of multiple predator species. Oecologia 141: 171-178

Werner EE, Gilliam JM, Hall DJ, Mittelbach GG (1983). An experimental test of the effects of predation risk on habitat use in fish. Ecology 64: 1540-1548

Werner RG, Klindt R, Jonckheere B (1996). Vegetative characteristics of muskellunge (*Esox masquinongy*) spawning and nursery habitat in the 1000 Islands section of the St. Lawrence River. Great Lakes Research Review 2: 29-35

Weller JD, Leblanc JP, Liskauskas A, Chow-Fraser P (2015). Spawning-site fidelity in sub-populations of muskellunge in Georgian Bay: Implications of habitat loss. Transactions of the American Fisheries Society (in submission)

Table 3.1. List and ecological interpretation of variables used in this study. Habitat variables apply to the water zone defined by 0.5 and 1.0 m contours. Protocols described in Leblanc et al. (2014) were used to sample the fish community and fish habitat. Variable names in brackets are the acronyms and citations for variable description reflect wetland features previously identified as important to suitable muskellunge nursery habitat.

	Variable Name	Variable Description
Habitat Variables	**Substrate-covering SAV (Sub SAV) [a]**	Mean stem density of all substrate-covering SAV species (Murry and Farrell 2007; Kapuscinski and Farrell 2014). Data were $\log_{10}$ (n+1) transformed.
	Canopy SAV [a, b, c] (Can SAV)	Mean stem density of canopy-structuring SAV taxa (Craig and Black 1986; Murry and Farrell 2007). Data were $\log_{10}$ (n+1) transformed.
	Floating & Emergent vegetation [a]	Mean stem density of combined emergent and floating vegetation (Craig and Black 1986). All data were $\log_{10}$ (n+1) transformed. This variable was considered an additional variable to infer habitat structure in the upper water-column in the wetland.
	Macroalgae SAV[a]	Mean stem density of *Chara* sp. + *Najas* sp. only. This variable was included because previous studies indicated that macroalgae were negatively associated with the quality of muskellunge nursery habitat (Murry and Farrell 2007); *Najas* sp. and *Chara* sp. have similar vegetative structure and presumably similar habitat structuring effects. All data were $\log_{10}$ (n+1) transformed.
	Proportional abundance of *V. americana* [a, b, c]	*Vallisneria americana* was the dominant taxon of Canopy SAV found at all wetlands surveyed (Murry and Farrell 2007). This variable is intended to reflect the diversity of the canopy-forming SAV community, with high values indicating a more monoculture of *Vallisneria*. All data were arcsine-square root transformed.
	Substrate Slope [a, b, c]	Estimate of the substrate slope within the wetland. Substrate slope was estimated with the protocol by Leblanc et al. (2014). All values were $\log_{10}$ transformed.
	Stem Density Ratio (Sub SAV:Can SAV) [a, b, c]	Ratio of stem density of Sub SAV-to-Can SAV. Values <1 indicated that the site had more Can SAV than Sub SAV. All data were $\log_{10}$ (n+1) transformed.
Fish Variables	**Proportional abundance of Yellow Perch [c, d]**	Indicative of relative impact of potential egg depredation (Murry and Farrell 2007; Leblanc et al. 2015, CH2). All data were arcsine-square root transformed.
	Proportional abundance of Cyprinid species [c, d]	Indicative of conditions that promote good growth and survival for YOY; cyprinid species are assumed to be preferred forage for YOY muskellunge (Kapuscinski et al. 2012).
	Residual spp. richness [c, d]	An additional metric of the habitat complexity of the wetland that may also promote YOY muskellunge survival by limiting YOY predation risk (Wahl 1999).

[a] used in MANOVA analysis

[b] used in DFA with habitat variables only

[c] used in DFA with all ecosystem variables

[d] see Leblanc et al. (2015, CH2) for more detailed explanation regarding the fish variables

Table 3.2. Frequency of occurrence (%) and mean (± S.E.) stem densities of species specific substrate-covering (Sub SAV) and Canopy-structuring SAV (Can-SAV) sampled at YOY-Musky and No-Musky sites at depths > 0.5 m. Untransformed means displayed for presentation purposes.

		YOY Muskellunge		**No-Musky**	
	Species	**Freq. Occ. (%)**	**Mean (± S.E.)**	**Freq. Occ. (%)**	**Mean (± S.E.)**
Sub-SAV	Slender water nymph (*Najas flexilis*)	100	**10.61** (3.67)	92.3	**12.75** (2.56)
	Quillwort (*Isoetes spp.*)	75	**37.69** (14.91)	87.2	**120.94** (30.63)
	Fern-leaf pondweed (*Potamegeton robbinsii*)	75	**7.50** (2.64)	74.4	**15.75** (4.84)
	(*Chara sp.*) [a]	43.8	**1.59** (1.11)	69.2	**4.47** (1.18)
Can SAV	Water celery (*Vallisneria americana*)	100	**78.54** (14.87)	100	**63.24** (6.72)
	Clasping-leaved pondweed (*Potamogeton richardsonii*) [a]	100	**6.77** (1.09)	89.7	**3.35** (0.57)
	Common waterweed (*Elodea canadensis*) [a]	87.5	**15.03** (3.47)	82.1	**7.17** (2.29)
	Flat-stemmed pondweed (*Potamogeton zosteriformis*)	81.3	**12.66** (5.52)	82.1	**6.11** (1.86)
	Coontail (*Ceratophyllum demersum*) [a]	75	**3.30** (0.90)	38.5	**0.60** (0.22)
	Eurasian milfoil (*Myriophyllum spicatum*)	56.3	**0.96** (0.45)	53.8	**0.91** (0.26)
	Slender pondweed (*Potamogeton pusillus*)	56.3	**2.88** (1.44)	64.1	**1.28** (0.33)
	Variable pondweed (*Potamogeton gramineus*)	50	**2.07** (0.71)	43.6	**2.09** (0.82)
	Beck's water marigold (*Bidens beckii*)	37.5	**0.87** (0.41)	46.2	**0.44** (0.19)
	Large-leaved pondweed (*Potamegeton amplifolius*)	37.5	**1.07** (0.70)	30.8	**0.93** (0.41)
	Northern water-milfoil (*Myriophyllum sibiricum*)	12.5	**0.09** (0.07)	20.5	**0.13** (0.07)

[a] denotes significant differences between site types (i.e., YOY-Musky and No-Musky site) with respect to median stem densities based on Mann-Whitney U Tests ($p < 0.05$).

Table 3.3. Raw (unstandardized) and standardized coefficients, and factor structure correlations of the variables for the canonical axis obtained from the Discriminant Function Analysis on the 4 selected habitat variables. Variables with positive loadings are associated with YOY-Musky sites, while those with negative loadings are associated with No-Musky sites.

Habitat Variables	**Raw Coefficients for Canonical Variables**	**Standardized Coefficients for Canonical Variables**	**Factor Structure Correlations for Canonical Root**
Canopy SAV (m^{-2})	1.285	0.393	0.418
Substrate Slope (°)	1.521	0.494	0.664
Proportional abundance of *V. americana*	-2.237	-0.519	-0.623
Stem Density Ratio (Sub SAV-to-Can SAV)	-1.126	-0.284	-0.650
Constant	-0.398		
Eigen value	0.488		

Table 3.4. Discriminant Function Analysis (DFA) based all ecosystem variables to define the suitability of muskellunge nursery habitat. The DFA model (Wilks $\lambda = 0.575$, $F_{7, 47} = 4.955$, $p = 0.00029$) correctly classified 87.5% (14 of 16) of the nursery sites and 89.1 % (35 of 39) sites where YOY muskellunge had not been caught. Positive and negative coefficients and correlations are associated with sites with and without YOY, respectively. Only sites that had both fish and habitat variable estimates were included in the DFA ($n_{total} = 55$).

	DFA Variable	**Raw Coefficients**	**Standardized Coefficient**	**Factor Structure Correlation**
Wetland Fish Variables	Proportional abundance of Yellow Perch	-0.7740	-0.1497	-0.2120
	Proportional abundance of Cyprinid species	1.4524	0.4018	0.2320
	Residual spp. Richness	0.1594	0.4030	0.3762
Wetland Habitat Variables	Can SAV (m^{-2})	1.2723	0.3885	0.3403
	Substrate Slope (°)	1.7532	0.5694	0.5406
	Proportional abundance of *V. americana*	-2.1184	-0.4913	-0.5064
	Stem Density Raito (Sub SAV-to-Can SAV)	-0.2596	-0.0655	-0.5286
	Constant	-2.3941		
	Variation Explained (%)	73.8		

Table 3.5. Results from Discriminant Function Analyses (DFA) with different combinations of variables. Slope=substrate slope; Sub:Can = stem density ratio of substrate-covering SAV to Canopy SAV; Can-SAV = stem density of Canopy structuring SAV; Pr. *V. am* = proportional abundance of *V. americana*; Cyp = proportional abundance of cyprinid species; YP = proportional abundance of yellow perch; Spp. = residual fish species richness. Only DFA models that correctly classified > 50 % of YOY-Musky sites (numbered 1 – 16) are presented. All models were significant ($p < 0.001$). Models are presented in order of % True +ve (percentage of YOY-Musky sites correctly identified) followed by the fewest number of variables included in the DFA (k). % False +ve = percent of No-Musky sites (n = 39) classified as YOY-Musky sites. ● = correctly identified; x = incorrectly identified.

Variables included in the DFA	**k**	**% True +ve**	**% False +ve**	**DFA models**															
				1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**
Slope, Sub:Can, Can-SAV, Pr.*V. am*, Cyp, YP, Spp.	7	87.5	10.3	●	●	●	●	●	●	●	●	●	●	●	●	●	●	x	x
Slope, Sub:Can, Can-SAV, Pr. *V. am*, Cyp, Spp.	6	81.3	10.3	●	x	●	●	●	●	●	●	●	●	●	●	●	●	x	x
Slope, Cyp, Spp.	3	75.0	10.3	●	●	●	●	●	●	●	●	●	●	●	●	x	x	x	x
Slope, Sub:Can, Can-SAV, % V. am	4	75.0	10.3	●	●	●	●	●	●	x	●	●	●	●	x	x	●	●	x
Slope, Cyp, YP, Spp.	4	75.0	10.3	●	●	●	●	●	●	●	●	●	●	●	●	x	x	x	x
Slope, Sub:Can, Cyp, Spp.	4	75.0	12.8	●	●	●	●	●	●	●	●	●	●	●	●	x	x	x	x
Slope, Sub:Can, Can-SAV, Pr. *V. am*, Spp.	5	75.0	10.3	●	●	●	●	●	●	●	●	●	●	●	x	x	●	x	x
Slope, Sub:Can, Cyp, YP, Spp.	6	75.0	12.8	●	●	●	●	●	●	●	●	●	●	●	●	x	x	x	x
Slope, Sub:Can, Can-SAV, Pr.*V. am*, YP, Spp.	6	75.0	10.3	●	●	●	●	●	●	●	●	●	●	●	x	x	●	x	x
Slope, Spp.	2	68.8	10.3	●	●	●	x	●	●	●	●	●	●	●	●	x	x	x	x

Table 3.5. Continued

Variables included in the DFA	k	% true positive	% false positive	DFA models															
				1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Slope, YP, Spp.	3	68.8	10.3	●	●	●	x	●	●	●	●	●	●	●	●	x	x	x	x
Slope, Sub:Can, Can-SAV, Pr. *V. am*, YP	5	68.8	10.3	●	●	●	●	x	●	x	●	●	●	●	x	x	●	●	x
Slope, Pr. *V. am*, Cyp, YP, Spp.	5	68.8	10.3	●	x	●	●	●	●	●	●	●	x	●	●	x	●	x	x
Slope, Can-SAV, Cyp, YP, Spp.	5	68.8	10.3	x	●	●	●	●	●	●	●	●	●	●	●	x	x	x	x
Slope, Sub:Can, Can-SAV, Pr. *V. am*, Cyp, YP	6	68.8	10.3	●	x	●	●	x	●	x	●	●	●	●	●	●	●	x	x
Slope, Sub:Can, Can-SAV, Pr. *V. am*, Cyp	4	62.5	10.3	●	x	●	●	x	●	x	●	●	●	●	●	x	●	x	x
Slope, Sub:Can, Can-SAV	3	56.3	10.3	●	●	●	●	x	●	x	x	●	●	●	●	x	x	●	x

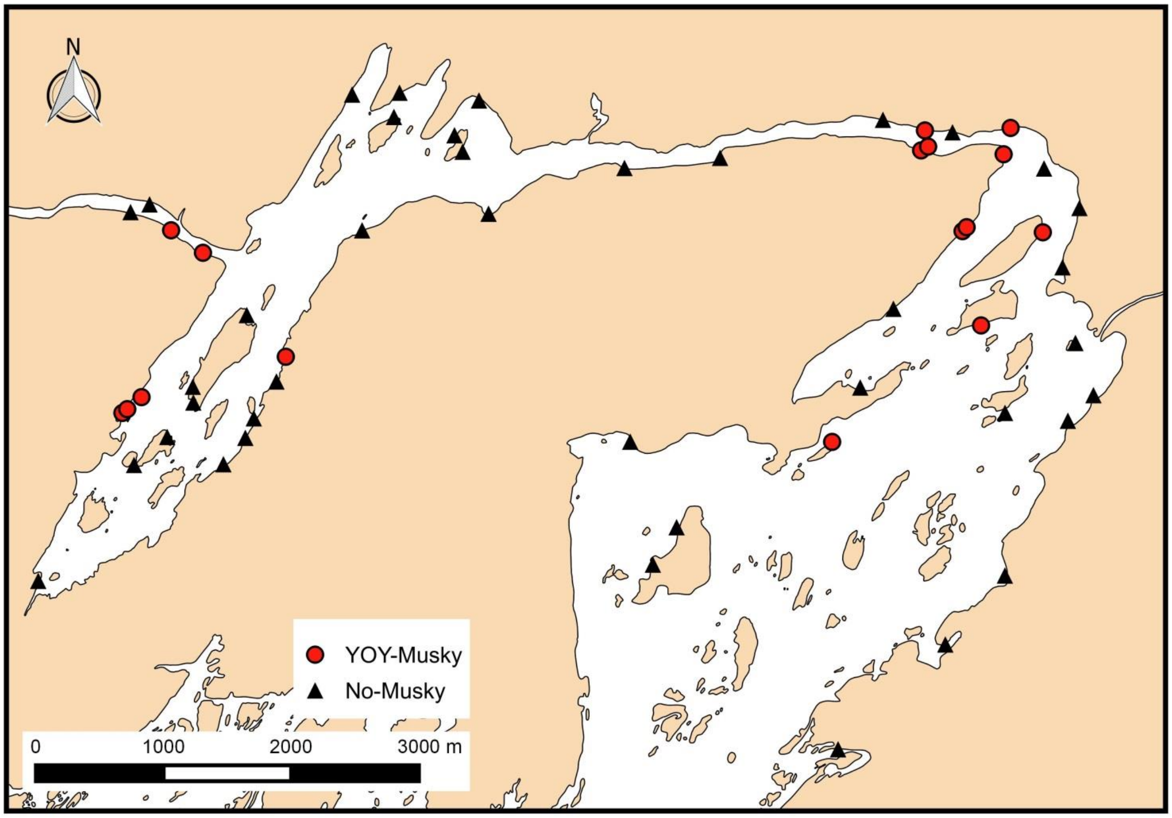


Figure 3.1. Locations where YOY muskellunge were present (YOY-Musky sites denoted by circles; n = 16) and absent (No-Musky sites denoted by triangles; n = 39) in coastal wetlands of northern Georgian Bay. See Leblanc et al. (2015, CH2) for study-site descriptions. The No-Musky sites were randomly selected for habitat assessments from the 67 sites originally identified as such from seining the wetlands in July (Leblanc et al. 2015, CH2).

