Movement, resource use, and life history strategies of Black Bay Walleye (*Sander vitreus*)

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Abstract

Resource distribution across the landscape can drive movement strategy selection, from sedentary to highly mobile individuals. When paired with other forms of analysis, movement ecology can provide insight into the resource use, habitat selection, and life history strategies of fish. Acoustic telemetry has greatly improved our understanding of fish movement in the Laurentian Great Lakes, and Walleye (*Sander vitreus*), as a fish of great economic and social importance, have been intensively studied. While the degree of migration through the Great Lakes has been assessed, there remains a knowledge gap surrounding within-population variation in this movement.

Black Bay once supported the largest commercial fishery for Walleye on Lake Superior, until its collapse in the late 1960s, and the recovery of this population has become a management priority on the lake. Management decisions have however, lacked precise information on the spatial extent, resource use, and life history of Black Bay Walleye. My thesis makes use of a two year acoustic telemetry study to assess Walleye movement within Black Bay and into the main body of Lake Superior. This was done with the goal of identifying Walleye movement patterns, and the influence of thermal-optical habitat and forage availability on these movement patterns.

Black Bay Walleye have distinct migratory and resident groups, where migrators leave Black Bay during part of the year, and residents remain within Black Bay all year. Using a traditional Von-Bertalanffy model to describe growth, I found that migratory Walleye achieved a greater asymptotic length than residents, but that the curvature of these growth patterns did not differ between groups. Thermal-optical habitat conditions outside of Black Bay influence occupancy of this region by migrants, but occupancy of the north end of Black Bay is not limited

by available thermal-optical habitat. Migratory and resident Walleye from Black Bay did not differ in prey use (assessed using stable isotopes), and forage availability did not differ between regions within and outside of Black Bay. Historical differences in coregonid abundance between Black Bay and the region outside of the bay may, however, have led to the disparity in movement strategies still observed today.

Lay Summary

Walleye in Black Bay, Lake Superior have become a management priority following population collapse in the 1960s due to overfishing and the loss of potential spawning habitat. Until recently, however, little has been known about the distribution of this population, its resource use, or its habitat use. I tracked Black Bay Walleye in order to better understand how these fish move through the bay, and to determine if any individuals migrate out of the bay and into the main basin of Lake Superior. Black Bay Walleye demonstrate diversity in movement strategies, with resident fish that remain within the bay all year, and migratory fish that exit the bay in late summer and early fall, returning in the winter months. Walleye migrating out of Black Bay grow larger than their resident counterparts, and do not exit the bay until temperature and light conditions in the main basin meet their preferred levels. Surprisingly, I found no difference in prey species use between migratory and resident fish, despite the larger size of the migrators. This may be due to the timing of migration corresponding to a period where energy is allocated to reproduction rather than growth, and cannot be detected by my methods.

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1. General Introduction

1.1 Background

The movement of animals across the landscape has important implications with regards to their access to forage and breeding sites, as well as population dispersal (Mueller & Fagan 2008). In ecology, movement patterns are typically separated into three categories: sedentary ranges (or resident), migration, and nomadism (Mueller & Fagan 2008). Sedentary ranges are characterized by individuals that use a relatively small area compared to the entire population (Roshier & Reid 2003). This movement strategy is typical on landscapes with homogenous resource distributions, and is often conceptualized with the construction of home ranges (Mueller & Fagan 2008; Roshier & Reid 2003). Burt (1943) defined the home range as the area used by an individual during its normal activities of gathering forage, breeding and raising young. As this definition suggests, animals who are resident to a particular area must be able to fully complete their life cycle within this home range. If movements outside of the home range occur infrequently, they can be considered exploratory, rather than part of the home range (Burt 1943).

If animals must move between habitats in order to obtain transitory resources, then migration may become beneficial (Hayden et al. 2014; Mueller & Fagan 2008). While the exact definition of migration seems to differ between sources, most descriptions point to temporally predictable patterns to the movement between habitats as a key characteristic (Brönmark et al. 2014). These patterns often follow seasonal periodicity, but may range from as long as a single lifetime round trip (e.g. Pacific salmonids; Buchanan & Skalski 2010) to as short as diel migration of many planktonic animals (Brierley 2014).

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Nomadism is another strategy that involves a great deal of movement however, it differs from migration in that it does not follow any predictable, periodic pattern (Mueller & Fagan 2008). Nomadic animals are typically wanderers that must search for resources that vary greatly in their abundance spatially and temporally which results in populations that do not maintain a consistent spatial distribution (Mueller & Fagan 2008). Examples of this are often seen in fish inhabiting the open ocean such as tuna and billfish, which must cover great distances in order to find isolated pockets of resources (Kraus et al. 2011).

In order for these more mobile strategies to be selected for in a population, the benefits of acquiring resources spread over a larger area must outweigh the costs of simply relocating to these areas (Roff 1988). Animals may migrate in order to optimize their food intake, reduce predation risk or find mates and improve nest survival (Brönmark et al. 2014; Hayden et al. 2014). The decision of which movement strategy an animal uses is not made consciously in most species, but is a by-product of an evolutionary history tailored toward maximizing reproductive success (Brönmark et al. 2014). Like all characteristics of animals shaped by natural selection, there is likely a degree of within-population variation to the type and amount of movement.

In addition to defining the types of movement patterns exhibited by animals, Mueller and Fagan (2008) suggested three mechanisms that drive animal movement. The first of these is a non-oriented mechanism, in which an animal moves randomly through its habitat (Mueller & Fagan 2008). This is most akin to diffusion, and the only factor that affects the animal's movement is the stimuli from its immediate environment such as visual, auditory or chemosensory cues (Mueller & Fagan 2008). An animal may also move with an oriented mechanism where stimuli from beyond its immediate environment influences movement decisions (Mueller & Fagan 2008). Magnetism is a stimulus used by many migrating animals in

order to orient movements however, visual cues of distant landmarks or celestial bodies, as well as olfactory cues from outside of the immediate environment are also used (Akesson 1994; Collett 2010; Ueda 2012). Finally, a memory mechanism may influence an animal's movements based on previous information on a movement target (Mueller & Fagan 2008). Mueller and Fagan (2008) further suggest that these mechanisms can also be integrated by the same animal in order to make decisions about its movement. Examples of this may be found in the migration of fish to spawning habitats, which often is based off of some type of memory, and the subsequent dispersal throughout a waterbody based on perceived resource abundance.

Recent advances in animal tracking technology have greatly improved the number and accuracy of location estimates (Kie et al. 2010). In the world of fisheries researchers, acoustic telemetry has opened many possibilities for tracking aquatic animals (Huveneers et al. 2016). This tool has allowed for both the tracking of fish migrations, as well as better understanding of fish residency (Huveneers et al. 2016).   Today, reduced cost and advancements in passive tracking technology have allowed researchers to deploy acoustic telemetry arrays across various spatial scales (Kessel et al. 2013). Using this technique, multiple individuals can be tracked constantly without interruption during the study period (Kessel et al. 2013). This has allowed researchers to collect a great deal of information on the spatial ecology of fish, and when combined with other analyses has revealed a great deal of information about resource use, habitat use and even life history variability (Mueller & Fagan 2008).

Acoustic telemetry has begun to reveal insights into the spatial ecology of the fishes in the Laurentian Great Lakes, many of which are of economic importance and cross geo-political boundaries. In addition, other factors such as climate change, and invasive species may affect native species in ways that are as of yet largely unknown (Ng & Gray 2011; Walsh et al. 2016). Due to its importance in both recreational and commercial fisheries, Walleye (*Sander vitreus*)

have become one of the more intensely studied species in the field of Great Lakes fish

movement (Landsman et al. 2011). Using acoustic telemetry, Hayden et al. (2014)

demonstrated that Walleye in Lake Huron can migrate up to 350km from their spawning sites

and often return in the same year. Despite their popularity as a study species among

researchers, there remains a gap in knowledge of Walleye spatial ecology in the Great Lakes.

While our knowledge of Walleye migration, as well as preferences for resources and habitat is

improving, the degree of variation in resource and habitat use as it relates to movement has not

been well studied.

Walleye are a piscivorous top predator found throughout the Great Lakes (Pothoven et

al. 2016). They exhibit a great degree of flexibility in forage species use based on available prey

(Herbst et al. 2016; Pothoven et al. 2016). While young Walleye typically feed on zooplankton

and aquatic insects, use of these food sources can also occur in adult fish when they are readily

available (Herbst et al. 2016). Adult Walleye will largely feed on fish, particularly young Yellow

Perch (*Perca flavescens*) which overlap in habitat use with the adult Walleye (Herbst et al. 2016;

Pothoven et al. 2016). As generalists, Walleye will readily shift their diet when other forage

species become available, such as Rainbow Smelt (*Osmerus mordax*) and coregonids (Pothoven

et al. 2016). Further, some work has shown that Walleye feeding on large pelagic forage such as

Lake Herring (*Coregonus artedi*) tend to grow to sizes that are larger than Walleye that have

only Yellow Perch as a prey item (Henderson et al. 2004).