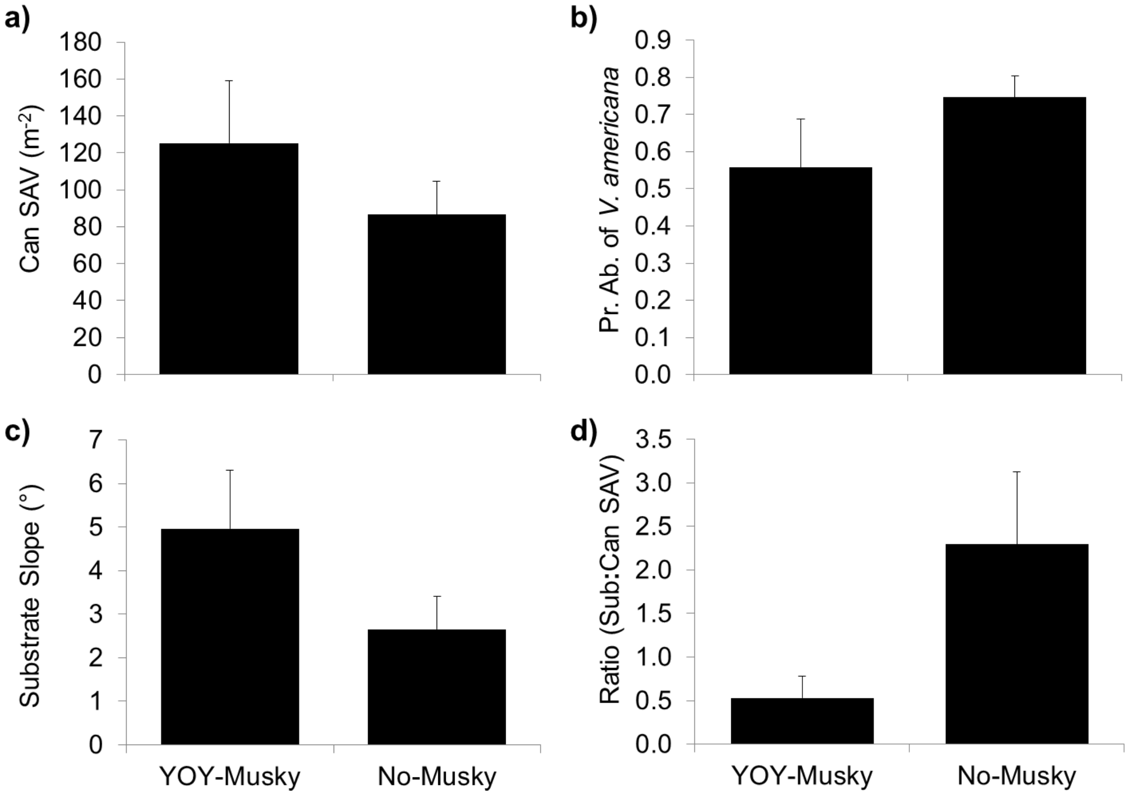


Figure 3.2. Means ± 95% confidence intervals of univariate habitat variables that differed significantly ($p < 0.05$) between sites with (YOY Musky) and without YOY muskellunge (No-Musky). Data correspond to depths > 0.5 m. Variables include the stem density of Canopy structuring SAV (Can SAV), Proportional abundance (Pr. Ab.) of *V. americana*, the substrate slope of the wetland, and the ratio of Sub**:**Can SAV stem densities. Untransformed data are displayed.

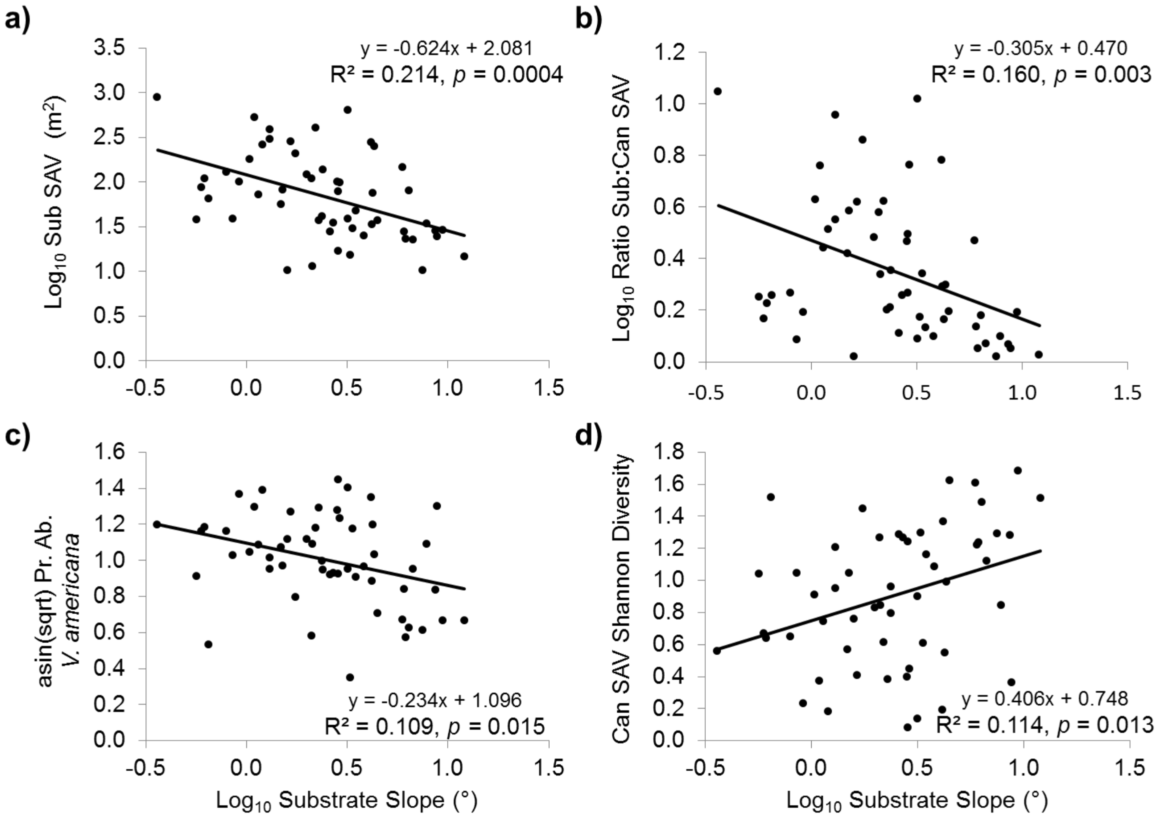


Figure 3.3. Linear regression relationships between variables concerned with the macrophyte community and substrate slope. Linear regression of **a)** Stem density of Sub SAV, **b)** Ratio of Sub**:**CanSAV, **c)** Proportionate abundance of *V. americana*, and **d)** Shannon diversity of Can SAV against substrate slope. R^2 and *p*-values displayed in respective panels.

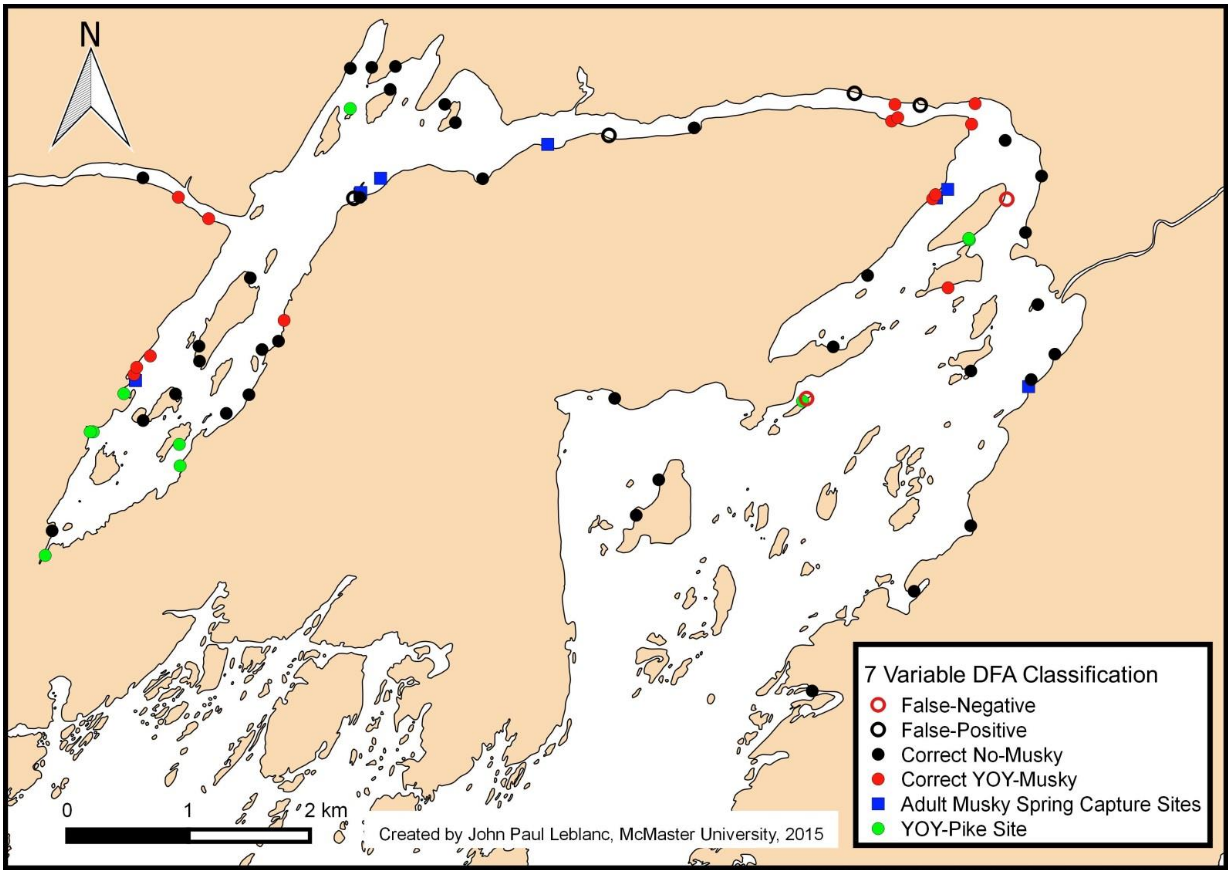


Figure 3.4. Classification of cases from the 7-variable Discriminant Function Analysis (DFA). False-Negative denotes YOY-Musky sites that were classified as No-Musky sites, while False-Positive denotes No-Musky sites classified as YOY-Musky sites. Locations where adult muskellunge were caught during the spawning season and identified northern pike nurseries (YOY-Pike Site) are presented for reference.

Chapter 4:

Index of Nursery Habitat Suitability for muskellunge in Georgian Bay, Lake Huron

For submission: Leblanc JP, Chow-Fraser P (2015, CH4). Index of Nursery Habitat Suitability for muskellunge in Georgian Bay, Lake Huron

Abstract

To support Georgian Bay's self-sustaining muskellunge (*Esox masquinongy*) fisheries, we developed two Index of Nursery Habitat Suitability (INHS) models that can be used to identify and monitor the quality of muskellunge nursery habitats in coastal wetlands. The INHS models were based on habitat features found in wetlands with young-of-the-year (YOY) muskellunge identified at two large embayments in northern Georgian Bay. One INHS model had 5 variables that included relative abundance of yellow perch (*Perca flavescens*), relative abundance of Cyprinids, residual fish species richness, the wetland's substrate slope and a metric related to macrophyte abundance. The other INHS model included only three variables from the 5-variable INHS, omitting information on macrophyte and fish species richness. When they were applied to an independent dataset, both INHS models successfully tracked deterioration in nursery suitability after 15 years of sustained low water levels in Georgian Bay, but the 5-variable INHS had higher overall accuracy and showed stronger discrimination between sites with and without YOY. We applied the 3-variable model to classify coastal wetlands in other regions of Georgian Bay and obtained a false negative rate <13%. We also obtained a higher false-positive rate with the 3-variable model compared with the 5-variable model (54% vs 31%) because it required a lower threshold to indicate suitability (0.6 versus 0.70, respectively). These INHS models should allow managers to screen for suitable nursery habitat near current spawning sites across Georgian Bay, and allow managers to predict how changes in water-level regimes might affect the suitability of spatially explicit wetland units.

Keywords: Habitat Suitability Index, Muskellunge, Nursery Habitat, Georgian Bay, Water Levels

Introduction

The muskellunge (*Esox masquinongy*) fishery of Georgian Bay (Lake Huron) is well known for its trophy status, for producing fish that reach world record sizes, and that are of great economic and ecological value to Ontario (Kerr et al. 2011). Since 2001, a restrictive harvest regulation that prohibits anglers from harvesting fish smaller than 137 cm (54 inches) has been effective in keeping many of the spawning individuals alive in the population. Adult mortality is further minimized through voluntary catch-and-release by many dedicated anglers. Despite these conservation measures which have successfully limited the exploitation rate of adults in Ontario to < 1% (Kerr 2007), the muskellunge population in Georgian Bay could still be vulnerable to collapse if suitable nursery habitat becomes unavailable (Kapuscinski et al. 2014; Leblanc et al. 2014). That is why many Great Lakes jurisdictions, including Ontario, now focus on conserving habitat for early-life stages as part of the overall management strategy of muskellunge (Farrell et al. 2007; Liskauskas 2007).

To implement this aspect of the management strategy, agencies must be able to first identify nursery habitat. For muskellunge, this has been difficult because only a few studies have been published to provide guidance. One of the earliest studies was conducted by Craig and Black (1986), who showed that young-of-the-year (YOY) are most often found in shallow portions of coastal wetlands from shore to approximately 1.0 m depth. More recent studies have provided further refinement by pointing out that suitable habitat must also include a structurally complex macrophyte community that allows YOY to hide from predators (Murry and Farrell 2007; Kapuscinski and Farrell

2014; Leblanc and Chow-Fraser 2015, CH3; Wagner et al. 2015) while simultaneously allowing them to ambush their preferred prey (i.e., soft-rayed fusiform fish; Wahl and Stein 1988; Kapuscinski et al. 2012; Leblanc et al. 2015, CH2). With such information, it is now possible and desirable to develop an index that can be used to identify suitable habitat for YOY before any development can occur. Once a site has been identified as being suitable, a more detailed study can be carried out to confirm the presence of YOY. This index could be philosophically similar to the standard Habitat Suitability Index (HSI), except that the index should focus only on early-life habitat instead of habitat of all life stages (US Fish and Wildlife Service 1981; Ahmadi-Nedushan et al. 2006; De Kerckhove et al. 2008). To differentiate it from the HSI, our index should be referred to as an Index of Nursery Habitat Suitability (INHS).

The goal of this paper is to develop INHS models for YOY muskellunge in Georgian Bay. We want to constrain this development to minimize false-negatives (i.e. the incidence of nursery sites being misclassified as unsuitable) since we want to err on the side of conservation. At least one of the INHS models to be developed should contain only variables that are readily measured and available to fisheries biologists to ensure that the INHS will be appropriate for biologists in most management agencies. The INHS should not be confused with the Habitat Suitability Models (HSM) or Species Distribution Models (SDM) that predict species distributions over a large geographic region in response to climatic or environmental features (Guisan and Thuiller 2005). Instead, the INHS is a site specific indexing tool for a particular wetland.

Like the HSI score, the INHS score should take on a value ranging from zero (indicating completely unsuitable habitat) to one (indicating entirely suitable habitat) (US Fish and Wildlife Service 1981), and may be used to reflect the degree of change in suitability of a habitat that was positively or negatively impacted by natural (e.g. water levels of a lake) or human-induced disturbances (e.g. lakeshore modifications) (De Kerckhove et al. 2008). We will also use a suite of suitability index (SI-) variables similar to those in HSI, that correspond to quantifiable dimensions of the habitat and which are scaled from zero to one. These SI-variables will be based on habitat features that can discriminate between sites with and without YOY muskellunge in wetlands of Georgian Bay including stem density of various groups of submersed aquatic vegetation (SAV), the relative abundance and species richness of fish taxa, as well as the substrate slope of the wetland (Leblanc and Chow-Fraser 2015, CH3). We will compare the performance of various INHS models and use independent data to validate the best model. Development of these indices will help protect critical nursery habitat and complement existing efforts to minimize mortality of spawning adults, both of which are necessary for the muskellunge population in Georgian Bay to be managed as a self-sustaining fishery.

Methods

Data and INHS Development

The data used to for this study come from two large embayments in northern Georgian Bay (see Leblanc et al. 2015, CH2 for site description; Figure 4.1). Leblanc and Chow-Fraser (2015, CH 3) collected parallel information at sites where YOY muskellunge were (YOY-Musky sites) and were not caught (No-Musky sites) by seines, to determine variables that differed significantly between site types. To develop the INHS models, we considered seven variables that differed significantly between YOY-Musky and No-Musky sites. These were as follows: (1) stem density of canopy-forming SAV (Can SAV), (2) proportional abundance of *Vallisneria americana* in the Can SAV, (3) stem density ratio of substrate-covering SAV (Sub SAV) to Can SAV (Sub SAV**:**Can SAV), (4) the wetland's substrate slope, (5) relative abundance of yellow perch, (6) relative abundance of Cyprinid species and (7) residual fish species richness. All of the plant information was collected at wetland depths between 0.5 and 1.0 m (Leblanc and Chow-Fraser 2015, CH3), and all fish community variables were calculated with fish data collected in a standard seine haul, after excluding YOY (Leblanc et al. 2015, CH2).