Due to the size of the Great Lakes, they encompass a variety of species across multiple

habitat types (Sierszen et al. 2014). Lake Superior is no exception to this however, it does vary

from the other Great Lakes in the level of change seen both physically and ecologically (Sierszen

et al. 2014). The southern Great Lakes have seen many changes since the 1970s including

overfishing of native species, introduction of non-native species, eutrophication, addition of

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contaminants and climate change (Sprules 2008). This has led to a change in the species

structure that maintains the functioning food web in these lakes (Sprules 2008). Lake Superior

has had the least divergence in its ecological structure of all of the Great Lakes, and therefore

provides a model ecosystem against which to compare changes in the other Great Lakes

(Sierszen et al. 2014).

Lake Superior's food webs vary according to the habitat in which they are found

(Sierszen et al. 2014). This variation is largely linked to differences in depth, such as the greater

abundance of *Diporiea* in shallow, nearshore sites than deeper offshore sites (Scharold et al.

2004). Moving up the food chain, forage fish used by Walleye differ in their spatial distribution

as well. In nearshore environments Yellow Perch and smelt are common (Mercado-Silva et al.

2006; Parker et al. 2012). Further from shore in deeper water, Cisco become much more

prevalent (Gorman et al. 2012). Forage species have been shown to vary in their proportional

contribution to Walleye diets depending on the region of the waterbody used by Walleye, or the

time of year (Pothoven et al. 2016). Yellow Perch are common in the diet throughout the year,

however, Rainbow Smelt are typically preyed upon more heavily early in the summer, while

coregonids make up a greater proportion of the late summer diet (Pothoven et al. 2016).

Identifying forage use through stable isotope analysis has provided detail of changing

forage use over time by individuals, as well as connections between food webs (Hobson 1999).

Analysis of stable carbon-13 isotopes (^{13}C) has allowed delineation of food webs in lake

ecosystems, particularly benthic and pelagic food webs (Harrison et al. 2016; Hobson 1999).

Complimentary to this, nitrogen-15 (δ^{15}N) is a valuable tool for determining the trophic position

of consumers (Post 2002; Vander Zanden & Rasmussen 2001). Combining these two isotopic

signatures can provide valuable insight into the niche space of populations, and how they fit into

the greater food web. New techniques in stable isotope analysis allow non-lethal sampling of

fish tissues, provided a relationship is created for the isotopic values of the sampled tissue, and white muscle (typically used in lethal sampling; Fincel et al. 2012). This will allow studies using acoustic telemetry to identify the forage use of tagged fish, and compare them to differences in movement and space use.

Another factor that is tied with Walleye space use, and therefore potentially movement patterns, is habitat. Walleye habitat preferences have been well studied in the literature in the context of productivity (Chu et al. 2004; Lester et al. 2004; Pandit et al. 2013), but not movement. It is well established that thermal-optical habitat conditions are among the most important factors influencing Walleye productivity and habitat use in lake ecosystems (Bowlby & Hoyle 2011; Chu et al. 2004; Lester et al. 2004; Pandit et al. 2013). Walleye are a cool water fish, preferring a temperature range between 18°C and 22°C (Chu et al. 2004), and given a lifestyle not limited by diet, Walleye growth rate is maximized at 21°C (Lester et al. 2004). With changes in water temperature beyond the preferred range for Walleye, habitat suitability quickly declines (Chu et al. 2004).

Water temperature varies both spatially and temporally in the Great Lakes. As such, the distribution and habitat use of Walleye within these lakes can vary accordingly (Peat et al. 2015). During the warmer summer Walleye tend to inhabit warmer waters near the 21°C optimum, while in spring and fall they experience temperatures near 10°C (Peat et al. 2015). Walleye will use habitats with different water temperatures both between and within lakes, presumably depending on individual preference (Peat et al. 2015). This may be a result of different life stages, such as young fish remaining in warm shallow bays, while mature fish migrate to the main basin of a large lake (Bowlby & Hoyle 2011; Chu et al. 2004).

While all Walleye prefer water conditions with reduced light, juveniles may prefer environments with a further reduction in light created by increased turbidity (Pandit et al. 2013). These environments are typically found in shallow embayments, and are thought to be used as a way to maximize food capture while reducing predation risk (Pandit et al. 2013). Walleye have adapted to hunting in low light conditions by developing a *tapetum lucidum* within the retina, and as such, darker or more turbid water tends to be associated with increased hunting activity (Einfalt et al. 2012). Indeed, Walleye occurrence and productivity peaks around a secchi depth of 2m (Lester et al. 2004). Water clarity above or below the optimum preferred by Walleye results in a dramatic decrease in habitat suitability however, adults have been shown to have a higher variability to preferences in water clarity than juveniles (Chu et al. 2004; Lester et al. 2004). While most juvenile Walleye tend to remain within shallow regions of lakes, some adults may migrate to the main basin of lakes during the summer where the water is cooler and more clear (Chu et al. 2004). To compensate for the clear water, Walleye presumably move deeper in the water column, where light intensity decreases (Brandt et al. 2011). While knowledge of Walleye responses to thermal-optical water conditions are well understood in the southern Great Lakes, knowledge of potential climate-specific adaptations to these preferences remains limited (Lester et al. 2004). The Canadian waters of Lake Superior remain particularly understudied in this regard.

Variability in habitat and resource use is often associated with differences in life history, and this variability in life history traits can occur within a species, between populations or even within a population (Réale et al. 2010). The variability in life history strategies allows a level of plasticity to environmental changes, permitting populations to adjust to these changes (Lester et al., 2004). The pace of life syndrome (POLS) hypothesis predicts that individuals should differ in a suite of traits associated with differences in life history (Martin et al. 2006; Réale et al. 2010).

Recently, this has been extended to the idea of behavioural differences between individuals which can include variation in habitats and the resources associated with them (Réale et al. 2010).

Movement patterns are a behavioural trait that have been linked to life history variation and POLS (Nakayama et al. 2016). The rate of movement of an animal affects how it uses its habitat and resources, and habitat and resource use in turn are related to its eventual growth (Nakayama et al. 2016). Thus, movement, resource use, and habitat preference are all important traits when considering the life history characteristics of an animal (Mueller & Fagan 2008; Quist et al. 2003). While some fish will exhibit a highly mobile, active life history, others may show a more sedentary lifestyle (Nakayama et al. 2016). This relates to differences in growth and survival, as the active fish capture more prey and grow faster, while the sedentary fish grow more slowly, but encounter fewer predators (Nakayama et al. 2016).

Lester et al. (2014) found variation in Walleye life history throughout North America, and demonstrated how this can be used to calculate sustainable exploitation across the continent. In fact, largely due to the popularity of Walleye as a commercially and recreationally exploited fish, productivity has seen the most attention when analyzing the effects of differences in life history traits for this species (Lester et al. 2014; Zhao et al. 2008).

Growth patterns are often used to elucidate information about life history, and in cases where animals must be kept alive for movement studies, non-lethal sampling techniques are required to assess growth. Walleye dorsal spines can be non-lethally sampled, and can be used to both age an individual and back calculate its length at age (Borkholder & Edwards 2001). This allows for comparisons of growth patterns to movement subsequently determined with the use of acoustic telemetry. While scales have been used frequently in the past to age fish and back

calculate length at age, the scale annuli can become crowded at the outer edge in older fish

making accurate measurements difficult (Borkholder & Edwards 2001). Dorsal spine annuli do

not experience this crowding to the same degree, and are therefore a more accurate method for

determining age and length at age in older fish (Borkholder & Edwards 2001).

Lake Superior has received a great deal of attention from scientists studying coarse

resolution fish movement however, this work has largely focused on Lake Sturgeon (*Acipenser

fluvescens*), Lake Trout (*Salvalinus namaycush*), and Brook Trout (Landsman et al. 2011). In

addition, there have been relatively few acoustic telemetry studies developed on the lake

(Landsman et al. 2011). Recently, however, managers have begun to take advantage of this new

technology to implement fish migration projects across the lake. This includes the study of

Walleye movement within Black Bay.