Suitability-Index (SI) curves were superimposed over the frequency distribution of YOY muskellunge associated with different levels of the SI-variable (see Appendix); the untransformed mean ± 2 SE was given a SI value of 1.0, while other values on both shoulders of the SE would take on values between 1.0 and zero. Thus, SI curves are representative of habitat-use indices or comparable to a category-II HSI (Ahmadi-Nedushan et al. 2006). In many cases, the shoulders on either side of the mean were simply extended linearly from one to zero to intercept the x-axis at locations that bracket observed distributions. When there were insufficient data, the line was subjectively broken or bent to reflect uncertainty of the relationship. As a result, SI curves should be considered hypotheses of suitable habitat relationships for YOY muskellunge that require further testing and refinement.

The SI scores for each variable were calculated for each site. Since there was relatively low correlation between all SI-variable pairs (i.e., $r \leq 0.30$), we suggest that the SI-variables are statistically independent. Additionally, no single variable was deemed to be more important than others with regards to habitat suitability, and SI-variables were assumed to be compensatory. Therefore, we propose to create a composite INHS by calculating the arithmetic mean of all SI-variables using the following formula:

$$\mathrm{INHS} = \left(\sum_{i=m}^{\mathrm{n}} Vi\right)/\mathrm{n} \qquad [1]$$

where Vi is the SI-value for the i^{th} SI-variable, and n is the number of SI-variables used to calculated the INHS score.

We could have used the lowest SI value as the criterion for overall suitability, but an arithmetic mean of the variables is less biased towards unsuitability (Ahmadi-Nedushan et al. 2006), something that we were aiming for, to minimize the number of cases in which YOY-Musky sites would be misclassified as being unsuitable (i.e., a false-negative). Furthermore, we wanted to ensure that all SI-variables had equal weighting, since the SI curves were created with a small sample size that had high site-specificity.

To determine what combination of SI-variables could effectively identify the suitability of YOY-Musky sites, multiple logistic regression and Akaike information criterion (AIC) model selection was used with the 7 SI-variables in Statistica 8.0 (StatSoft Inc. 2007). The combination of SI-variables that produced the best fit of the data (based on AIC values), and were most consistent with the near-shore features hypothesized to promote suitable nursery habitat, comprised the final list of variables for the INHS (equation [1]). To aid interpretation of INHS scores, we divided the range (from 0 to 1) into four categories to represent high, moderate, low and no suitability (US Fish and Wildlife Service 1981). The cut-off points separating these categories were modified to minimize the false-negative rate while maximizing overall accuracy of classification. This was guided by the Receiver Operating Characteristic (ROC) curve that compares the true-positive (sensitivity) and false-positive (1 – specificity) rates among all potential threshold points to discriminate between the YOY-Musky and No-Musky sites (Fielding and Bell 1997). The ROC curve was used to identify the cut-off that maximizes the sensitivity at the lowest false-positive rate (i.e., sensitivity – false-positive) that is independent of the prevalence of the species and potential threshold effects from presence-absence models (Pearce and Ferrier 2000; Manel et al. 2001). This allowed us to evaluate the usefulness or conservation value of the model (Fielding and Bell 1997; Pearce and Ferrier 2000).

The Area Under the Curve (AUC) from the ROC was also used to evaluate the "discrimination capacity" of the INHS model (Fielding and Bell 1997; Pearce and Ferrier 2000). The AUC can be interpreted as an index of the probability that the model will correctly distinguish between a randomly selected YOY-Musky and No-Musky sites (e.g., AUC = 0.80 means that 80% of the time the model will correctly identify the YOY-Musky site; Fielding and Bell 1997; Pearce and Ferrier 2000). AUC values range between 0.5 (no discrimination capacity) and 1.0 (perfect model with no overlap of the category's scores; Fielding and Bell 1997) and models with AUC values between: 0.5 – 0.7 are considered "poor"; between 0.7 – 0.9 = "reasonable"; while AUC ≥ 0.9 are considered "very good" discriminating models (Pearce and Ferrier 2000).

We further evaluated the performance of the selected INHS model by applying it to an independent dataset that consisted of published information corresponding to sites in southeastern Georgian Bay that no longer supported YOY muskellunge (Leblanc et al. 2014), but which had been nursery sites for muskellunge in 1981 (Craig and Black 1986). We expected this model to correctly classify sites as being unsuitable in 2012.

Development of Alternative INHS Model

We know that data on the wetland macrophyte community are not readily available to fishery managers. Therefore, we combined different fish-community variables and substrate slope information from the northern Georgian Bay data to develop an alternate INHS model that may be less effective but still useful for screening purposes. The ROC and AUC for each model were used to determine precision of classification and to determine the cut-off point that could be used to maximize the sensitivity and, as much as possible, limit the false-positive rate among the various INHS models. Once an appropriate suitability threshold was determined, all of the INHS models were applied to data from southeastern Georgian Bay to determine transferability of models from region to region. The INHS model that yielded the lowest false-negative rate (i.e., highest sensitivity) was further validated with data that had been collected in eastern Georgian Bay as part of a separate study (Cvetkovic et al. 2012). Fish species composition and presence of YOY muskellunge had been collected during July 2007 with paired fyke-nets. We calculated the substrate slope by estimating the distance from shore to the 1.0 m contour (we assumed that the location of the large nets was at or near 1.0 m because this was a depth requirement for fyke-net deployment). We replicated this procedure for six additional, randomly selected, wetlands from the same study that did not support early life-stages of muskellunge.

Finally, we wanted to develop a simple metric that could be used to infer habitat complexity of the macrophyte community without the need for counting stems in the field. Macrophyte *biovolume,* which reflects the percentage of the water column occupied by SAV, can be estimated with hydroacoustic equipment or estimated in the field (Weaver et al. 1997; Valley et al. 2005), for which field derived and remotely sensed estimates are highly correlated (Valley et al. 2005). Biovolume is also similar to other indices that have been used to characterize the macrophyte community in habitats used by YOY muskellunge in the lower Great Lakes (see Kapuscinski and Farrell 2014; Murry and Farrell 2007), which are associated with intermediate densities of SAV in the water column.

At its simplest, biovolume can be derived by taking the mean SAV height, dividing it by the depth at which the SAV was measured, and then expressing it as a percentage (Valley et al. 2005). For each site with available data (n = 14 YOY-Musky sites and n = 37 No-Musky sites), mean SAV height (estimated to the nearest cm) was divided by the respective depth (cm) from which plants were found. These estimates of biovolume were restricted to the last quadrant of the three transects used during habitat assessments and a mean for each site was calculated. We restricted estimates of biovolume to this region of the wetland in order to make it consistent with data that would have been collected by hydroacoustic equipment (e.g. approximately 1.0 m; Weaver et al. 1997). Prior to incorporating biovolume into the INHS, its relationship with other SAV related SI-variables was inspected to determine the degree of auto-correlation.

Results

Multiple logistic regression and AIC model selection identified 7 candidate INHS models within 2 units of the lowest AIC value (Table 4.1). The second ranked AIC model consisted of 5 variables (i.e., proportional abundance of yellow perch, residual species richness of fish, proportional abundance of Cyprinid species, substrate slope of the wetland and stem density ratio of Sub**:**Can SAV; Table 4.1). This 5-variable INHS model yielded scores that had a highly significant logistic fit of the northern Georgian Bay data ($X^2 = 29.871$, $p < 0.001$; odds ratio = 36.0). We could use the model to correctly classify 12 of the 16 (75 %) YOY-Musky and 36 of the 39 (92.3 **%**) No-Musky sites (Figure 4.2) and the ROC plot indicated "very good" discriminatory capacity of this model (AUC = 0.911).

To more appropriately quantify variation in the INHS scores, we manipulated the threshold from the logistic regression when classifying YOY-Musky sites. The ROC analysis indicated that a threshold of 0.70 was associated with the highest sensitivity and lowest false-positive rate among all threshold values. Given our overall objective was to minimize the false-negative rate, we came up with a lower suitability cut-off of 0.60, and break points at 0.70 and 0.80 to derive three suitability categories as follows: (Figure 4.2):

≥ 0.8	high suitability
0.7 – 0.79	moderate suitability
0.6 – 0.69	low suitability
≤ 0.59	no suitability

This framework facilitated interpretation of the scores derived from the 5-variable model so that all of the YOY-Musky sites were correctly identified with at least moderate suitability (INHS score ≥ 0.70; Figure 4.3), while 12 of the 39 No-Musky sites were assessed as being suitable (INHS score ≥ 0.70; Figure 4.3). We applied this 5-variable model to the 2012 data corresponding to sites that had supported YOY historically in southeastern Georgian Bay, and found it successfully classified all of the 2012 sites as having “low” or “no” suitability for YOY muskellunge (Figure 4.4).

Development of Alternative INHS Model

Notwithstanding the relative importance of SAV as a component of suitable habitat for YOY muskellunge (minimum one SAV-related variable within all candidate INHS models; Table 4.1), stem density estimates are rarely available to fishery managers; therefore, we investigated whether or not an alternative INHS model could be developed that did not require use of stem counts (Table 4.2). We found that all logistic regressions of INHS scores resulting from models without a SAV variable were statistically significant ($X^2 \geq 14.60$, $p < 0.001$, for all INHS models; Table 4.2). Nevertheless, only 10 of the 16 (62.5 %) YOY-Musky sites and 36 of the 39 (92.3 **%**) No-Musky sites were correctly classified in northern Georgian Bay. Even so, the AUC value indicated that the models had “reasonable” discriminatory power (AUC < 0.840) when compared with the 5-variable INHS. Based on the ROC of these various INHS models, we found that when the logistic regression threshold was manipulated, a suitability threshold value of 0.6 maximized the number of correctly classified YOY-Musky sites. Using 0.6 as the cut-off to indicate suitability, the INHS model that included all fish variables as well as substrate slope of the wetland (i.e., $\text{INHS}_{\text{No-SAV}}$) identified all YOY-Musky sites correctly, but also had a correspondingly high false-positive rate > 50% (Table 4.2; Figure 4.5). All other

INHS models (see Table 4.2) had relatively low false-negative rates and comparable false-positive rates as the $\mathrm{INHS}_{\mathrm{No\text{-}SAV}}$ when 0.6 was used to indicate suitability (Table 4.2).

To assess the transferability of the INHS models, we applied them to an independent dataset and compared their performance. We found that a 3-variable model that included the proportional abundance of yellow perch, proportional abundance of Cyprinids and substrate slope (i.e., $\mathrm{INHS}_{\mathrm{YP\text{-}CYP\text{-}Slope}}$) was associated with the lowest false-negative rate (12.5 %; Table 4.2; Figure 4.6). All other INHS models had false-negative rates ≥ 25.0 % (Table 4.2), which is unacceptably high considering our conservation goals. Using this INHS model, we were successful in differentiating between YOY-Musky and No-Musky sites within northern and southeastern Georgian Bay (Tukey-HSD, $p < 0.001$), but we also found a significant interaction between site type and region ($F_{1,\,82} = 2.946$, $p = 0.029$; Figure 4.7). In both regions, the mean $\mathrm{INHS}_{\mathrm{YP\text{-}CYP\text{-}Slope}}$ scores for YOY-Musky sites were similarly high (INHS > 0.7: Tukey-HSD, $p > 0.5$), whereas the mean for No-Musky sites was significantly higher for the northern sites than for southeastern Georgian Bay (Tukey-HSD, $p < 0.001$; Figure 4.7).

To further assess the transferability of the $\mathrm{INHS}_{\mathrm{YP\text{-}CYP\text{-}Slope}}$ model, we applied it to a site in eastern Georgian Bay that had supported YOY-Muskellunge, and the 6 other wetlands sampled in an identical fashion that were not known to have supported YOY muskellunge. The $\mathrm{INHS}_{\mathrm{YP\text{-}CYP\text{-}Slope}}$ correctly classified the one YOY-Musky site as being suitable ($\mathrm{INHS}_{\mathrm{YP\text{-}CYP\text{-}Slope}} = 0.65$), and the 6 other eastern Georgian Bay wetlands as being unsuitable (Figure 4.8).

Compared to all other INHS models that excluded SAV variables, we found that the $\text{INHS}_{\text{YP-CYP-Slope}}$ to be the most accurate for classifying YOY nursery habitat (14 of the 16 correctly classified). It was able to detect changes in habitat suitability for sites in southeastern Georgian Bay, even though it had been derived with data from northern Georgian Bay; however, because of the greater variability in INHS scores, we had to use a lower suitability threshold (0.6) than that used for the 5-variable INHS (0.7). Nevertheless, this 3-variable INHS failed to classify 2 YOY-Musky sites as being suitable in each region of Georgian Bay (Table 4.2; Figure 4.6).

We found YOY-Musky sites associated with a significantly higher biovolume ($\bar{x}$ ± S.E.: 49.0 ± 2.4%; n = 14) than at No-Musky sites ($\bar{x}$ ± S.E.: 32.9 ± 1.9%; n = 37; $t_{49} = 4.701$, $p < 0.001$), and that YOY muskellunge were never found at sites with biovolumes < 30% or > 70%. Additionally, we found that biovolume was significantly correlated with all SI-variables related to macrophytes: positively related to stem density of Can SAV ($r = 0.609$, $p < 0.0001$), negatively related to stem density ratio (Sub**:**Can SAV), and negatively related to the proportional abundance of *V. americana* SI-variables ($r < -0.464$, $p < 0.001$). When biovolume was substituted into the 5-variable INHS, we found a significant logistic relationship ($X^2 = 23.302$, $p < 0.001$, odds ratio = 20.6) that correctly classified 10 of the 14 (71.4%) YOY-Musky and 33 of the 37 (89.2%) No-Musky sites. The INHS with biovolume appeared to have very "reasonable" discriminatory capacity (AUC = 0.898) and the ROC plot indicated that a suitability threshold of 0.7 was still optimal for minimizing the false-negative rate. Using this threshold, 13 of the 14 YOY-

Musky sites (92.3%) were correctly classified while 9 of the 37 No-Musky sites were assessed as being suitable (INHS ≥ 0.70; Figure 4.9).

Discussion

Of the models we tested, the 5-variable model performed best, even when compared with models that included all seven variables. This 5-variable INHS included three variables related to fish (proportional abundance of yellow perch, residual species richness of fish, proportional abundance of Cyprinid species), one related to site geomorphology (substrate slope) and one related to the macrophyte community (Sub**:**Can SAV ratio). Information to populate the first four variables would have to be collected by fishery biologists in the field or, for substrate slope from existing digital elevation models. The last variable, however, may require additional expertise and effort to collect, but since it can be substituted with biovolume, fisheries biologists can estimate this using hydroacoustic technology (Weaver et al. 1997; Valley et al. 2005) without having to count stems of plant taxa. Another reason why we recommend this 5-variable INHS model is because it had very good discriminatory power (i.e. AUC value) when applied to the northern Georgian Bay data, being able to correctly classify all 16 of the YOY-Musky sites. When we applied this model to the 2012 data from southeastern Georgian Bay, all of the No-Musky sites were also correctly classified as being unsuitable (Leblanc et al. 2014).

All things considered, the 5-variable INHS is the one that we recommend to fisheries biologists to index suitability of habitat for YOY muskellunge. If, however, SAV information is unavailable, then we recommend the 3-variable $\text{INHS}_{\text{YP-CYP-Slope}}$ because this was able to identify suitable nursery habitat with a respectable false-negative rate < 13%, and correctly identified sites in southeastern Georgian Bay as being unsuitable when we were no longer able to find YOY muskellunge in any of the historic nursery sites in 2012 (Figures 4.4 and 4.6). While both models can correctly identify YOY-Musky sites, addition of SAV-related variables decreased the false positive rate by 23% (31% vs 54% for the 5-variable INHS and the $\mathrm{INHS}_{\mathrm{YP\text{-}CYP\text{-}Slope}}$ model, respectively), and this increased level of sensitivity is likely more acceptable in jurisdictions where development pressures are high.

Cook and Solomon (1987) developed a Habitat Suitability Index (HSI) that considered all life stages of the muskellunge. This model was developed for both small inland lakes as well as larger coastal systems up to 10 000 ha (Cook and Solomon 1987). It has not yet been applied to a system as large as Georgian Bay, with a surface area ~15 000 km^2. We compared the usefulness of this HSI model against our two INHS models. According to Cook and Solomon (1987), habitat for adult life stages are rarely limiting in large systems and therefore, we focused on their four proposed SI-variables for early life stages. The 4 SI-variables were (1) a decline in water levels between April and June (2) adequate dissolved oxygen concentration (DO) at the substrate-water interface (3) abundance of coastal wetlands and (4) adequate percentage cover of macrophytes.

These 4 SI-variables were difficult to apply to Georgian Bay. For example, the first SI variable could not be a limiting factor because water levels in Georgian Bay usually increase between April and early-June rather than decline, and are therefore suitable for promoting egg and larval survival (Cook and Solomon 1987). Dissolved oxygen at the substrate-water interface in wetlands of eastern and northern Georgian Bay are unlikely to be limiting because wetlands are at saturated oxygen concentrations

(Cvetkovic and Chow-Fraser 2011), levels that should not interfere with development of muskellunge eggs (Dombeck et al. 1984; Cook and Solomon 1987; Zorn et al. 1998). Both of the last two SI variables are too coarse to be applied to Georgian Bay, because virtually the entire eastern and northern shoreline of Georgian Bay are lined with abundant small wetlands (< 2 ha; Midwood et al. 2012) that have high percent cover of macrophytes (Croft and Chow-Fraser 2007; 2009). Therefore, although some metric of the plant community is no doubt an important component of habitat for YOY muskellunge (Murry and Farrell 2007, Kapuscinski and Farrell 2014; Leblanc and Chow-Fraser 2015, CH3), prior to our INHS models, there was no standardized way to quantify this for suitability assessment in Georgian Bay.

Since introduction of the HSI proposed by Cook and Solomon (1987), advances have been made to identify whole lake (e.g., Rust et al. 2002) and within-lake features (e.g., Nohner and Diana 2015) that can predict the self-sustaining status of muskellunge populations. Most efforts have focused on predicting the spawning locations selected by muskellunge. For instance, Nohner and Diana (2015) developed a GIS-based model to predict spawning sites selected by muskellunge within relatively small (50 ha) and large (1 500 ha) inland lakes of Wisconsin from remotely sensed information. Additionally, Crane et al. (2014) developed a model of the micro-habitat features related to the spawning locations selected by muskellunge in the Niagara River. Although specific features from the micro-habitat of the spawning sites appeared to differ greatly between lacustrine and riverine systems, and among the trophic status of inland lakes (e.g., Crane et al. 2014; Nohner and Diana 2015), the suitability of spawning habitat is consistently interpreted to provide appropriate dissolved oxygen levels (Dombeck et al. 1984; Zorn et al. 1998; Rust et al. 2002; Crane et al. 2014; Nohner and Diana 2015), which, as mentioned earlier, does not appear limiting in Georgian Bay.

There is no doubt that dissolved oxygen is important for muskellunge recruitment and identifying locations that muskellunge use for spawning is a necessary management strategy. Suitability of muskellunge spawning and nursery habitats, however, likely reflects different requirements for egg and YOY survival within the same wetland. Consistent with others who have suggested that spawning and nursery habitats are spatially linked (LaPan et al. 1996; Farrell et al. 2007), we also found that nursery sites occurred in close proximity (< 30 m to 1 km) to their presumed spawning sites (Weller et al. 2015). Furthermore, adults of muskellunge have shown high fidelity to particular spawning areas within a large region (Jennings et al. 2011). In Georgian Bay, for instance, muskellunge appear to have used very specific spawning sites within the Severn Sound region over a period of three decades (Weller et al. 2015), and continue to use wetlands that have nursery habitats with poor suitability (Leblanc et al. 2014). It remains unclear, however, if models developed to predict spawning-site selection can account for the requirements of spatially linked nursery habitats and site-fidelity behaviour of muskellunge in Georgian Bay. Thus, managers can more appropriately assess the self-sustaining capacity of muskellunge in Georgian Bay by using the INHS models to inspect the suitability of nursery sites near muskellunge spawning sites.

Management Implications

The recent and unprecedented period of sustained low water levels in Lakes Huron-Michigan (Sellinger et al. 2008) is one of the main threats to the quality (i.e., less diverse macrophyte and fish communities; Midwood and Chow-Fraser 2012) and quantity (i.e., lost access to wetlands by fish; Fracz and Chow-Fraser 2013) of wetland habitat in eastern Georgian Bay. The low water levels are also likely impacting the suitability of other coastal wetland used by muskellunge for early-life habitats because the aquatic plant community depends in large part on water-level fluctuations (Keddy and Reznicek 1986; Wilcox and Meeker 1991; Midwood and Chow-Fraser 2012). With expected changes in water-level regimes within the Great Lakes over the next 50 years due to global climate change (Angel and Kunkel 2010), Great Lakes fishery managers everywhere, but particularly those in Georgian Bay, are in urgent need of tools that can help them screen for suitable habitat for YOY muskellunge, and to assess how the suitability of the habitat would change in response to different water-level scenarios.

The INHS models proposed here provide a means to predict potential changes in the suitability of nursery habitat over time. By accounting for the response of macrophytes to water levels and the nearshore bathymetry, managers will have an indication of the potential suitability of nurseries near identified spawning sites under multiple water-level scenarios. Thus, managers can apply the INHS at locations with suspected declines in nursery suitability to determine if YOY muskellunge are present, the suitability status of the wetland, and potential rehabilitative efforts. The labour-intensive requirement to populate the INHS and the vast distribution of small coastal wetlands in Georgian Bay (Midwood et al. 2012), likely makes it impractical to index the suitability of nursery habitat from all early-life habitats used by muskellunge. It may therefore be more appropriate to establish sentinel sites at known early-life habitats used by muskellunge to be monitored on a regular basis. By stratifying sentinel sites to reflect the gradient of nearshore bathymetries within Georgian Bay, the recruitment potential of the various sub-populations of muskellunge in Georgian Bay can be assessed under different water level scenarios. Furthermore, the INHS models have the potential to promote restoration efforts by identifying and indexing wetlands with a higher likelihood of promoting early-life survival if stocking initiatives are deemed necessary.

Broad-scale approaches used to model a species' response to environmental change is no doubt necessary for conservation purposes (e.g., Species Distribution Models (SDM); Guisan and Thuiller 2005) and preferable than a site-specific assessment tool. Species distribution models typically operate at regional or global scales and include remotely sensed information that is easily accessible to populate the model. However, many SDM models use variables that are often indirect measures of ecological relationships assumed to structure a species' distribution (Guisan and Zimmermann 2000). As a result, SDM models can be practical by providing an inventory of potentially suitable habitat (e.g., Nohner and Diana 2015), but may lack the precision and resolution needed to identify underlying ecological relationships operating at the site level that accommodate requirements most limiting to a species (Randin et al. 2006). Ultimately, a regional SDM for Georgian Bay would have to account for processes that structure a suitable macrophyte community in the wetland and the life-history traits (spawning site fidelity) that likely increase the muskellunge's vulnerability to failed natural recruitment. Until then, the site-specific INHS models developed here, even though more labour intensive, are the most appropriate tools to satisfy management needs for muskellunge in Georgian Bay and to guide rehabilitative actions that appear to be necessary in southeastern Georgian Bay (Leblanc et al. 2014). Finally, we recommend that our proposed INHS models be used as a foundation on which to build a more regional model for Georgian Bay that is based on the ecological relationships identified to promote suitable early-life habitat for muskellunge.

Acknowledgments

We wish to thank Dan Weller, Chris Biberhofer and members of the Chow-Fraser lab and field technicians for their assistance with data collection between 2012 and 2014. We are indebted to Harvey and Lorna Meirke, Jerry Burke, and Pitfields General Store for providing lodging and boats while we were sampling in northern Georgian Bay. We are also grateful to the Ontario Ministry of Natural Resources and Forestry for their logistical support, advice and guidance when developing the HSI models. This project was funded in part by a research grant from the Sierra Club Canada Foundation, the Ontario Ministry of Natural Resources through the Canada-Ontario Agreement, the Ontario Graduate Scholarship Fund, The Dr. Ed. Crossman Scholarship Fund from Muskies Canada Inc., grants from the Great Lakes Basin Conservancy, and charitable contributions from the Georgian Bay Musky Association.

References

Ahmadi-Nedushan B, St-Hilaire A, Berube M, Robichaud E, Thiemonge N, Bobee B (2006). A review of statistical methods for the evaluation of aquatic habitat suitability for instream flow assessment. River Research and Applications 22: 503-523

Angel JR, Kunkel KE (2010). The response of Great Lakes water levels to future climate scenarios with an emphasis on Lake Michigan-Huron. Journal of Great Lakes Research 36: 51-58

Cook MF, Solomon RC (1987). Habitat suitability index models: muskellunge. U.S. Fish and Wildlife Service Biol. Rep. 82 (10.148). 33 pp. retrieved from http://www.nwrc.usgs.gov/wdb/pub/hsi/hsi-148.pdf

Craig RE, Black RM (1986). Nursery habitat of muskellunge in southern Georgian Bay, Lake Huron, Canada. American Fisheries Society Special Publication 15. Pp. 79–86, *in* Hall

Crane DP, Farrell JM, Kapuscinski KL (2014). Identifying important micro-habitat characteristics of muskellunge spawning locations in the upper Niagara River. Journal of Great Lakes Research 40: 325-335

Croft MV, Chow-Fraser P (2007). Use and development of the Wetland Macrophyte Index to detect water quality impairment in fish habitat of Great Lakes coastal marshes. Journal of Great Lakes Research 33: 172-197

Croft MV, Chow-Fraser P (2009). Non-random sampling and its role in habitat conservation: a comparison of three wetland macrophyte sampling protocols. Biodiversity and Conservation 18: 2283-2306

Cvetkovic M, Chow-Fraser P (2011). Use of ecological indicators to assess the quality of Great Lakes coastal wetlands. Ecological Indicators 11:1609-1622

Cvetkovic M, Kostuk K, Chow-Fraser P (2012). Gear-type influences on fish catch and a wetland fish index in Georgian Bay wetlands. North American Journal of Fisheries Management 32: 313-324

De Kerckhove DT, Smokorovski KE, Randall RG (2008). A primer on fish habitat models. Canadian Technical Report of Fisheries and Aquatic Sciences 2817: vi + 65 p

Dombeck MP, Menzel BW, Hinz PN (1984). Muskellunge spawning habitat and reproductive success. Transactions of the American Fisheries Society 113: 205–216

Farrell JM, Klindt RM, Casselman JM, LaPan SR, Werner RG, Schiavone A (2007). Development, implementation, and evaluation of an international muskellunge management strategy for the upper St Lawrence River. Environmental Biology of Fishes 79: 111-123

Fielding AH, Bell JF (1997). A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation 24: 38-49

Fracz A, Chow-Fraser P (2013). Impacts of declining water levels on the quantity of fish habitat in coastal wetlands of eastern Georgian Bay, Lake Huron. Hydrobiologia 705: 151-169

Guisan A, Thuiller W (2005). Predicting species distribution: offering more than simple habitat models. Ecology letters 8: 993-1009

Guisan A, Zimmermann NE (2000). Predictive habitat distribution models in ecology. Ecological Modelling 135: 147-186

Jennings MJ, Hatzenbeler GR, Kampa JM (2011). Spring capture site fidelity of adult muskellunge in inland lakes. North American Journal of Fisheries Management 31: 461-467

Kapuscinski KL, Farrell JM (2014). Habitat factors influencing fish assemblage at muskellunge nursery sites. Journal of Great Lakes Research 40: 135-147

Kapuscinski KL, Farrell JM, Murry BA (2012). Feeding strategies and diets of Young-of-the-year muskellunge from two large river ecosystems. North American Journal of Fisheries Management 32: 635-647

Kapuscinski KL, Farrell JM, Wilkinson MA (2014). Trends in muskellunge population and fishery characteristic in Buffalo Harbor (Lake Erie) and the Niagara River. Journal of Great Lakes Research 40: 125-134

Keddy P, Reznicek A (1986) Great Lakes vegetation dynamics: the role of fluctuating water levels and buried seeds. Journal of Great Lakes Research 12: 25–36

Kerr SJ (2007). Characteristics of Ontario Muskellunge (*Esox masquinongy*) fisheries based on volunteer angler diary information. Environmental Biology of Fishes 79: 61-69

Kerr SJ, Kirkpatrick A, Haxton TJ (2011). Characteristics of trophy-sized muskellunge (*Esox masquinongy*) angled from Ontario waters, 1917-2010. Fisheries Policy Section, Biodiversity Branch. Ontario Ministry of Natural Resources. Peterborough, Ontario. 7 p. + appendices.

LaPan SR, Schiavone A, Werner RG (1996). Spawning and post-spawning movements of the St. Lawrence River muskellunge (*Esox masquinongy*). In Managing muskies in the '90s. Workshop Proceedings [eds. Kerr, S. J. and C. H. Olver]. Ontario Ministry of Natural Resources, Southern Region Science and Technology Transfer Unit Workshop Proceedings WP-007. Pp. 73-82

Leblanc JP, Chow-Fraser P (2015, CH3). Nearshore ecosystem features predict suitability of muskellunge nursery habitats in Georgian Bay, Lake Huron (Chapter 3)

Leblanc JP, Weller JD, Chow-Fraser P (2014). Thirty-year update: Changes in biological characteristics of degraded muskellunge nursery habitat in southern Georgian Bay, Lake Huron, Canada. Journal of Great Lakes Research 40: 870-878

Leblanc JP, Weller JD, Chow-Fraser P (2015, CH2). Similarities in fish communities between muskellunge nursery sites from two adjoining embayments in northern Georgian Bay, Lake Huron (Chapter 2)

Liskauskas AP (2007). Severn Sound muskellunge population assessment survey, 2007. Upper Great Lakes Management Unit, Ontario Ministry of Natural Resources. Unpublished technical report. 9pp

Manel S, Williams HC, Ormerod SJ (2001). Evaluating presence-absence models in ecology: the need to account for prevalence. Journal of Applied Ecology 38: 921-931

Midwood JD, Chow-Fraser P (2012). Changes in aquatic vegetation and fish communities following 5 years of sustained low water levels in coastal marshes of eastern Georgian Bay, Lake Huron. Global Change Biology 18: 93-105

Midwood JD, Rokitnicki-Wojcik D, Chow-Fraser P (2012). Development of an inventory of coastal wetlands for eastern Georgian Bay, Lake Huron. International Scholarly Research Network (ISRN Ecology) 2012: 1-13

Murry BA, Farrell JM (2007). Quantification of native muskellunge nursery habitat: influence of body size, fish community composition, and vegetative structure. Environmental Biology of Fishes 79: 37-47

Nohner JK, Diana JS (2015). Muskellunge spawning site selection in northern Wisconsin Lakes and a GIS-based predictive habitat model. North American Journal of Fisheries Management 35: 141-157

Pearce J, Ferrier S (2000). Evaluating the predictive performance of habitat models developed using logistic regression. Ecological Modelling 133: 225-245

Randin CF, Dirnbock T, Dullinger S, Zimmermann NE, Zappa M, Guisan A (2006). Are niche-based species distribution models transferable in space? Journal of Biogeography 22: 1689-1703

Rust AJ, Diana JS, Margenau TL, Edwards CJ (2002). Lake characteristics influencing spawning success of muskellunge in northern Wisconsin Lakes. North American Journal of Fisheries Management 22: 834-841

Sellinger C, Stow C, Lamon E, Qian S (2008). Recent water level declines in the Lake Michigan−Huron system. Environmental Science & Technology 42: 367–373

StatSoft, Inc. (2007). STATISTICA (data analysis software system), version 8.0. www.statsoft.com.

Szendrey TA, Wahl DH (1996). Size-specific survival and growth of stocked muskellunge: effects of predation and prey availability. North American Journal of Fisheries Management 16: 395-402

US Fish and Wildlife Service (1981). Standards for the development of suitability index models. Ecology Service Manual 103, U.S. Fish and Wildlife Service, Division of Ecological Sciences, Washington, DC, USA

Valley RD, Drake MT, Anderson CS (2005). Evaluation of alternative interpolation techniques for the mapping of remotely-sensed submersed vegetation abundance. Aquatic Botany 81: 13-25

Wagner CP, Weber MJ, Wahl DH (2015). Structural complexity influences littoral coarse woody habitat selection by juvenile muskellunge. North American Journal of Fisheries Management 35: 14-19

Wahl DH (1999). An ecological context for evaluating the factors influencing muskellunge stocking success. North American Journal of Fisheries Management 19: 238-248

Wahl DH, Stein RA (1988). Selective predation by three esocids: the role of prey behavior and morphology. Transaction of the American Fisheries Society 117: 142-151

Weaver MJ, Magnuson JJ, Clayton MK (1997). Distribution of littoral fishes in structurally complex macrophytes. Canadian Journal of Fisheries and Aquatic Sciences 54: 2277-2289

Weller JD, Leblanc JP, Liskauskas A, Chow-Fraser P (2015). Spawning-site fidelity in sub-populations of muskellunge in Georgian Bay: Implications of habitat loss. Transactions of the American Fisheries Society (in submission)

Wilcox DA, Meeker JE (1991). Disturbance effects on aquatic vegetation in regulated and unregulated lakes in northern Minnesota. Canadian Journal of Botany 69: 1542–1551

Zorn SA, Margenau TL, Diana JS, Edwards CJ (1998). The influence of spawning habitat on natural reproduction of muskellunge in Wisconsin. Transactions of the American Fisheries Society 127: 995-1005

Table 4.1. Multiple logistic regression with AIC model selection of the suitability index (SI) variables used to predict the occurrence of YOY muskellunge. Ranks of models are sorted according to ascending AIC values, with the 7-variable model (i.e., Full) presented for reference. CYP = proportional abundance of cyprinids; RICH = residual fish species richness; Slope = substrate slope; Sub:CanSAV= ratio of stem densities of substrate to canopy SAV; YP = proportional abundance of yellow perch; *VALL* = proportional abundance of *Vallisneria americana*; and CanSAV = stem density of canopy structuring SAV. Respective Chi^2 and *p*- values are shown from the logistic regression for each IHSI model.