Black Bay is a large embayment in the northwestern region of Lake Superior covering

about 60 000 ha (Furlong et al. 2006). Water depth in Black Bay is shallow, with 30% of the bay

less than 5m deep and an additional 50% between 5 m and 15 m deep (Furlong et al. 2006).

Most of the shallow water is concentrated in the north end of Black Bay, with a channel running

to the mouth at the south end that reaches a depth of 64.5 m (Furlong et al. 2006). The bottom

substrate of Black Bay primarily consists of silt and clay, with a few cobble shorelines and bars

(Biberhofer 2006; Furlong 2006). There has been little development on the bay, most of which

is concentrated in a series of dwellings on the western shoreline (Furlong et al. 2006). The

largest tributary to Black Bay is the Black Sturgeon River, which is currently considered to be a

major spawning site for Walleye in the bay (Furlong et al. 2006; Wilson et al. 2007).

During the late 1800s to the 1960s, Black Bay accounted for 90% of Lake Superior's

commercial Walleye harvest (Furlong et al. 2006; Garner et al. 2013). Following intense fishing

pressure, and the construction of the Camp 43 dam on the Black Sturgeon River (1960), the

Walleye population collapsed in 1968 (Berglund 2014; Bobrowicz 2012; Furlong et al. 2006). A

moratorium was placed on the commercial Walleye fishery of Black Bay in 1971, and

recreational fishing on the northern half of the bay, as well as the lower Black Sturgeon River

was closed in 1999 (Berglund 2014; Bobrowicz 2012). Numerous stocking efforts have been

attempted in Black Bay, but the results have been inconsistent (Garner et al. 2013). Evidence

from the last decade suggests that the Walleye population has increased in Black Bay however,

it remains a fraction of historic levels (Berglund 2014). This has led to the belief that habitat loss

may have contributed to the decline and lack of recovery of Walleye in Black Bay, and not

overfishing alone. For this reason, the spawning potential of the Black Sturgeon River and the

prospective removal of the Camp 43 dam has received a great deal of attention (Bobrowicz

2012; Furlong et al. 2006; Garner et al. 2013).

Radio telemetry study of a small number of Walleye in Black Bay and the Black Sturgeon

River tracked movements between the river and the bay (Furlong et al. 2006). The historical

significance of this river as spawning habitat has been largely debated, however, as anecdotal

evidence from commercial fishermen indicates that Walleye in Black Bay may have been

primarily spawning on shoals (Goodyear et al. 1982). Genetic work suggests that Walleye found

in Black Bay share a common gene pool with Walleye from the Black Sturgeon River, both above

and below the dam (Garner et al. 2013). While a great deal of work has been conducted on fish

movement between Black Bay and the Black Sturgeon River, little tracking of Walleye has been

done throughout Black Bay. As such, the geographic extent of the Black Bay Walleye population

remains unknown. Genetic analysis, supported by mark recapture work, suggests that Walleye

populations in Black Bay and Nipigon Bay are distinct (Ryder 1968; Wilson et al. 2007), but there

is no information on the connectivity of Black Bay Walleye with nearby Thunder Bay. Given the

potential for long distance migration of Walleye discovered by Hayden et al. (2014), this

intermixing of populations is a distinct possibility over the geographical range between Black

Bay and Thunder Bay.

While a great deal of information exists describing Walleye resource and habitat

preferences in the Great Lakes, movement patterns have only just begun to be better

understood. Understanding of these movements will provide valuable information about the

geographical extent of a population, as well as the connectivity of populations. Relating

movement patterns to resource and habitat use will also aid researchers in elucidating the

proximate reasons behind fish movement patterns, as well as understanding any within

population variability to the life history choices associated with movement and resource use.

Acoustic telemetry has revealed a great deal of information about fish movement in the

southern Great Lakes however, as of yet there remains a knowledge gap of fish movement

ecology in Lake Superior, the northernmost and least disturbed of the lakes.

1.2 Hypotheses

By making use of an acoustic telemetry study, my proposed work aimed to test the

hypothesis that Black Bay Walleye exhibit variation in their movement patterns, displaying both

migratory and sedentary individuals (H1). In order to test the hypothesis that walleye

occupancy in a region is related to the amount of available habitat (H2), I applied a thermal-

optical habitat model to Black Bay against which fish locations were compared. Through use of

stable isotope analysis taken from non-lethal samples of tagged fish, in tandem with prey

density analysis from the regions within and immediately outside of Black Bay, I tested the

hypothesis that forage use by Black Bay Walleye differs between migratory and resident fish

(H3). Finally, I compared the above factors to the growth trajectories of Walleye in Black Bay

determined from the back calculated length at age using dorsal spine sections. This allowed me to test the hypothesis that the more active life history strategy employed by migratory fish when compared to residents leads to faster growth (H4).

1.3 Significance

This information will help improve understanding of fish movement in the Great Lakes and potential influences on this movement. It will also provide greater insight into the POLS hypothesis as it may relate to fish movement and the level of variability within a population. From a management perspective, this study will aid in decisions regarding the potential removal of the Camp 43 dam and inform on the effectiveness of the recreational fishing sanctuary on Black Bay, thereby supporting the recovery of Walleye in Black Bay. On a broader scale this work will provide significant ecological knowledge to barriers of Walleye rehabilitation and the appropriate spatial scales at which management practices may need to be applied in order to be most effective.

2. Movement, habitat use, and life history of Walleye (*Sander vitreus*) in Black Bay, Lake Superior

2.1 Abstract

Studies of animal movement rarely incorporate life history into the understanding of within

population variability in movement patterns, despite the fact that variations in such behavioral

traits may lead to a range of responses by animals to changing environmental conditions. I

aimed to identify movement strategies of Walleye (*Sander vitreus*) in a recovering population

from Black Bay, Lake Superior by making use of an acoustic telemetry study during the years of

2016-2017. Having identified migratory and resident individuals, I assessed differences in their

growth using measurements of dorsal spine annuli to back calculate length at age. I then

developed a thermal-optical habitat model for Black Bay and the waters immediately outside of

the bay in order to determine if habitat availability acts as a driver of migration. Migratory Black

Bay Walleye left the bay mostly during the late summer and early fall, while residents remained

within Black Bay for the entire year. The curvature of growth did not differ between migratory

and resident fish however, the maximum asymptotic length of migratory Walleye was 55 mm

longer than residents. Increasing thermal-optical habitat area outside of Black Bay led to

increasing Walleye occupancy in this area, but it did not limit occupancy within the bay. This

work indicates that variation in movement strategies are linked to different life history

strategies in Black Bay Walleye, and that the departure of migratory individuals from the bay is

dictated by optimal habitat availability. This improves our knowledge of how behavioral

differences within a population are linked to disparate life history strategies.

2.2 Introduction

Variability in movement and resource use in fish can often be associated with differences in life history (Nakayama et al. 2016). Movement patterns can range from sedentary individuals, who remain resident within a relatively small area when compared to the larger population, to migrators, who travel across the landscape in periodically predictable patterns (Mueller & Fagan 2008). The Pace of Life Syndrome Hypothesis (POLS) predicts that within a population, individuals will vary in a suite of physiological and behavioral traits, including movement (Nakayama et al. 2016; Réale et al. 2010). Highly active individuals typically cover a greater area, acquiring better resources, allowing for faster growth and higher reproductive output (Nakayama et al. 2016; Réale et al. 2010). This comes at the trade-off, however, of the higher energetic cost of long distance movement, as well as increased predation risk and higher overall mortality relative to more sedentary individuals (Nakayama et al. 2016; Réale et al. 2010). Variation in movement and life history is particularly important within a population given that it provides a degree of plasticity to environmental change (Lester et al. 2014).

Throughout North America, the life history and production of Walleye (*Sander vitreus*) has been well studied to best estimate sustainable levels of exploitation (Lester et al. 2014; Zhao et al. 2008). Research into Walleye productivity has led to a better understanding of Walleye resource use and habitat preferences (Chu et al., 2004; Lester et al. 2004; Pandit et al. 2013). As adults, Walleye are picivorous top predators and typically feed on Yellow Perch (*Perca flavescens*), but will readily shift their diets to other food sources such as aquatic invertebrates, Rainbow Smelt (*Osmerus mordax*), and coregonids when available (Herbst et al. 2016; Pothoven et al. 2016). Among the most important drivers of Walleye habitat use are the thermal and optical conditions found within a body of water (Bowlby & Hoyle 2011; Chu et al. 2004; Lester et al. 2004; Pandit et al. 2013; Peat et al. 2015). Walleye are a cool water fish, preferring

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temperatures between 18°C and 22°C, and maximize hunting activity in low light conditions

provided by turbid water or during the crepuscular periods of early morning and late evening

(Chu et al. 2004). As water temperature and clarity changes away from these optimal values,

Walleye habitat suitability quickly declines leading to reductions in growth and reproductive

output (Chu et al. 2004).

Temperature and light conditions vary both spatially and temporally within large bodies

of water which can lead to differential habitat use throughout the year (Pandit et al. 2013; Peat

et al. 2015). Adult Walleye tend to inhabit shallower, more turbid water in the spring, moving

out into the deeper, clearer main basin of lakes when temperatures in the shallow bays exceed

optimal values (Peat et al. 2015). In order to compensate for the increased light penetration in

the main basin, adult Walleye presumably shift lower in the water column (Brandt et al. 2011).

Seasonal habitat shifts by Walleye into the main basin of a large lake may result in long

distance migrations. Acoustic telemetry provides high resolution spatial data from the

continuous tracking of multiple individuals, allowing researchers to investigate fish migration

and residency at multiple spatial scales (Huveneers et al. 2016; Kessel et al. 2013; Kie et al.

2010). In Lake Huron, Walleye were tracked as far as 350 km from their spawning site in the

Tittabawassee River into the main basin of the lake (Hayden et al. 2014). This migration was not

consistent across the population, and while Hayden et al. (2014) found no difference in the

migration routes of male and female Walleye, the timing of these migrations did differ between

sexes; females in Lake Huron tended to out migrate from the Tittabawassee Reiver and Saginaw

Bay prior to males (Hayden et al. 2014). Contrary to this, sex based differences in migration

strategy have been observed in jaw tagged Walleye from Lake Huron, where female recaptures

in the main basin of the lake outnumbered male recaptures (Fielder 2016).

Walleye are found throughout the Great Lakes, which cover a vast area and cross multiple geo-political boundaries. Because of this, and their importance to commercial, recreational, and subsistence fisheries, their ecology in these waterbodies has been heavily studied (Landsman et al. 2011). While the southern Great Lakes have received a great deal of attention, Lake Superior remains particularly understudied. This is the case despite the fact that it remains the least changed, both physically and ecologically, of all of the Great Lakes (Sierszen et al. 2014), which make it a model system against which to compare ecological change in the other Great Lakes.

Black Bay is a large, shallow embayment in the northwestern region of Lake Superior, covering 60 000 ha (Furlong et al. 2006). The shallow water and fine substrate of the bay results in high turbidity when compared to the main basin of Lake Superior. Between the late 1800s and the 1960s, Black Bay produced 90% of Lake Superior's commercially caught Walleye (Furlong et al. 2006; Garner et al. 2013). This intense fishing pressure led to the collapse of Walleye in Black Bay in 1968, resulting in a moratorium of the commercial fishery in 1971 (Berglund 2014; Bobrowicz 2012; Furlong et al. 2006).

Since the collapse of the Walleye fishery, Black Bay has been the subject of continued rehabilitation attempts including several stocking events that saw little integration into the larger population (Garner et al. 2013). In 1999, the northern half of Black Bay, as well as the lower Black Sturgeon River were closed to recreational fishing, which was followed by an end to the commercial Yellow Perch fishery in 2002 (Berglund 2014; Bobrowicz 2012). In the last decade, this has led to an increase in Walleye abundance in Black Bay however, the population has plateaued at a level that is below historic numbers (Berglund 2014).

Much of the recent attention surrounding Walleye recovery in Black Bay has focused on the Black Sturgeon River, the largest tributary to Black Bay, and its contribution to Walleye spawning (Furlong et al. 2006; Wilson et al. 2007). Radio telemetry and genetics suggest a link between Walleye from Black Bay and those from the Black Sturgeon River, but anecdotal evidence indicates that prior to collapse Black Bay Walleye were primarily spawning on shoals in the north end of the bay (Furlong et al. 2006; Garner et al. 2013; Goodyear et al. 1982). Genetic analysis of Walleye found in nearby parts of Lake Superior indicates that Black Bay Walleye are genetically distinct from Nipigon Bay Walleye (Wilson et al. 2007), but there exists little knowledge as to the connectivity of Black Bay with nearby Thunder Bay. Despite the focus on Walleye surrounding the Black Sturgeon River system, there remains little understanding of the spatial structure of the Black Bay Walleye population as a whole.

Objectives

Through the use of acoustic telemetry, my study aimed to test the hypotheses that the trajectory of Walleye movement between Black Bay and the main basin of Lake Superior outside of the bay varies temporally, and that movement direction depends on the previous location of Walleye. I also aimed to test the hypothesis that within the Black Bay population of Walleye, there is variation in movement strategies with some individuals undertaking active migrations, while others remain as sedentary residents. I then sought to evaluate the hypothesis that active migratory Walleye grow larger and faster than their resident counterparts. Finally, I assessed thermal-optical habitat conditions available to Walleye in different areas of Black Bay and the nearby portions of Lake Superior's main basin, and compared this to Walleye occupancy of these regions to test the hypothesis that the timing of Black Bay Walleye movement is driven by the spatial and temporal availability of optimal thermal-optical habitat conditions. This

information will add to the body of knowledge describing Walleye movement strategies and life history variation.

2.3 Methods

Fish capture and tagging

Adult Walleye were captured within Black Bay, immediately outside of the mouth of Black Bay, as well as along the lower Black Sturgeon River (Table 2.1; Figure 2.1). These fish were intra-coelomically fitted with acoustic tags (Vemco V16, V13) and released at their respective capture sites. Acoustically tagged Walleye were also fitted with an external Floy tag for identification in the case of recapture. In total, 155 Walleye were tagged during the spring and summer seasons (May to July) of 2016 (n=94) and 2017 (n=61). Walleye tagging followed procedures approved by the Canadian Council on Animal Care (Lakehead University AUP #05 2017) and took place on shore near capture locations. Initial tagging procedures used clove oil (60 mg clove oil/L water) in order to anesthetize Walleye, and in 2017 electric fish handling gloves (32 V-39 V, 4 mA-25 mA; Smith-Root, Vancouver, WA) were adopted. Electric fish handling glove settings were adjusted to individual fish, initially exposing the Walleye to low electrical current and voltage, and increasing both until the fish was immobilized. Anesthetized Walleye were placed in a padded trough for surgery, where an acoustic transmitter was inserted into each fish via a small incision on the ventral side posterior to the pelvic girdle. Walleye gills were irrigated throughout the surgery process, and the incision was closed using 3 sutures (polydioxanone absorbable monofilament; Ethicon, Somerville, NJ). In order to promote high and consistent fish survival and recovery, only two experienced surgeons carrying out the same procedures were used in this study. Walleye anesthetized using clove oil were allowed to recover in an aerated tank for 15-30 minutes prior to release, while Walleye anesthetized using

electro-anesthesia gloves were released as soon as possible due to their rapid recovery time (typically less than 30 seconds).

Fish tracking

During the open water season of 2016 (May-November) acoustic receivers (n=32; Vemco VR2W, VR2AR; 69 kHz) with omnidirectional hydrophones were deployed within and outside of Black Bay as part of the Great Lakes Acoustic Telemetry Observation System (GLATOS) to detect acoustically tagged Walleye. All receivers were deployed using an anchor and float system, resulting in the receiver being suspended 0.5-1.5 m off bottom. The receivers were arranged in 5 gates at significant ecological and management boundaries (Figure 2.2). These correspond with the boundary of the recreational fishing sanctuary at Bent Island (BEI; n=9), the mouth of Black Bay at George Point (GEP; n=5), Edward Island outside of the mouth of Black Bay (EDI; n=7), the Sibely Peninsula towards Thunder Bay (SIP; n=2), and the Black Bay Peninsula towards Nipigon Bay (BLP; n=3). In addition to this, 6 receivers were deployed in sentinel positions (Figure 2.2), corresponding to the Black Sturgeon River Mouth (BSR), Hurkett Cove (HUC), the Wolf River Mouth (WOR), Pearl Harbour (PER), Copper Point (COP), and Squaw Bay (SQB). Hayden et al. (2014) spaced gate receivers in Lake Huron 1000 m apart based on simulations to ensure 100% detection efficiency of passing Walleye. Because changing environmental conditions can influence detection range (Kessel et al. 2013), the gate receivers used in this study were placed 800 m apart to further ensure maximum detection rate.