	SI-Variables Included										
Rank	CYP	RICH	Slope	Sub:CanSAV	YP	VALL	CanSAV	**# of Variables**	**AIC value**	**Chi^2**	***p***
1	○	○	○	○				4	46.72	29.61	< 0.0001
2	○	○	○	○	○			5	47.44	30.88	< 0.0001
3	○	○	○	○		○		5	47.54	30.78	< 0.0001
4	○	○	○	○	○	○		6	48.42	31.90	< 0.0001
5	○	○		○	○	○		5	48.65	29.68	< 0.0001
6	○	○		○		○		4	48.68	27.65	< 0.0001
7	○	○	○	○			○	5	48.71	29.61	< 0.0001
16 (Full)	○	○	○	○	○	○	○	7	50.42	31.91	< 0.0001

Table 4.2. Comparison of false-negatives (i.e. nursery sites classified as not suitable) and false positives (i.e. non-nursery sites classified as suitable) associated with various INHS models developed without SAV-related variables and applied to data collected in northern (i.e., calibration) and southeastern (i.e., validation) Georgian Bay. Receiver Operating Characteristic plots from the various INSH models from the northern Georgian Bay data was subsequently used to derive INHS scores to interpret suitable nursery habitat for muskellunge (INHS ≥ 6.0).

	INHS Name	**Variables Included**	**False-Negative (%)**	**False-Positive (%)**
Northern Georgian Bay	$\mathrm{INHS}_{\text{No-SAV}}$	YP, CYP, RICH, Slope	0.0	51.3
	$\mathrm{INHS}_{\text{YP-CYP-Rich}}$	YP, CYP, RICH	6.3	56.4
	$\mathrm{INHS}_{\text{YP-CYP-Slope}}$	YP, CYP, Slope	12.5	53.8
	$\mathrm{INHS}_{\text{YP-Rich-Slope}}$	YP, RICH, Slope	12.5	59.0
	$\mathrm{INHS}_{\text{CYP-Rich-Slope}}$	CYP, RICH, Slope	18.8	43.6
Southeastern Georgian Bay	$\mathrm{INHS}_{\text{YP-CYP-Slope}}$	YP, CYP, Slope	12.5	18.8
	$\mathrm{INHS}_{\text{YP-Rich-Slope}}$	YP, RICH, Slope	25.0	12.5
	$\mathrm{INHS}_{\text{No-SAV}}$	YP, CYP, RICH, Slope	31.3	18.8
	$\mathrm{INHS}_{\text{YP-CYP-Rich}}$	YP, CYP, RICH	37.5	18.8
	$\mathrm{INHS}_{\text{CYP-Rich-Slope}}$	CYP, RICH, Slope	56.3	12.5

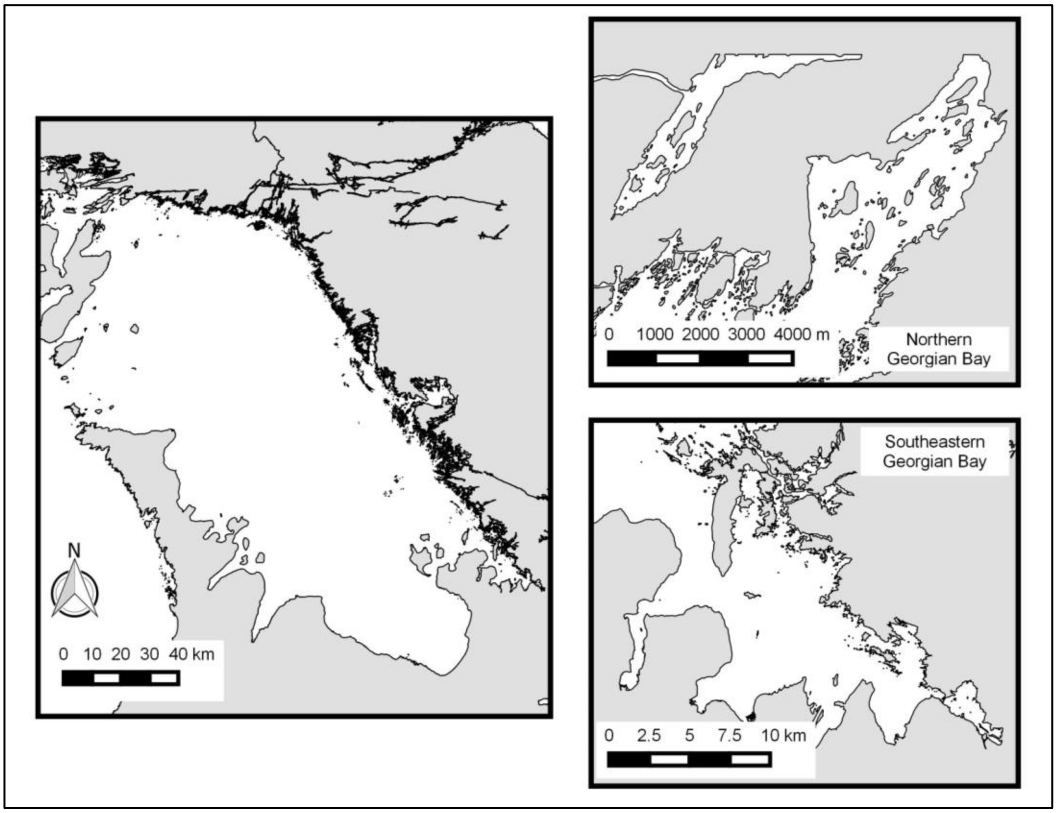


Figure 4.1. Location of study sites in northern and southeastern Georgian Bay. Data collected in northern Georgian Bay were used to create the INHS models (see Leblanc et al. 2015, CH2), and was applied to independent data from southeastern Georgian Bay (see Leblanc et al. 2014 for study site description) to determine the transferability of the INHS models throughout Georgian Bay.

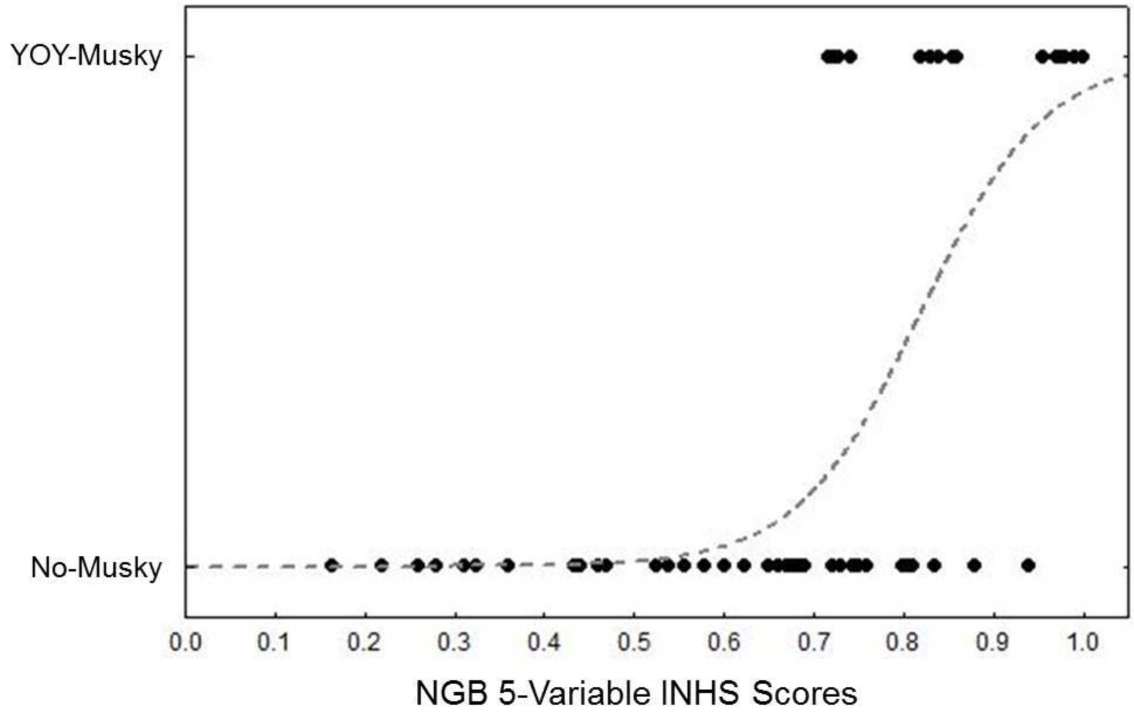


Figure 4.2. Logistic regression of the scores associated with the 5-Variable INHS model for the northern Georgian Bay (NGB) data. A significant logistic fit was observed ($X^2 = 29.871$, $p < 0.001$**;** odds ratio = 36.0) where 75 % of the YOY-Musky sites (12 of 16) and 92.3 % of the No-Musky sites (36 of 39) were correctly classified. We interpret INHS scores ≥ 0.7 to be “good” to “excellent” suitability, scores 0.6 – 0.69 to have “limited” suitability, whereas scores ≤ 0.59 to have “poor” suitability.

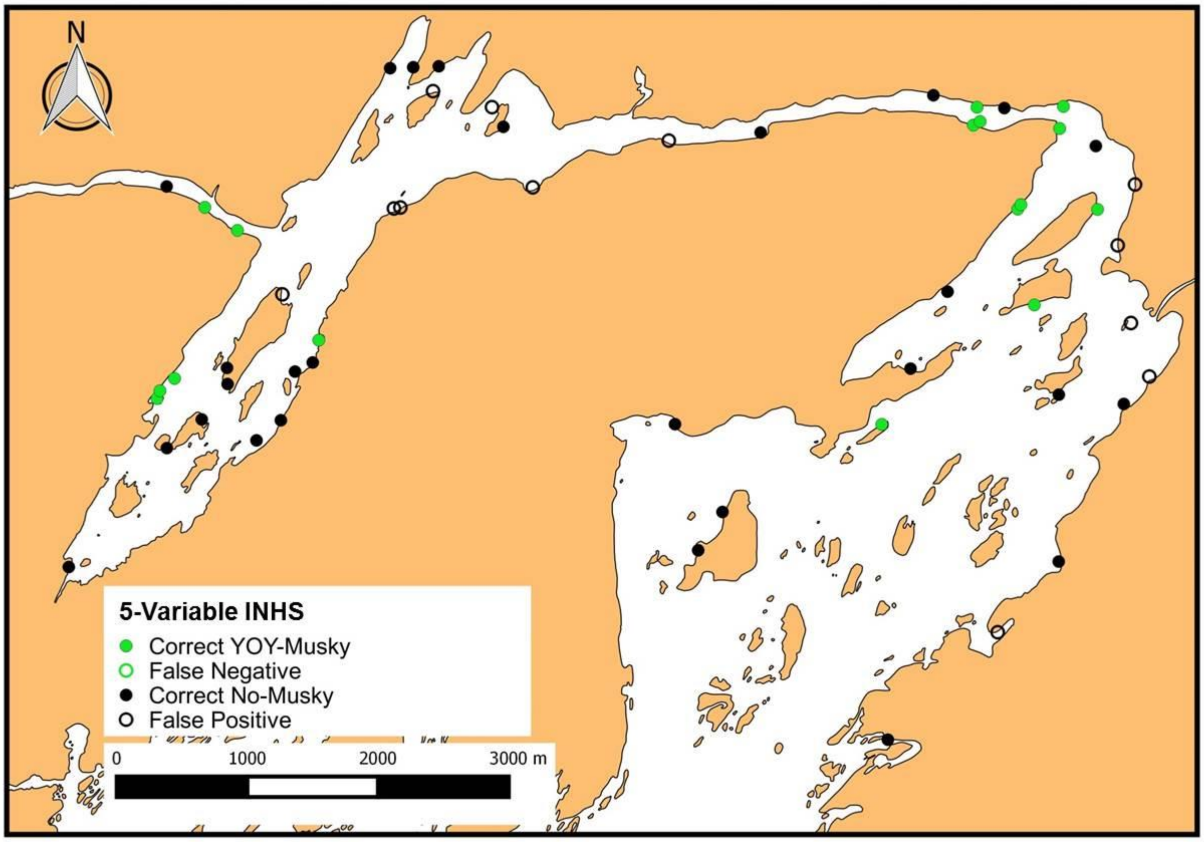


Figure 4.3. 5-Variable INHS applied to northern Georgian Bay data. All YOY-Musky sites were identified as such (HSI score ≥ 0.70). Twelve of 39 No-Musky sites were classified as YOY-Musky sites (i.e., False Positive).

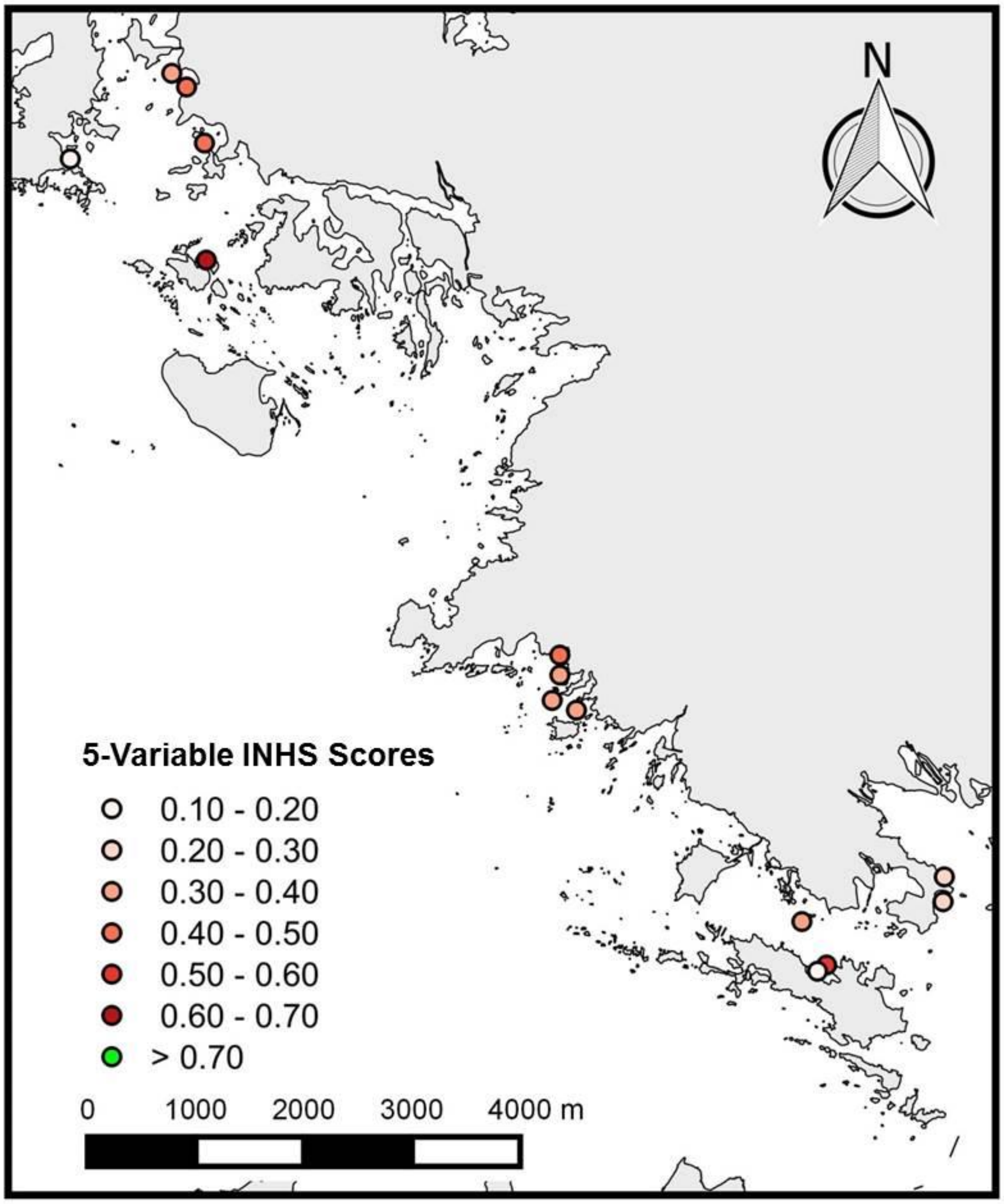


Figure 4.4. 5-Variable INHS applied to the 2012 data from southeastern Georgian Bay. All sites were correctly identified as No-Musky sites (INHS score < 0.70).