In order to confirm high detection efficiency at the BEI, GEP, and EDI receiver gates, I simulated receiver line performance based on range testing carried out by the Ontario MNRF. Logistic regressions were fit to the range test data, and used to characterize the probability of detection with increasing distance from a receiver in each gate. Simulated passes of 10000

Walleye were then pushed through each receiver line at swim speeds of 1.0 m/s, which is above

the maximum sustained swimming speed for Walleye found by Peake et al. (2000). Tag

transmission intervals ranged from 120-360 seconds to match the minimum time delay between

transmission in tags deployed in this study, and potential maximum time delay between tag

transmissions in the case of misfires. Walleye detection probability for each gate was

determined by the proportion of fish detected at least twice in the simulation.

Prior to ice up, receivers in water shallower than 5 m were removed to prevent receiver

damage and loss, leaving 24 receivers over winter (November-May). All gate receivers were re-

deployed for open water season of 2017 (May-November), as well as an expansion of the array

to include a grid-work of receivers in the north end of Black Bay (Figure 2.3; NOR; n=13, 5 km

spacing), and sentinel positions (Figure 2.3; Black Sturgeon River-BSR, Wolf River-WOR, Thunder

Cape-CAP, Sawyer Bay-SAW; n=4). Receiver maintenance and data downloads took place each

spring and fall.

Movement and survival

Walleye movement and survival was determined using a multistate mark-recapture

model (Brownie et al. 1993; Hestbeck et al. 1991) analyzed in Program MARK (White & Burnham

1999). States were designated as the areas between receiver gates (Figure 2.4), and state

occupancy by each fish for each capture occasion was determined by a weighted average of

detections across both gates and sentinel receivers placed in the north end of Black Bay. This

produced a condensed encounter history for each acoustically tagged Walleye describing

movement throughout and outside of Black Bay. A tagged Walleye could transition from one

state to another with probability $\psi_{h,k}$ (where h denotes the initial state, and k denotes the next

location) or remain in the initial state with probability 1-ψ_h where $\psi_h=\sum\psi_{h,k}$ for all possible k. An

assumption of the multistate mark-recapture model is that prior to detection in the next capture

occasion, each detected Walleye has survived the previous occasion in its initial state with

probability S_h. There is an additional capture probability term that states that a Walleye may be

captured with a probability of p_k. If a Walleye is not detected it may have perished (with a

probability of $1-S_h$) or simply not been observed (with a probability of $1-p_k$). Each parameter of

the multistate-mark recapture model can be time dependent (t), state dependent (g), constant

across states and time (.), or dependent on both time and state (t*g).

Movement and survival were assessed with capture occasions every month, as well as

every two weeks. Candidate models were constructed and run in Program MARK, and top

explanatory models for both monthly and bi-weekly occasions were selected on the basis of AIC_c

where a ΔAIC_c of greater than 2 was used to indicate that models were not the same (Burnham

& Anderson 2002). The top model chosen was used to determine time and state dependence

on the transition, survival, and capture probabilities. Parameter estimates from the top

candidate model were then used to assess movement and survival throughout, and immediately

outside of Black Bay.

Walleye detected in both 2016 and 2017 (n=62) were selected from the larger study

population and assigned migration patterns based on the maximum outbound extent from the

mouth of the Black Sturgeon River at the northern end of Black Bay. Since almost all fish were

detected on the receiver grid in the north end of Black Bay at some point, this was considered

an appropriate indicator of migration distance. Any Walleye detected beyond the George Point

(GEP) receiver line (mouth of Black Bay) were considered migratory, while Walleye whose

maximum outbound detection was at, or within the George Point receiver line were considered

resident. A paired *t*-test of maximum travel distance achieved by each fish in 2016 and 2017

was used to test for consistency in migration patterns between years. Differences in age and

total length between migratory and resident Walleye were evaluated with Welch two sample *t*-tests in order to account for unequal variances (resulting in degrees of freedom that are not whole numbers), using fish for which these data existed (n=53).

Growth

Walleye growth patterns were determined by back calculating length at age using the Fraser-Lee method. All spines were prepared by an experienced technician at the MNRF. Only those spines with clearly defined annuli were used in this analysis (n=53). Measurements of dorsal spine annuli were carried out in Image J (Schneider et al. 2012), and were taken from the focus to the edge of each annulus along the horizontal elongated transect. The Fraser-Lee assumption of proportional growth between dorsal spine radius and total length was assessed for Black Bay Walleye by regressing length at capture against dorsal spine radius at capture with a linear model. Von-Bertalanffy growth curves ($L = L_\infty(1 - e^{-k(t-t_0)})$), where: *L*= length (mm) at age *t* (yr), L_∞=asymptotic maximum length (mm), *k* is the Brody growth rate coefficient (yr^{-1}), and t_0= hypothetical age at which length is 0 mm), were fitted to both the migratory and resident Walleye back calculations of length. For both migratory and resident growth curves, t_0 was constrained to zero to avoid variation in this value impacting comparisons of L_∞ and *k* between migratory and resident fish, as parameters within the Von-Bertalanffy equation can be correlated (Pilling et al. 2002). Error around parameter estimates were generated using bootstrapping, and comparisons of parameter estimates and associated confidence intervals were used to determine significant differences between the growth patterns of resident and migratory Walleye from Black Bay.

Habitat use

Optimal Walleye habitat area was defined as the available optimal thermal-optical

habitat area (TOHA), or the benthic area where temperature and light conditions were optimal

for Walleye productivity. For the northernmost and southernmost states, monthly secchi disk

readings were taken during the open water season of 2017. Data on surface illuminance for

2017 was collected from the Experimental Lakes Area near Kenora, Ontario using a Kipp and

Zonen SP Lite Sensor (Data provided by Ken Sandilands, IISD-ELA). Due to its similar latitude and

climate patterns to Black Bay (Columbo et al. 2007), and lack of illuminance data for the Black

Bay region, this station was used as a proxy of average monthly surface illuminance. The hourly

maximum and minimum depths at which optimal light conditions existed for Walleye in Black

Bay were calculated using the equation: $z = \frac{-z_{sec}}{k} \cdot log_e(\frac{I}{I_{0,t}})$, where: z=depth in m (calculated

for both maximum and minimum preferred light intensity of Walleye), z_{sec}=secchi depth in m, k

is a turbidity parameter (set to 2.1), I=light intensity in lux (68 lux for maximum preferred light

intensity by Walleye, 8 lux for minimum preferred light intensity by Walleye), and $I_{0,t}$=surface

light intensity in lux for each hour as in Lester et al. (2004). Hourly maximum and minimum

optical depth preferences were averaged for each monthly period corresponding to the

multistate mark-recapture model in order to determine the depth range providing Walleye with

preferred light intensities for each monthly period. A vertical temperature profile was also

created for the northernmost (max depth=14 m) and southernmost (max depth =70 m) states

from temperature loggers deployed at 1m intervals from 2-20 m depth, 5 m intervals from 20-40

m depth, and a logger at 50 m depth. Monthly temperature averages at each depth were used

to determine the depth range at which conditions were optimal for Walleye productivity. The

overlap in depth ranges from the optimal optical habitat, and optimal thermal habitat, were

then used to determine the optimal thermal-optical habitat depth range for Walleye in each

state during each capture occasion. TOHA was calculated for both states during each monthly

capture occasion by calculating the bottom area of Black Bay that fell within the optimal depth

ranges in ArcGIS 10.5 (Environmental Systems Research Institute, Redlands, California) using a

digital bathymetry model on a 30m by 30m cell raster derived from a 5m contour map of Black

Bay.

Walleye habitat occupancy for each monthly capture occasion was determined by the

number of fish assigned to each state used in the multi-state mark recapture model. Walleye

occupancy in the northernmost and southernmost states was then compared to the available

TOHA in the respective state using a linear regression. Data on Walleye occupancy and TOHA

was then combined from both states and fit to a linear model to determine if a significant trend

exists across states.

2.4 Results

Walleye tagged in 2016 ranged in age from 5 to 16 years (mean=9.6 years) and ranged

in length from 471 mm to 782 mm (mean=612 mm). Walleye tagged in 2017 ranged in age from

4 to 14 years (mean=9.5 years) and ranged in length from 389 mm to 792 mm (mean=590 mm).

Of the 155 Walleye fitted with acoustic transmitters over both years, 144 were detected at least

once on the receiver array (n=84 tagged in 2016, n=60 tagged in 2017). 138 of the tagged

Walleye were detected north of the Bent Island gate at least once, and Walleye were detected

within the north end of Black Bay throughout the tracking period. Detections of Walleye on the

George Point and Edward Island receiver gates began in June, and Walleye began to be detected

on the peninsular receiver gates in July and August. Throughout 2016 and 2017, 65 Walleye

were detected at or beyond the Edward Island receiver gates, with the number of detections at

these gates peaking in September and October. In 2016, of the 37 Walleye that were detected

outside of Black Bay, all but one returned to the bay by the following winter. Individual

movement patterns were highly variable with some fish exhibiting a great deal of movement

back and forth between gates, while others traveled in a more linear fashion (Figure 2.5).

Simulated detection probabilities were above 99% for each gate enclosed by land (BEI=99.98%,

GEP=99.99%, EDI=99.95%).

The top candidate models from the multistate mark recapture modelling for both

monthly and bi-weekly capture occasions were $\psi(g)p(t)S(.)$, indicating that for the period of

tracking, Walleye movement was not time dependent. Transition probabilities from one state

to another (ψ) did, however, depend on the original state (Figure 2.6). The probability of

acoustically tagged Walleye being detected (p) was not state dependent, but did vary with time,

with detection probabilities remaining above 80% except for the months of October-February

(Figure 2.7). Finally, the survival probability from one month to another (S) of acoustically

tagged Walleye was 97.9% and was consistent across states and time. For monthly capture

occasions, the ΔAIC_c for the closest alternative model [$\psi(g)p(t)S(t)$] was 5.238 (Table 2.2),

indicating differences do exist between the top model and all other candidate models (Burnham

and Anderson 2002). This is also true for the bi-weekly capture occasions closest alternative

model [$\psi(g)p(t)S(g)$] (ΔAIC_c=3.7836; Table 2.3).

Migration patterns among Black Bay Walleye did not follow consistent patterns across

the population. While almost all fish were detected in the north end of Black Bay during the

winter months, the outbound extend of migration could be split into two sub-groups. Of the 62

Walleye detected in both 2016 and 2017, 29 were not detected further south than the receiver

gate at George Point. These Walleye (hereafter referred to as 'resident') consistently remained

within Black Bay during both 2016 and 2017 (Figure 2.8). 33 Walleye detected in both 2016 and

2017 were detected beyond the George Point receiver line, travelling as far as the Edward Island

gate, the Sibley Peninsula gate, or the Black Bay Peninsula gate (Figure 2.8). Of these migratory

fish that were detected in both years, only 3 undertook this migration in 2016, but not 2017. A

paired t-test of migration distance from the north end of Black Bay for fish detected in 2016 and

2017 indicated individual migration strategies did not significantly differ from year to year

(t=1.4017, df=61, p=0.1661). Migratory Walleye did not differ in mean age from resident

Walleye (t=-0.03, df=50.66, p=0.97) however, the total length of migratory Walleye

(mean=629mm) was greater than those that remained resident (mean=588mm; t=-2.91,

df=50.21, p=0.005).

When fit to Von-Bertalanffy growth curves, the 95% confidence intervals surrounding

the curvature parameter (Brody's k) of the resident and migratory Walleye overlap, indicating

the curvature of their growth patterns do not differ (Migratory: k=0.3685 95%CI=0.34486-

0.3939; Resident: k=0.4046 95%CI=0.3796-0.4317; Figure 2.9). The 95% confidence intervals

around the final asymptotic lengths for migratory and resident Walleye do not overlap,

however, indicating that migratory Walleye grow larger than their resident counterparts

(Migratory: L_∞=654.98 95%CI=642.49-667.17; Resident: L_∞=600.25 95%CI=590.79-609.95; Figure

2.9). A linear model showed a significant positive relationship between Walleye total length at

capture and dorsal spine radius at capture ($F_{1,51}$=36.22, R^2=0.40, p<0.0001).

Linear regressions relating occupancy to available TOHA suggest that Walleye increase

their use of habitat outside of Black Bay when the amount of available TOHA increases

($F_{1,3}$=99.26, R^2=0.96, p=0.002; Figure 2.10). While Walleye occupancy does not significantly vary

with available TOHA in the north end of the bay ($F_{1,3}$=0.03, p=0.87), the occupancy values fall

near to those predicted by the TOHA model from outside of Black Bay (Figure 2.10). A linear

regression of combined occupancy and TOHA data from both the north end of Black Bay, and

outside of Black Bay was significant ($F_{1,8}$=56.72, R^2=0.86, p<0.0001), but violated the assumption

of homoscedasticity (Figure 2.10).

2.5 Discussion

Acoustically tagged Walleye were detected at all of the receivers deployed within the study area. During the summers of 2016 and 2017, almost half (47%) of all detected Walleye left Black Bay for short durations. Many of these fish (23%) swam towards nearby Thunder Bay, while comparatively few (6%) swam outside of the Black Bay Peninsula towards Nipigon Bay. The remainder of the detected Walleye (53%) were consistently detected within Black Bay, and reached asymptotic lengths 55mm shorter than their migratory counterparts. Hayden et al. (2014) detected a slightly lower proportion of Walleye reaching the mouth of Saginaw Bay (56.5%) than were detected reaching the mouth of Black Bay in my study (66%). This is not surprising, given that Saginaw Bay is twice as long as Black Bay and has 5 times the surface area, affording Walleye in Saginaw Bay more potential habitat. However, unlike Black Bay, the thermal regime within Saginaw Bay often exceeds the preferences of Walleye and may provide a strong motivation for out migration (Hayden et al. 2014). Walleye detected in both 2016 and 2017 displayed largely consistent degrees of outbound migration suggesting that while movement patterns vary within the population of Black Bay Walleye, they do not vary considerably from year to year. Additional and ongoing tracking data from 2018 and beyond will help to confirm this pattern.

Sexual dimorphism presents an interesting hypothesis for the cause of the observed disparity in migration and growth patterns of Black Bay Walleye. While reliable sex identification was not available during the tagging of fish, some observations support the notion that migrants and residents are sexually segregated. First, the growth trajectories of migratory and resident Walleye closely resemble the sexual dimorphism seen in the growth of many species of percids, with females growing larger than males (Henderson et al. 2003). Second, both the migratory and resident growth plots contain a small group of fish that diverge from the

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growth trajectory of the majority of the fish and closely follow the trajectory of the opposite

movement strategy. This may be evidence of females having a higher propensity to migrate

than males, with only a few males showing migratory behavior, and a few females showing

resident behavior. Walleye in Lake Huron did not differ in overall migration distance based on

sex however, they did differ in the timing of migration, with females leaving spawning grounds

and reaching distant receiver gates prior to males (Hayden et al. 2014). If Walleye in Lake

Superior have a shorter migration period when compared to the southern Great Lakes due to a

shorter growing season, female Walleye may have a greater chance to leave the bay than males.

Male Walleye have been reported to have lower feeding activity compared to females in order

to reduce predation risk, resulting in slower growth (Rennie et al. 2008). Reductions in

predation risk seems unlikely given the large size that adult Walleye attain in Black Bay

regardless of sex however, male residency through life may be an artifact of reducing predation

risk as juveniles. Future tagging endeavors that are able to reliably determine sex, or the

development of reliable sexing techniques using genetics taken from already tagged Walleye

may help confirm this hypothesis.

As with the Walleye observed in this study, within-species variation in growth rates and

movement patterns have been documented in a number of species. Within Lake Superior,

coaster brook trout display two widely known variations in life history involving a migratory lake

dwelling group, and a resident stream dwelling group (Robillard et al. 2011). The brook trout

that enter Lake Superior grow faster and larger than those that remain in tributaries, with the

two groups existing in different trophic niches (Robillard et al. 2011). Likewise, acoustic

telemetry of Eurasian Perch (*Perca fluviatilis*) has revealed the presence of "fast and slow life

histories" (Nakayama et al. 2016). In this case the individuals may also fit into highly mobile or

more sedentary life history classes that utilize different niches, as predicted by the Pace of Life

Syndrome Hypothesis (POLS; Nakayama et al. 2016).

Overall movement patterns were spatially dependent, but did not vary temporally for

either the monthly or bi-weekly capture occasions. Transition probabilities from states within

Black Bay to those outside of Black Bay were lower than the probability of remaining within the

bay. This is probably due to the large number of resident Walleye which remained within Black

Bay all year and contributed a great deal to the likelihood of low rates of transition between

states. As Walleye were found further and further from the north end of Black Bay, their

probability of transitioning to the southernmost state increased. The inbound transition

probabilities of Walleye found outside Black Bay to any state closer to the north end of the bay

were very consistent. This suggests that once outside of Black Bay, some Walleye are likely

making slow, indirect movements back into the bay, while others are making fast, direct

migrations back to the north end. While migrations out of Black Bay were observed most often

during August, September, and October, the routes of migration varied a great deal. Some

Walleye took more direct routes, while others used frequent back and forth trips that were

short in duration. This likely led to difficulty in modelling temporal dependence in migration

timing. The outbound migrations of Walleye from Black Bay observed here were much later

than those from Saginaw Bay, which largely occurred in May, June, and July (Hayden et al.