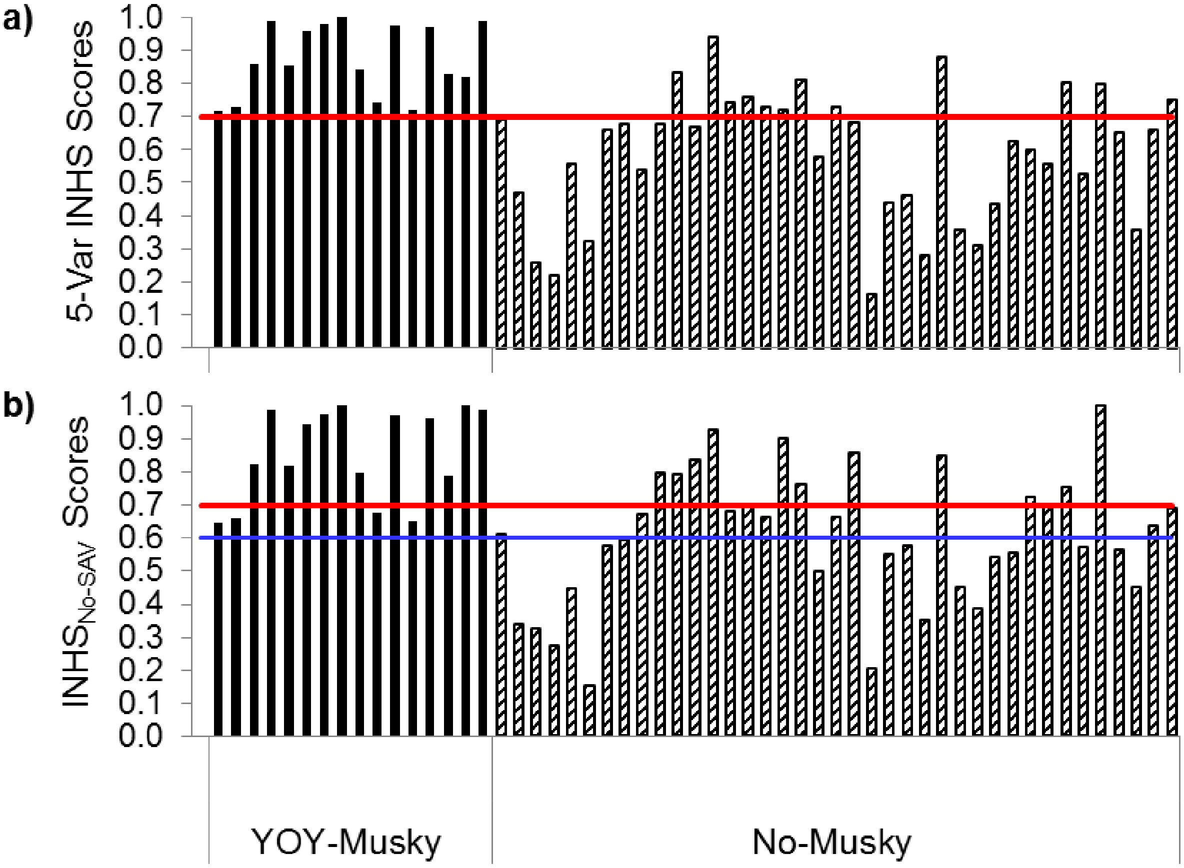


Figure 4.5. INHS scores for the YOY-Musky sites (solid black bars; n = 16) and No-Musky sites (black and white bars; n = 39) from northern Georgian Bay determined with the (**a**) 5-variable model and (**b**) $INHS_{No-SAV}$ model. Overlaying the figures are the INHS thresholds (red line = INHS ≥ 0.7 and blue line = INHS ≥ 0.6) used to identify suitable nursery habitat for both INHS models. Sites with INHS scores touching or above the respective horizontal lines were deemed suitable habitat for YOY muskellunge. To minimize the false negative rate in Figure (**b**), the threshold had to be lowered from 0.7 (red line) to 0.6 (blue line), but this elevated the false-positive rate.

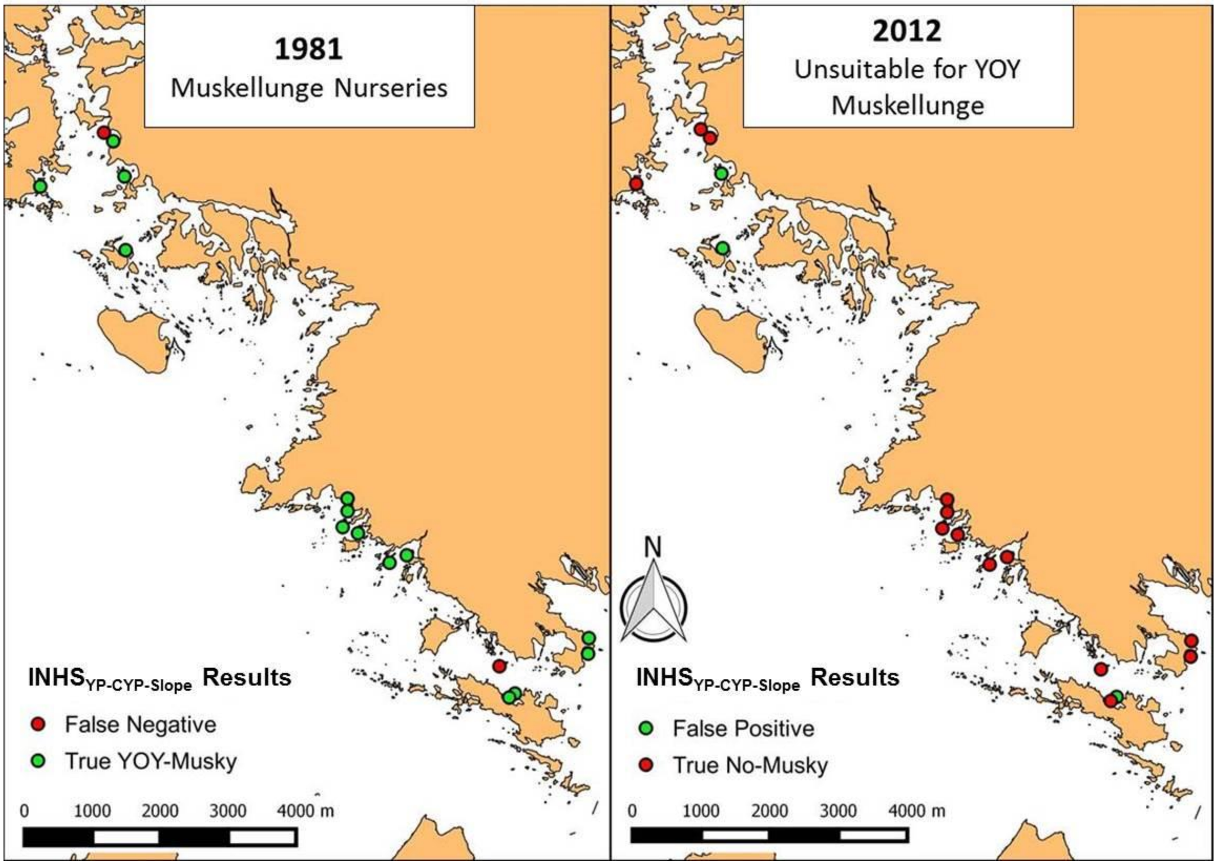


Figure 4.6. Application of INHS$_{YP\text{-}CYP\text{-}Slope}$ to data associated with historic nursery habitat identified in 1981 (Craig and Black 1986) and to sites that were no longer deemed suitable and did not support YOY muskellunge (Leblanc et al. 2014). False Negative has INHS score < 0.60 whereas False Positive has INHS score ≥ 0.60.

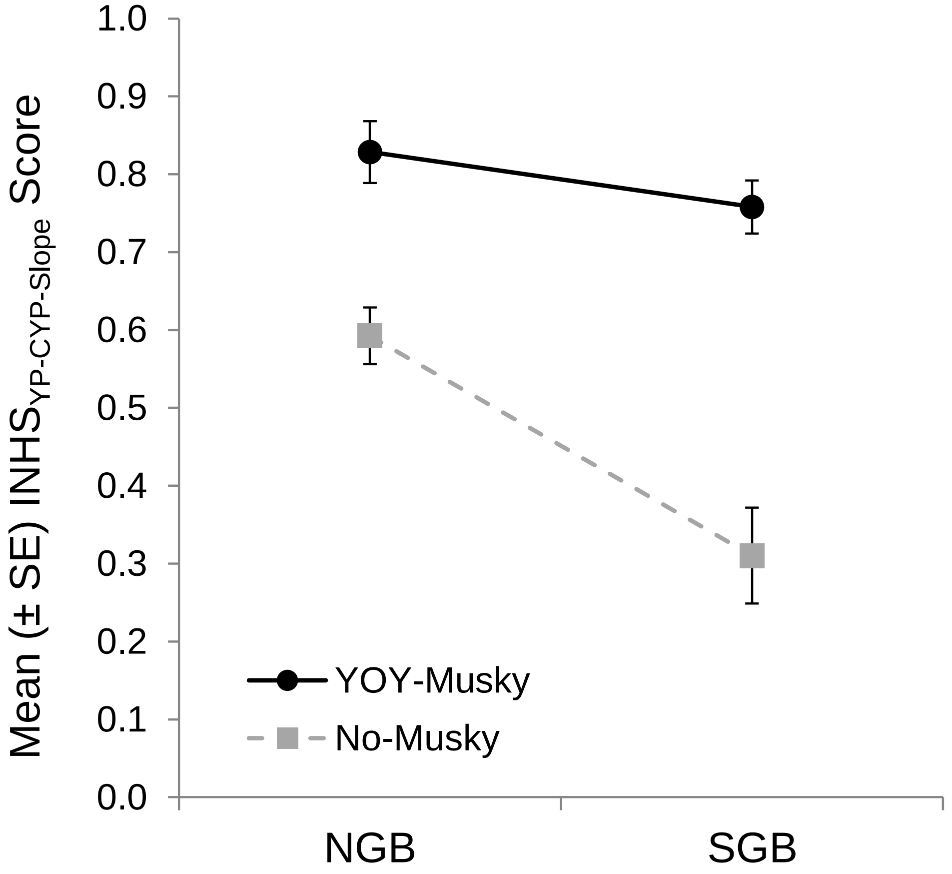


Figure 4.7. Mean (± S.E.) INHS$_{YP\text{-}CYP\text{-}Slope}$ scores associated with YOY-Musky and No-Musky sites from respective northern (NGB) and southeastern (SEGB) Georgian Bay. A two-way analysis of variance indicated a significant interaction ($F_{1,\,82} = 2.946$, $p = 0.029$). YOY-Musky sites did not differ between regions (Tukey-HSD, $p > 0.5$), but both were significantly higher than the No-Musky sites, regardless of region (Tukey-HSD, $p < 0.05$). Southeastern Georgian Bay No-Musky sites had significantly lower INHS$_{YP\text{-}CYP\text{-}Slope}$ than did the No-Musky sites in northern Georgian Bay (Tukey-HSD, $p < 0.05$).

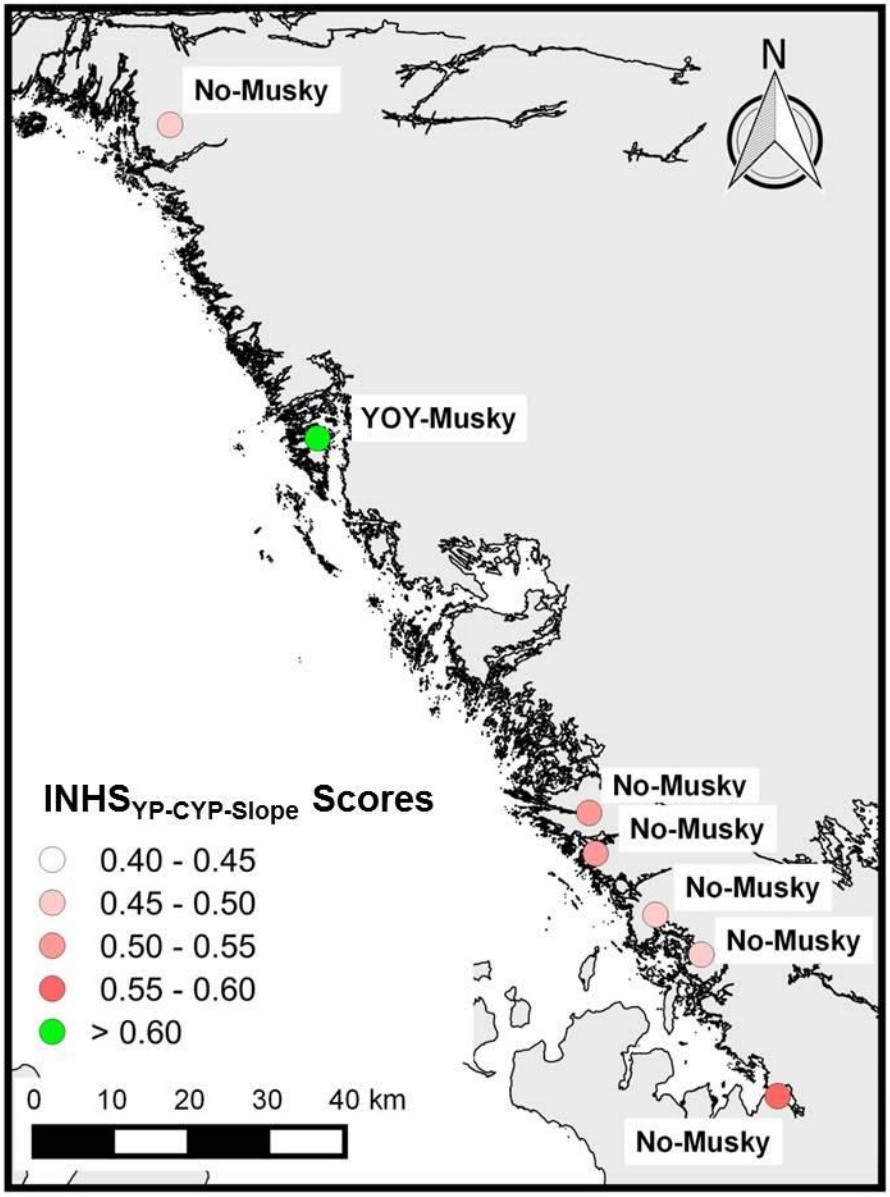


Figure 4.8. INHS$_{YP\text{-}CYP\text{-}Slope}$ scores of the only other confirmed muskellunge nursery sites (YOY-Musky) in eastern Georgian Bay and 6 randomly selected wetlands along eastern Georgian Bay that showed no evidence of being used by muskellunge (No-Musky). INHS$_{YP\text{-}CYP\text{-}Slope}$ scores ≥ 0.60 were considered suitable for YOY muskellunge. Wetland names, from south to north, are Matchedash Bay, Ganyon Bay, Longuissa Bay, Tadenac Bay 2, Hole in the Wall, Hermann's Bay and Key River.