2014). Likewise, Walleye tagged during spring spawning in the Thames River were found to

migrate out into Lake St. Clair, and from there travel to Lake Huron by the end of May (Ferguson

& Derksen 1971). Temperature is known to be among the most important factors influencing

Walleye production (Lester et al. 2004), and is thought to influence Walleye movement (Hayden

et al. 2014). Given the relatively cold water temperatures of Lake Superior when compared to

Lakes Huron and Erie, Walleye out migration from the comparatively warm waters of Black Bay may be delayed until adequate water temperatures are reached in the main lake basin.

Indeed, I found that Walleye do not make any appreciable use of the area outside of Black Bay unless the water conditions meet those within their thermal-optical optima. As the benthic area that falls within these requirements increases, so too does the occupancy of Walleye within this area. The secchi depths from outside of Black Bay did not vary greatly over time, except for one particularly deep reading in September. As such, changes in temperature likely represent a strong driver in the available habitat for Walleye outside of Black Bay. This trend of increased Walleye occupancy with increasing TOHA is not evident in the north end of Black Bay. An extension of the predictive trend of Walleye occupancy to available TOHA from outside of Black Bay does pass near the data from the north end of Black Bay, which suggests that TOHA is likely still an indicator of available Walleye habitat in the north part of the bay. However, the actual occupancy in the north end of Black Bay consistently falls just below the predicted occupancy from the trend outside of the bay. If Walleye are not yet limited by habitat in the north end of Black Bay, it may not act as a driver of occupancy to the same degree as it does outside of the bay. The thermal regime within Black Bay also never exceeded the optimal levels for Walleye, and therefore does not likely act as a driver of out migration in the same way that alternative forage might. Access to forage outside of Black Bay, however, may be limited by Walleye habitat availability until water temperatures increase to levels within Walleye preferences.

Two additional factors that can heavily influence habitat use and movement in fish are predation risk and growth (Brönmark et al. 2014). For Walleye in Black Bay, predators can come in the form of humans participating in the recreational fishery, or commercial by-catch. Surprisingly, survival estimates for Walleye within, and immediately outside of Black Bay

remained consistent spatially and temporally. Migration, therefore, is unlikely to provide any

refuge from predators. This may be due to an overall lack of fishing pressure on the bay, due to

the small number of anglers who access the resource and the lack of a commercial fishery.

Forage preferences or density may, however, cause a Walleye to make the decision to migrate

out of Black Bay.

Optimization of forage intake can be a strong driver behind migration, leading to a

greater energetic surplus that can be directed towards growth and reproduction, than more

sedentary strategies (Roff 1988). In the case of Black Bay Walleye, migratory and resident fish

follow similar rates of approach to asymptotic length however, the asymptotic length reached

by the migratory Walleye exceeds that of their resident counterparts by 55 mm. This suggests

that, although migratory Walleye are expending more energy than the resident fish in order to

travel greater distances, the forage that they are accessing likely has a greater energetic value

than that found within Black Bay. Roff (1988) demonstrated that migratory species tend to

grow larger and faster than resident species. This concept may hold true for within population

variants as well, given that Walleye in Black Bay grow to different sizes depending on their

movement pattern.

There are a number of potential factors that can drive the divergence in behavioral

strategies observed in Black Bay Walleye. In addition to sex, genetics and age have both been

proposed as candidate variables in other populations. Genetically separate subgroups of

Walleye populations have been shown to exist in Lake Erie however, these groups are separated

by the use of different spawning areas (Ferguson & Derksen 1971; Strange & Stepien 2007). The

Walleye from Black Bay appear to be largely descendants of those from the Black Sturgeon

River, suggesting a common genetic source (Garner et al. 2013). Furthermore, the collapse of

the Walleye population in Black Bay in the 1960s represented a genetic bottleneck (Garner et al.

2013), further reducing diversity and the chances that genetic divergence might drive the within

population differentiation observed here. Since stocking events appear to have contributed

very little to the genetic pool of Black Bay Walleye (Garner et al. 2013), there is little evidence

that genetic differences between wild and introduced populations are divergent life history

strategies. If a lack of genetic differentiation between migratory and resident Walleye in Black

Bay exists, it would be similar to the circumstances surrounding coaster brook trout migration,

where lake and tributary dwelling variants return to the same areas to spawn and do not

represent genetically distinct populations (Robillard et al. 2011).

Ontogenetic shifts are also unlikely to be contributing to the differences in movement

strategy, as I found no difference in ages between migratory and resident fish. All Walleye

tagged in this study were between 4 and 16 years old. Age at maturity for Walleye in

Northwestern Ontario is typically 4-5 years (Morgan et al. 2002), suggesting the majority of

tagged fish were beyond their juvenile stage, the transition from which being where one would

expect to see a change in behavior. Additional study, such as tagging juvenile fish and tracking

them through maturity, is required to assess the changes in movement behavior involved with

maturation of Walleye in Black Bay, as has been observed in Lake Ontario (Chu et al. 2004).

There was little movement of Walleye from Black Bay towards Nipigon Bay, via the

outside of the Black Bay Peninsula. This complements previous Walleye mark recapture work in

Nipigon Bay and Black Bay that found a very low proportion of Nipigon tags in Black Bay, and no

Black Bay tags in Nipigon Bay (Ryder 1968). A large proportion of Walleye did, however, migrate

from Black Bay towards nearby Thunder Bay, providing evidence of a possible association

between populations from the two bays. Interestingly, Garner et al. (2013) reported genetic

associations between Black Bay Walleye, and those from Thunder Bay. Genetic data from

historical samples of Black Bay Walleye consistently showed weak relationships with those from

an inland lake, initially stocked with individuals from Thunder Bay (Garner et al. 2013). In addition to this, Walleye deemed to be genetically similar to those from Thunder Bay have been found in Black Bay (Garner et al. 2013). Since their year class was not consistent with those of stocked fish, they are believed to have been migrants from nearby Thunder Bay (Garner et al. 2013). While the genetic relationship between Black Bay and Thunder Bay reported by Garner et al. 2013) was weak, observations from the current study of Black Bay Walleye demonstrating migration towards Thunder Bay lends support to the idea of some degree of mixing between the two populations that deserves further study. Population mixing by Walleye in other Great Lakes has been well documented; both lakes Huron and Erie contain panmictic Walleye populations, and mixing between the two lakes can occur (Hayden et al. 2014; Strange & Stepien 2007).

Detection probabilities were spatially consistent throughout the tracking period, and remained high (>80%) during the open water season. In addition to this, simulated detection probabilities along receiver lines were very high (>99%). This suggests that during the tracking period, receivers were appropriately deployed to assess Walleye space use within the study region. Detection probabilities declined drastically during the months of October-February, likely due to two factors: (1) reduced receiver coverage, and (2) reduced Walleye activity. In order to avoid ice damage, acoustic receivers in less than 5m of water were removed during winter, providing a greater area for tagged Walleye to avoid detection. The detection probabilities during March and April (prior to ice out and receiver re-deployment), however, rose back above 80%, indicating that receiver coverage at the gates was still high enough to detect increased Walleye movement as spawning approached. Prior to ice up, Walleye concentrated in the north end of Black Bay, which may act as a winter refuge before spawning. This area is large and shallow, preventing the use of acoustic receivers to track Walleye during the winter, and thereby providing a large area for Walleye to avoid detection. The lack of

detections along gates, however, indicates that Walleye did not leave the north end of Black Bay during this period.

The understanding of the migratory potential of Walleye in Lake Superior found here builds on that carried out in the southern Great Lakes. Only recently has behavioral data on Walleye movement become available, reflecting only single year patterns (Hayden et al. 2014). My study provides evidence for repeated annual patterns of residency and migration for Walleye in the Great Lakes, and begins to propose potential connections to life history and potential population mixing for a group of fish previously thought to be distinct from others in Lake Superior. This understanding of migration patterns and population mixing for an exploited species is important when considering management actions on a waterbody that crosses many borders. Continued cooperation by researchers and expansion of telemetry arrays across Lake Superior, as has been done on the other Great Lakes, will lead to further discoveries related to the extent of migration and population mixing. This will allow the distinction of appropriate management zones when setting harvest limits and fishing sanctuaries.