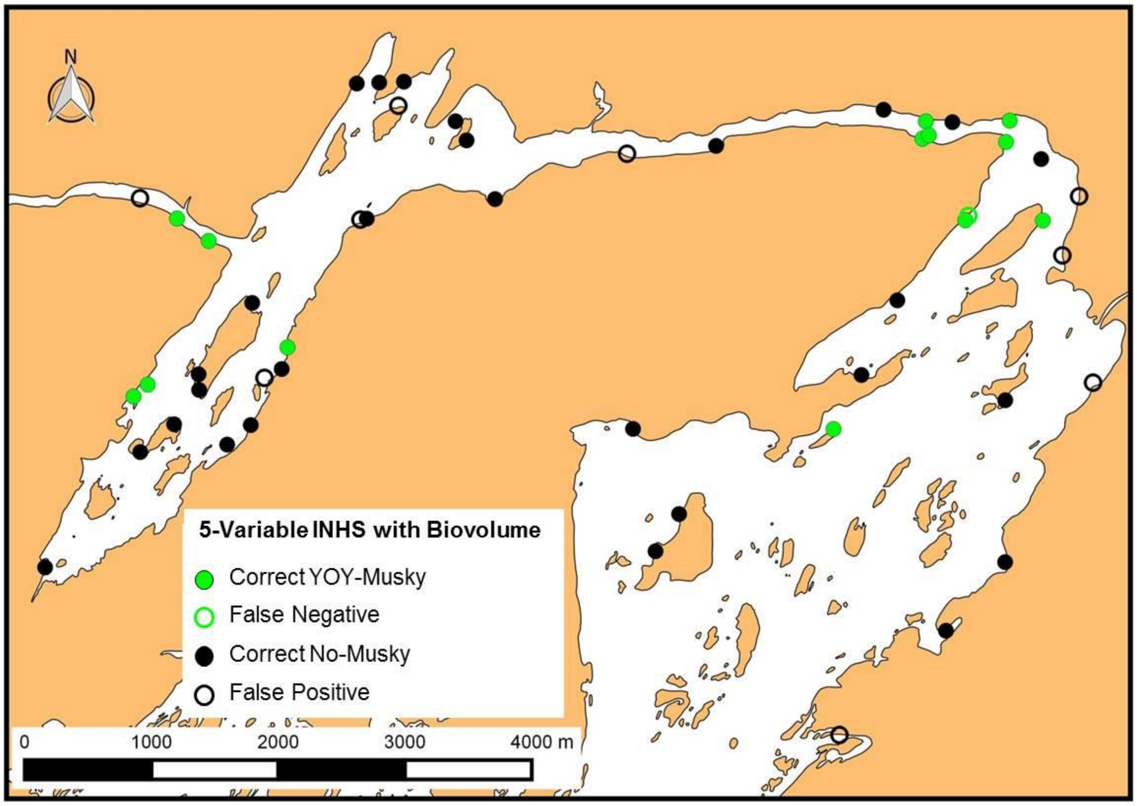
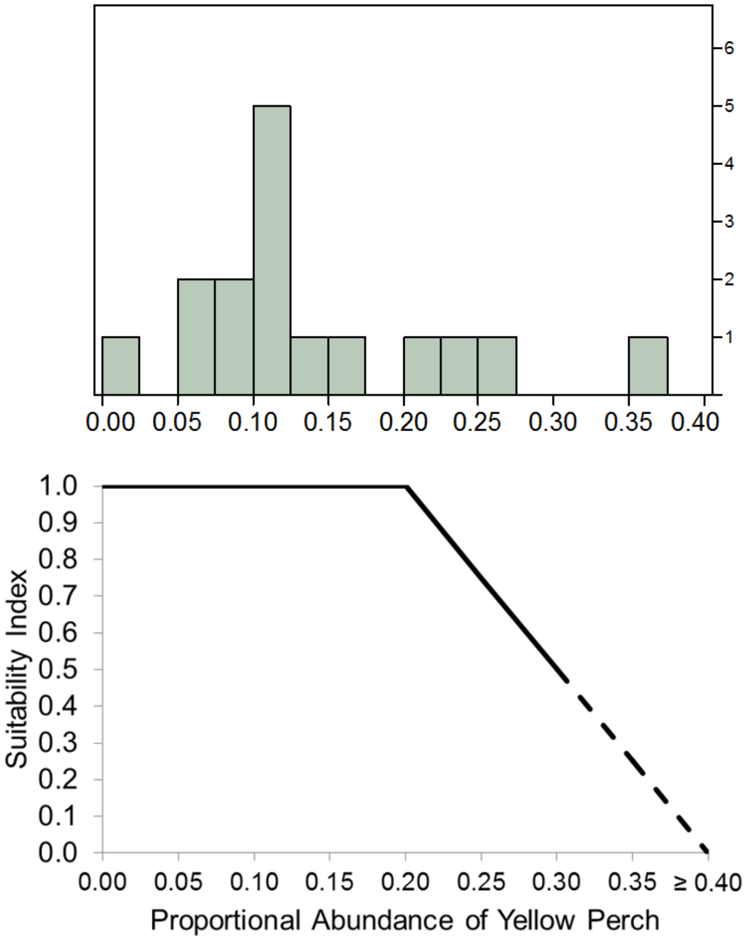


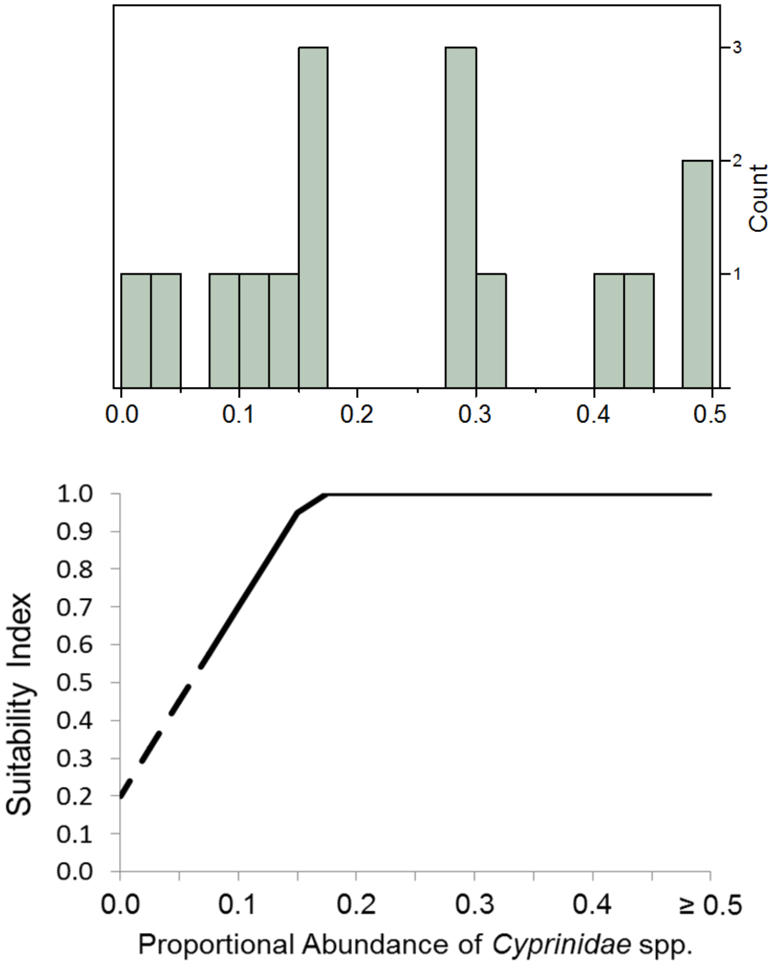
Figure 4.9. 5-variable INHS with biovolume substituted for the SAV variable applied to the northern Georgian Bay data. When an INHS score ≥ 0.70 was used to identify suitable nursery habitat, only 1 of the 14 YOY-Musky sites was classified as a No-Musky site (False Negative). Nine of the 37 No-Musky sites were wrongly classified as YOY-Musky sites (False Positive).

APPENDIX

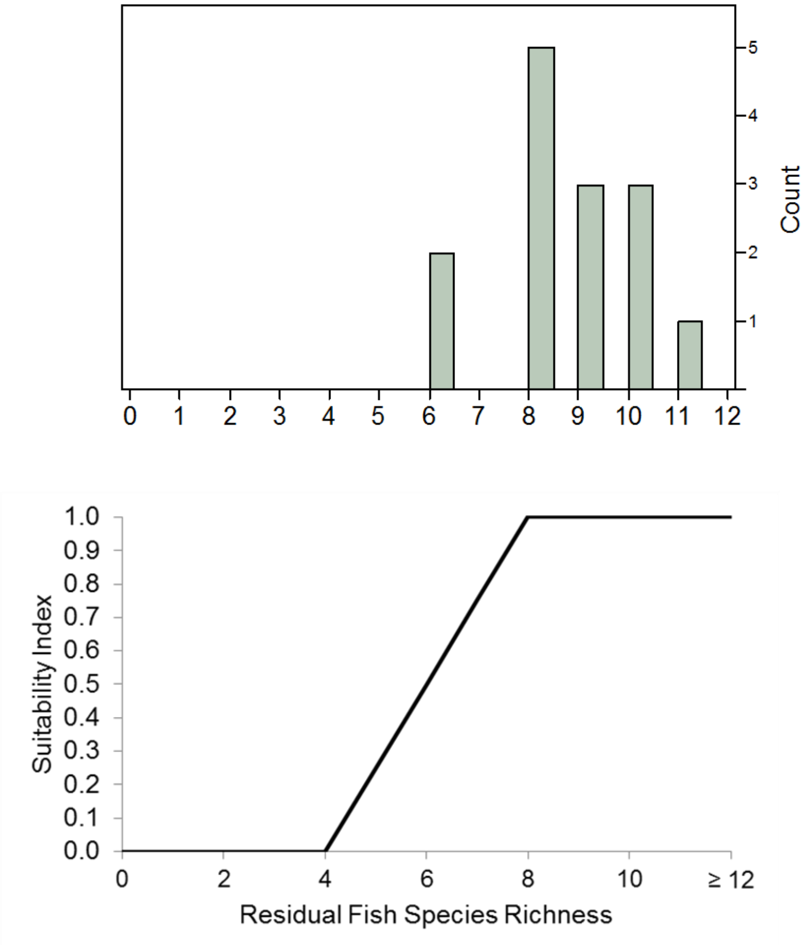
The following are frequency distributions and derived suitability index curves for all variables used in developing the Index of Nursery Habitat Suitability (INHS) for muskellunge. Suitability index curves were derived solely from the patterns observed with YOY muskellunge and ecological justification for the curves is provided. All estimates of the fish community were collected with the seining protocol described by Leblanc et al. (2014) in July of 2012 and 2013. All habitat variables were estimated from depths in the wetland between 0.5 and 1.0 m (Leblanc and Chow-Fraser 2015, CH3) in August of the respective years, and habitat data were collected with the protocol described by Leblanc et al. (2014). Suitability index curves should be considered hypotheses that require further testing and refinement, but are intended to reflect a continuum in suitability index scores. When data were insufficient, suitability index curves were bent or broken to reflect uncertainty in the relationships. Only those SI variables that contributed to the final INHS models are presented.



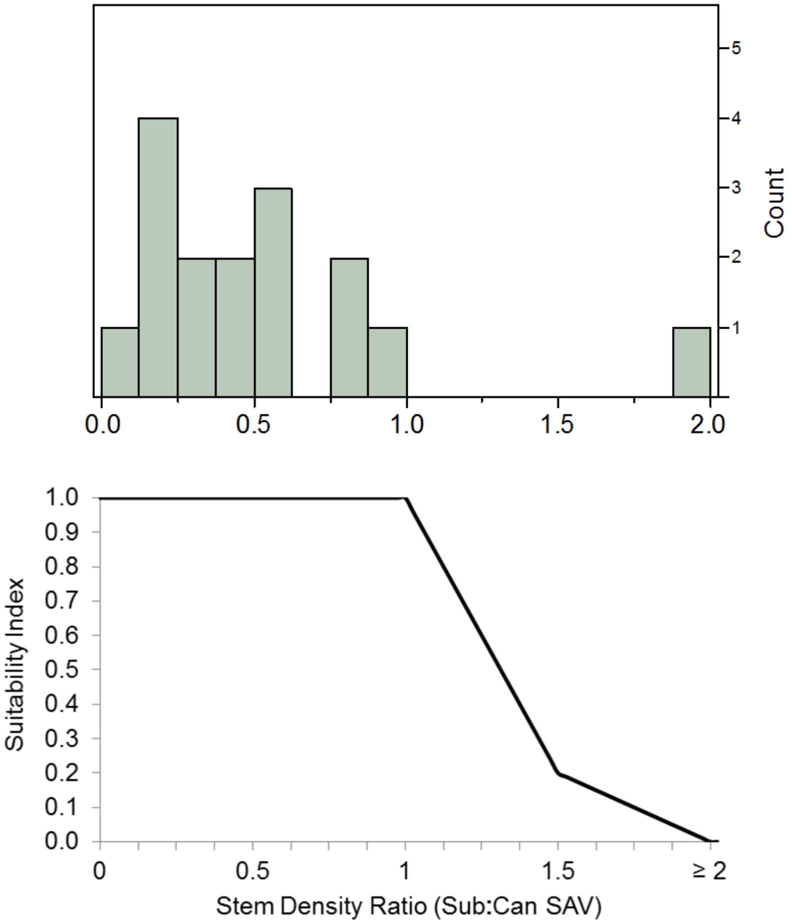
Variable 1: Frequency distribution and derived suitability index curve for the proportional abundance of yellow perch. Yellow perch were identified as a source of muskellunge early-life mortality (Leblanc et al. 2015, CH2), and were never found in excess of 40 % of the fish community with YOY muskellunge in northern Georgian Bay. Yellow perch abundance has also been negatively related to the presence and abundance of YOY muskellunge from the lower Great Lakes (Murry and Farrell 2007; Kapuscinski and Farrell 2014).



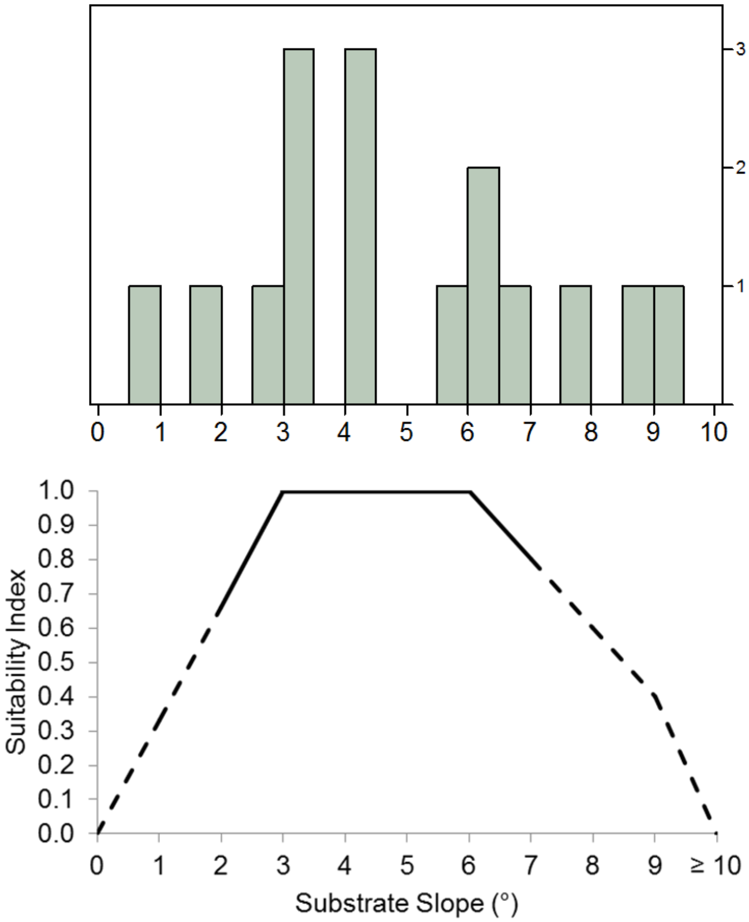
Variable 2: Frequency distribution and derived suitability index curve for the proportional abundance of cyprinid species. Cyprinids were considered preferred forage for YOY muskellunge (i.e., soft-rayed and fusiform species; Kapuscinski et al. 2012) and when at suitable abundances, that should translate into better growth and survival for the YOY (Szendrey and Wahl 1996).



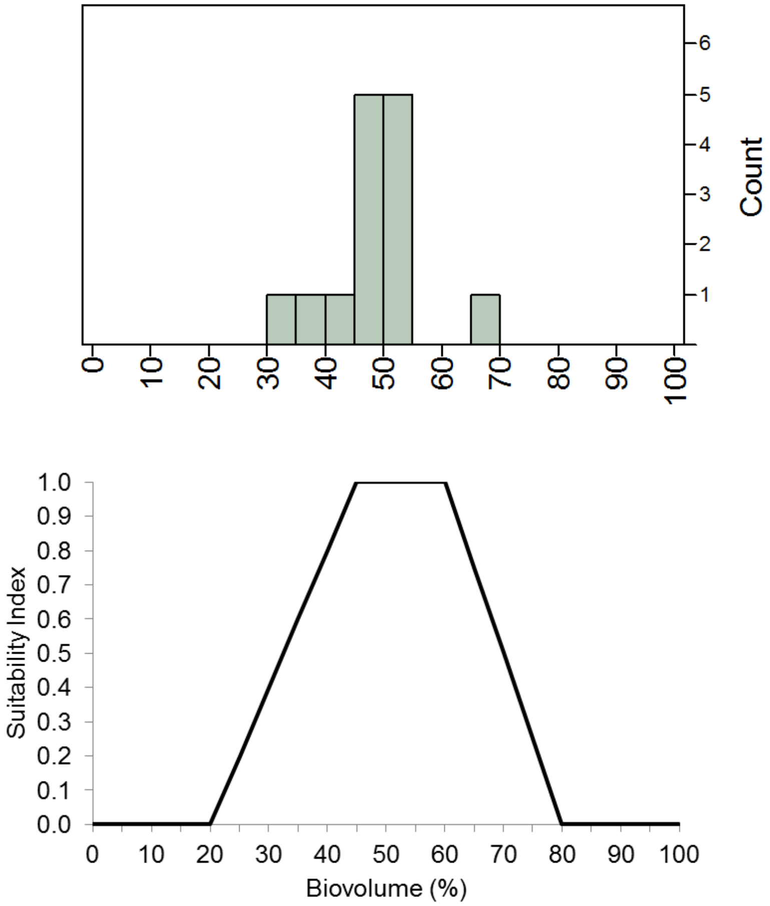
Variable 3: Frequency distribution and derived suitability index curve for the residual species richness of the fish community. YOY muskellunge were found in wetlands with overall higher fish species richness than at sites where they were not found. High diversity in the fish community is also hypothesized to promote YOY survival by providing alternative prey to predators of YOY muskellunge (Wahl 1999). Furthermore, high diversity in the fish community of a wetland is often related to greater habitat complexity that favours YOY survival.



Variable 4: Frequency distribution and derived suitability index curve for the stem density ratio of substrate-covering (Sub) SAV-to-canopy-forming (Can) SAV. Ratios less than 1 indicate a higher stem density count of Can SAV and limited contribution of Sub SAV. This variable was considered a metric of the combined contribution of different SAV growth forms in the water-column. YOY muskellunge have been negatively associated with high densities of Sub SAV while positively related with intermediate densities of Canopy SAV (Murry and Farrell 2007). Only one YOY muskellunge occurred in habitat where this ratio exceeded 1.



Variable 5: Frequency distribution and derived suitability index curve of the wetland's substrate slope, estimated between 0.5 and 1.0 m depth. The shallower substrate slopes that were exposed by the decade of low water levels appeared to be a primary cause for the change in nursery suitability for YOY muskellunge in southeastern Georgian Bay (Leblanc et al. 2014). Thus, substrate slope appears to be an important variable to infer how the suitability of a wetland changes in response to different water level scenarios in Georgian Bay for YOY muskellunge. Substrate slope explained some of the variation of the macrophyte community observed in the wetlands, where steeper substrate slopes promoted a more diverse community of Canopy SAV and precluded the establishment of Sub SAV (Leblanc and Chow-Fraser 2015, CH3). Although YOY muskellunge were observed over a range of substrate slopes, most YOY were found in wetlands with intermediate slopes (3 to 7°). Steeper slopes may also provide an additionally structural feature in the wetland, and thus add to the structural complexity of the habitat.



Variable 6: Frequency distribution and derived suitability index curve for *SAV biovolume*. Biovolume is a measure of the percent contribution of SAV making up the water column, and can be acquired with hydroacoustic techniques. It was measured as the mean height of the SAV divided by the depth of the water where the SAV was found (Valley et al. 2005). Thus, biovolume can be considered a surrogate metric of habitat complexity of the macrophyte community, and would not require physical stem counts. Although our estimates of biovolume were made without hydroacoustic equipment, field derived estimates are highly correlated with those acquired by remote sensing (Valley et al. 2005). Our estimates of biovolume appeared consistent with previous observations that suitable nursery habitat has intermediate densities of SAV in the upper water column (Craig and Black 1986; Murry and Farrell 2007). Additionally, biovolume has the potential to reflect multiple scales of habitat complexity of the SAV community composition (e.g., patchiness; Weaver et al. 1997), which may be more important when identifying nursery suitability for YOY muskellunge (Leblanc and Chow-Fraser 2015, CH3).

GENERAL DISCUSSION

Thesis Summary

The objectives of this thesis were to understand the impact that Georgian Bay's novel hydrological regime poses to the self-sustaining capacity of its muskellunge and provide the necessary information to manage the fishery effectively. Specifically, in Chapter 1, I established that the sustained low water levels and increased shoreline modification in Georgian Bay can severely limit the quality of suitable early-life habitat for successful recruitment of muskellunge in southeastern Georgian Bay. Despite observing a suitable spawning environment and congregating adult muskellunge at the historic sites during the spawning season in 2012, young-of-the-year (YOY) could not be found. The lack of YOY appeared attributed to low water levels that exposed a shallower bathymetry and increases in shoreline modification. This in turn likely mediated the loss of habitat complexity in the upper water column of the nurseries, and a shift in the fish community to higher abundances of early-life predators.

In Chapter 2, I identified that the wetlands where YOY muskellunge occurred in northern Georgian Bay had a unique fish community compared with those in which they were not found. Higher relative abundances of fish species considered preferred forage for YOY, higher overall fish species diversity and lower relative abundances of yellow perch (*Perca flavescens*) characterized muskellunge nurseries. Yellow perch was also identified as a likely source of early-life mortality for muskellunge.

In Chapter 3, I found that the wetlands supporting YOY muskellunge had unique habitat features. Muskellunge nurseries were characterized by higher densities and greater diversity of aquatic vegetation that structures the upper portion of the water column and by steeper bathymetries. The steeper substrate slopes appeared to be an important feature defining suitable nursery habitat since it was directly related to aspects of the macrophyte community. The steeper slopes may also be an added structural feature of the wetland that allows the YOY to be successful as an ambush predators, and an important variable to screen for suitable habitat.

From an ecological perspective, the features that were identified as unique to muskellunge nurseries suggested greater survivorship for the YOY, by providing refuge from predators and opportunities to efficiently forage on high quality prey. These features could also be used to statistically differentiate wetlands where YOY muskellunge were and were not found. These results are interpreted to provide the first quantifiable definition of suitable muskellunge nursery habitat in Georgian Bay. Encouragingly, the patterns that were observed between locations where YOY muskellunge were and were not found in northern Georgian Bay appeared transferable to conditions observed at the historic muskellunge nurseries in southeastern Georgian Bay before and after low water levels, respectively. The findings from the first three Chapters further suggest that YOY muskellunge are sensitive to the conditions of their nursery habitat, illustrating the importance of identifying and protecting those habitats.

In Chapter 4, an Index of Nursery Habitat Suitability (INHS) for muskellunge was developed as a management tool to identify and monitor suitable nursery habitats. Two INHS models were found effective at indexing suitable nursery habitats for muskellunge and to track the change in suitability at the historic nursery sites in southeastern Georgian

Bay from the 14 years of sustained low water levels. The 5-variable INHS, which included the relative abundance of yellow perch, relative abundance of Cyprinids, residual fish species richness, wetland's substrate slope and a macrophyte related metric, had the highest overall model accuracy and highest discriminatory capacity between suitable and unsuitable nursery sites. A potential caveat to the 5-variable INHS is the inclusion of a macrophyte related metric that requires physical stem counts, which may make it difficult for management agencies to populate the 5-variable INHS. To circumvent this issue, we found that a measure of the macrophyte community that can be acquired from hydroacoustics (i.e., *biovolume*) appeared to be an effective alternative for physical stem counts.

To account for situations when information on the aquatic plant community is not available, the utility of an INHS that completely excludes a macrophyte related metric was also investigated. An INHS with as few as three variables (i.e., relative abundance of Cyprinids, relative abundance of yellow perch, and wetland bathymetry; $\text{INHS}_{\text{YP-CYP-Slope}}$) was successful at identifying suitable from unsuitable nursery habitats for muskellunge when applied to independent data. However, the $\text{INHS}_{\text{YP-CYP-Slope}}$ was less reliable than the 5-variable INHS, with a higher false-negative and false-positive rates. Ultimately, the INHS models developed in Chapter 4 appear relevant as a site-specific assessment tool to indicate the recruitment potential of the nursery habitats near where muskellunge spawn.

In summary, prior to this study, the only information of muskellunge early-life habitat in Georgian Bay was from a descriptive study conducted 30 years ago, or had to be extrapolated from studies conducted in the lower Great Lakes, both of which provided insufficient information to predict how, in the unique landscape of Georgian Bay, an unprecedented period of sustained low water levels affected the suitability of muskellunge early-life habitat or to remediate degraded sites. The results from this thesis will better equip management agencies to achieve those goals. Adoption of the recommendations and future avenues of research suggested herein will further efforts to conserve the uniqueness of Georgian Bay’s trophy muskellunge.

Recommendations

Based on the major findings from this thesis, below are recommendations to more effectively manage the self-sustaining muskellunge fisheries in Georgian Bay.

1. A current priority of muskellunge management involves protecting identified spawning habitat. Although spawning grounds within the historic early-life habitats in southeastern Georgian Bay appear to be suitable, the quality of nursery habitat is very poor and therefore likely contributes little towards recruitment of this sub-population. Future studies should be carried out to determine the recruitment potential of existing nursery habitats and to determine the degree to which spawning and nursery sites are still spatially linked. Results of such a study could offer guidance on management actions that may be taken to restore this ecosystem function.
2. Given that the muskellunge continue to use historic early-life habitats in Severn Sound to spawn, despite the degraded nature of the nursery habitat, it is important that these historic nursery sites be rehabilitated. If possible, the shoreline contours should be re-built to provide steeper slopes so that suitable macrophyte communities will be re-established. Considering that the sustained low water levels appeared to be a major cause for the degradation of the nursery habitat in Severn Sound, restoring/managing water levels to mimic historic fluctuations may be the most efficient long-term management action. Natural water-level fluctuations would return the disturbance regime that structures suitable early-life

habitats for muskellunge as well as other important wetlands throughout Georgian Bay.

3. Despite recommendations of Craig and Black (1986) to protect early-life habitats, the density of docks at historic nursery sites has increased over the past three decades. This suggests that current regulatory tools to protect critical habitat from human disturbance are ineffective or perhaps pertinent information was unavailable to enforce regulations. Environmental agencies need to ensure that townships, planning units and local citizens of Georgian Bay are educated on the value of coastal wetlands, particularly those used by muskellunge. Furthermore, increasingly stringent policies should be incorporated into Official Plans to prevent critically important coastal wetland habitat from being modified by human activities.
4. I recommend the 5-variable INHS be used to systematically assess suitability of nursery habitat in eastern and northern Georgian Bay. Although the $\text{INHS}_{\text{YP-CYP-Slope}}$ requires less information, it was associated with a higher false-positive rate (> 50%) because it needed a lower INHS threshold to indicate habitat suitability (≥ 0.6) when compared with the 5-variable INHS (≥ 0.7). The $\text{INHS}_{\text{YP-CYP-Slope}}$ also classified two nursery sites as being unsuitable habitat in both northern and southeastern Georgian Bay. Thus, choice of model to be used should consider both management and conservation goals as well as resource implications (i.e. increased costs to collect information for the 5-variable INHS versus the elevated false-positive rate associated with the 3-variable model). Once appropriate

information becomes available, results of the 3-variable and 5-variable models should be compared directly to better understand the trade-offs of the two models as management tools. Future studies should also investigate the feasibility of using biovolume as a substitute for information on the aquatic plant community and habitat structure, to eliminate the tedious and time-consuming task of counting stems of SAV taxa.

5. Finally, I recommend that sentinel sites be established at known early-life habitats of muskellunge to be monitored on a regular basis. These sites should be stratified along Georgian Bay's shore and be representative of the various sub-populations in Georgian Bay. The 5-variable INHS and $\text{INHS}_{\text{YP-CYP-Slope}}$ were effective at monitoring changes in nursery suitability in southeastern Georgian Bay resulting from the low water levels and should continue to be used for this purpose. Additional sites in eastern Georgian Bay with different geomorphological features should also be monitored to determine how nursery suitability changes under different water level scenarios and/or human-induced disturbances.

Future Work

Below are suggestions for future research that will augment our understanding of muskellunge management, or novel questions that became apparent during the course of this research.

1. The definition for muskellunge nursery habitat and INHS models developed in this thesis are meant as site-specific assessment tools. As such, only a relatively small extent of the wetland is assessed. What remains unclear are the spatial requirements for YOY muskellunge within and between wetlands, and how habitat requirements scale with the growth of the YOY into its first winter. Furthermore, the INHS models and definition of suitable nursery habitat for muskellunge were based on presence-absence data. This binary nature produces polarized conditions (i.e. either suitable or not suitable), when in reality there is probably a range of conditions from highly unsuitable to highly suitable for YOY muskellunge. Although the INHS proposes such a continuum, it is unclear if the INHS values and break-points are related to the fitness of the YOY muskellunge or how many YOY the wetland can support. This information would further our understanding of the potential carrying-capacity of an individual wetland or complex of wetlands for YOY muskellunge and general population dynamics.
2. Reconciling true- *vs* pseudo-absence is a conservation concern when habitats are erroneously classified as unused because the species is not found at the time of sampling. This situation becomes increasingly problematic for species that are rare and difficult to capture because limiting habitats may not be afforded the

protection that the site deserves and the reliability of presence-absence models may diminish. Although greater sampling rigour can increase confidence in the true absence of a species, it is unclear how much added sampling effort is needed to ensure that the species is truly absence from the habitat. A better understanding of the spatial extent of the wetland habitat used by YOY muskellunge during the nursery period (i.e., home-range) can be used to optimize the level of sampling effort required. For example, the area sampled in a wetland could encompass the home-range of a YOY at the time of sampling. Although a radio-telemetry study would provide the most precise habitat-use data, the small size, approximately 120 mm total length in July, and sensitivity of the YOY may make attaching an appropriately sized transmitter difficult. Thus, it is prudent to determine if such a small scale radio-telemetry project is feasible or to conduct a methodology study to determine an optimal sampling effort that can reliably identify the presence or absence of YOY muskellunge.

3. Muskellunge were opportunistically observed returning to a specific area during the spawning season on a yearly basis. The specificity of this fidelity has not been fully tested in Georgian Bay, and it is unknown if muskellunge are returning to one wetland or a general area that has multiple wetlands available for spawning. This information would greatly assist with identifying the scale at which management strategies should be applied in Georgian Bay because of the large number of small wetland units that occur close to each other. A radio-telemetry study of adult muskellunge during the spawning period can be used to monitor the

wetlands used and/or the connectivity among wetlands used as early-life habitats. Furthermore, the apparent fidelity to a spawning site warrants that as many early-life habitats used by muskellunge are identified, because these sites likely occur disproportionately compared with otherwise available habitat.

4. Understanding what drives the apparent fidelity to a spawning site in muskellunge must be understood. If muskellunge imprint on the wetland where they were recruited, this has implications for stocking initiatives because the locations where the muskellunge are stocked will likely be used as the spawning and nursery habitat by those individuals once they mature. This requires that stocking locations be evaluated for both spawning and nursery habitat suitability if the goal is to promote naturally reproducing populations. If, however, muskellunge are selecting specific habitats, then we must identify the scale at which adults make these decisions, and investigate the spatial connectivity between the spawning and nursery habitats. By understanding the reason why muskellunge exhibit fidelity to a particular spawning location, we may also determine the potential plasticity of this behaviour, and use this information to understand meta-population dynamics in Georgian Bay.
5. The INHS developed in Chapter 4 is a site-specific assessment tool that requires on-the-spot habitat appraisal. We found, however, that the wetland's bathymetry was directly related to aspects of the macrophyte community, and this suggests that a more regional approach to map habitat suitability may be feasible. By understanding the physical characteristics that structures a suitable macrophyte

community and having greater access to high resolution imagery data (e.g., digital elevation maps, Light Detection and Ranging (LiDAR) technology, etc.), the INHS from Chapter 4 can be converted into a Habitat Suitability Model (HSM). The HSM could be used to identify wetlands with the greatest potential to support natural reproduction of muskellunge throughout Georgian Bay and model how different water level scenarios impact the suitability of those sites.

6. In Chapter 2, we identified yellow perch as a likely source of early-life mortality for muskellunge. This observation requires further confirmation in other sites. Identifying the impacts that known and potential early-life predators have on muskellunge recruitment would improve our understanding of how the composition of the fish community defines suitable early-life habitats. Even though we only observed a single round goby (*Neogobius melanostomus*) at the baited egg platform in Chapter 2, gobies are well established in southeastern Georgian Bay. Given the invasive nature of round gobies, investigating their impacts on muskellunge recruitment is warranted, especially since muskellunge do not protect their eggs or offspring.
7. Although rarely discussed in this thesis, we found that northern pike and muskellunge would sometimes use the same early-life habitats. Sympatric association between these congeners may be unique to the Great Lakes since other investigations have found northern pike to be competitively superior to muskellunge during the first year of life, and are thought to be able to exclude muskellunge where they co-occur. Future studies should be carried out to

determine if these congeners co-exist in other embayments of Georgian Bay, and to understand factors that govern when both species co-exist or exhibit competitive exclusion. Such a study would be of interest from an evolutionary and management perspective, since both species are of high value to the recreational fishery.