Given that Black Bay once provided the largest commercial harvest of Walleye on Lake Superior, and that Walleye from Black Bay out migrate, it has the potential to act as a source population to nearby portions of Lake Superior. Understanding the geographic extent of Walleye migration out of Black Bay, as well as the proportion of fish swimming to different portions of the lake will provide clues with respect to the degree of connectivity within the lake. If Black Bay is to act as a source population to other fisheries, appropriate management actions must be considered. The modelling framework used to assess Walleye movement and survival in this study will provide a method to determine if fish survival varies spatially or temporally in Black Bay, as well as other populations. This will allow managers to assess the effectiveness of

sanctuaries currently in place, such as that on the north end of Black Bay, or determine areas with reduced survival where sanctuaries can be created.

Understanding long term shifts in movement and survival is important when considering the management of fisheries in the face of climate change. Lake Superior has yet to see the level of ecological change experienced in the southern Great Lakes (Sierszen et al. 2014) however, climate change is expected to lead to a change in the species composition within the lake due to warming water temperatures (Cline et al. 2013). Climate change may have a particularly strong effect on the Lake Superior aquatic community, as it is one of the most rapidly warming lakes in the world (O'Reilly et al. 2015). In the face of ecological change, my study will provide a baseline of movement patterns against which to compare future changes.

The use of passive tracking acoustic telemetry technology has allowed me to elucidate a great deal of information about the broad scale movements of Walleye in Black Bay. However, there remains a large gap in knowledge surrounding the maximum extent of migration, as well as the fine scale spatial ecology of this population. Expansion of the receiver array across Lake Superior will allow future studies to determine how far these fish travel. Deployment of receivers in potential spawning areas will also allow researchers to quantify the proportion of Black Bay Walleye using each area. This is particularly important in the face of the decision to potentially remove the Camp 43 dam on the Black Sturgeon River. This dam acts as a barrier to both Walleye spawning from Black Bay, and invasive sea lamprey spawning (*Petromyzon marinus*; Furlong et al. 2006). The relative importance of this river to Walleye spawning in Black Bay, however, is poorly understood. This is important when considering the impacts of its removal.

Further study should also combine acoustic telemetry data with other forms of analysis, such as gender identification, genetics, and spatial connectivity of food webs. This will reveal in greater detail the drivers of migration and how they relate to differences in life history. It will also improve our understanding of the connectivity of habitats and populations across Lake Superior.

2.6 Figures and Tables

Tables

Table 2.1. Number of Walleye fitted with acoustic transmitters from each capture location within the Black Bay system. Captures in 2016 and 2017, as well as total captures shown.

Capture Location	Number (2016)	Number (2017)	Number (Total)
Black Sturgeon River	37	22	59
Hurkett Cove	41	6	47
Delany Island	0	14	14
Coldwater Creek Mouth	0	19	19
Pearl Harbour	3	0	3
Squaw Bay	13	0	13

Table 2.2. Top 5 candidate models for monthly capture occasions describing the effects of time dependence (t), state dependence (g), time and state dependence (t*g), and no time or state dependence (.) on transition probabilities (ψ), capture probabilities (p) and survival probabilities (S) in acoustically tagged Black Bay Walleye. AIC_c, ΔAIC_c, AIC_c weight, model likelihood, number of parameters and deviance shown.

Model	AIC_c	ΔAIC_c	AIC_c Weight	Model Likelihood	Number of Parameters	Deviance
ψ(g)p(t)S(.)	2407.8557	0.0000	0.93207	1.0000	30	1619.2802
ψ(g)p(t)S(t)	2413.9037	5.2380	0.06793	0.0729	45	1663.9335
ψ(g)p(t*g)S(.)	2433.9134	26.0577	0.0000	0.0000	81	1601.9016
ψ(g)p(t*g)S(g)	2434.4543	26.5986	0.0000	0.0000	84	1595.2231
ψ(g)p(t*g)S(t)	2442.6430	34.7873	0.0000	0.0000	97	1571.5340

Table 2.3. Top 5 candidate models for bi-weekly capture occasions describing the effects of time dependence (t), state dependence (g), time and state dependence (t*g), and no time or state dependence (.) on transition probabilities (ψ), capture probabilities (p) and survival probabilities (S) in acoustically tagged Black Bay Walleye. AIC_c, ΔAIC_c, AIC_c weight, model likelihood, number of parameters and deviance shown.

Model	AIC_c	ΔAIC_c	AIC_c Weight	Model Likelihood	Number of Parameters	Deviance
ψ(g)p(t)S(.)	4862.4568	0.0000	0.86896	1.0000	50	4163.5488
ψ(g)p(t)S(g)	4866.2404	3.7836	0.13104	0.1508	53	4160.9546
ψ(g)p(t*g)S(t)	4972.8223	65.3655	0.0000	0.0000	197	3887.0301
ψ(.)p(t*g)S(.)	5059.4471	196.9903	0.0000	0.0000	3	4457.5627
ψ(g)p(t*g)S(t*g)	5186.1336	323.6768	0.0000	0.0000	307	3843.2729
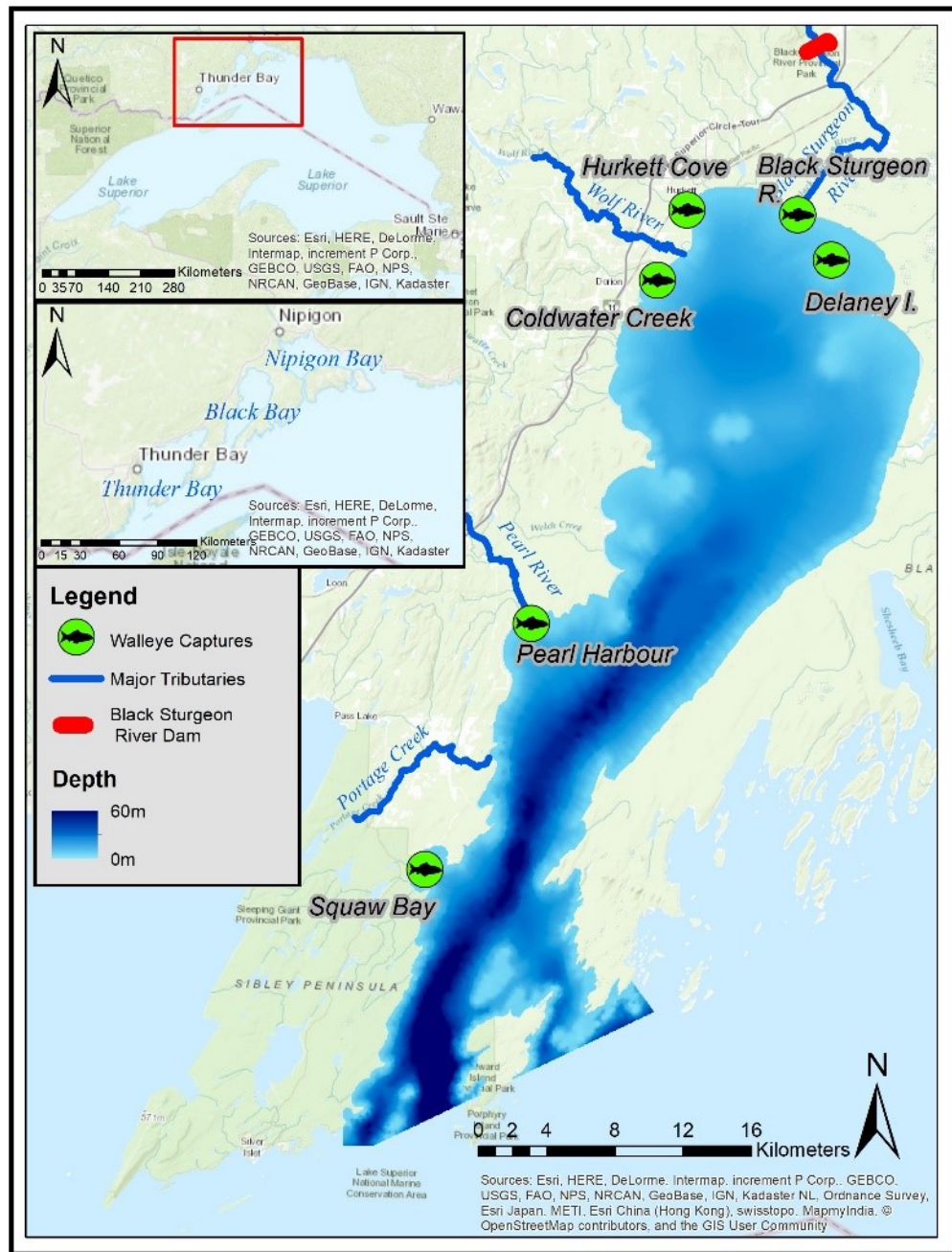
Figure 2.1. Capture locations for Walleye captured from the Black Bay study system and fitted with acoustic transmitters in 2016 and 2017.
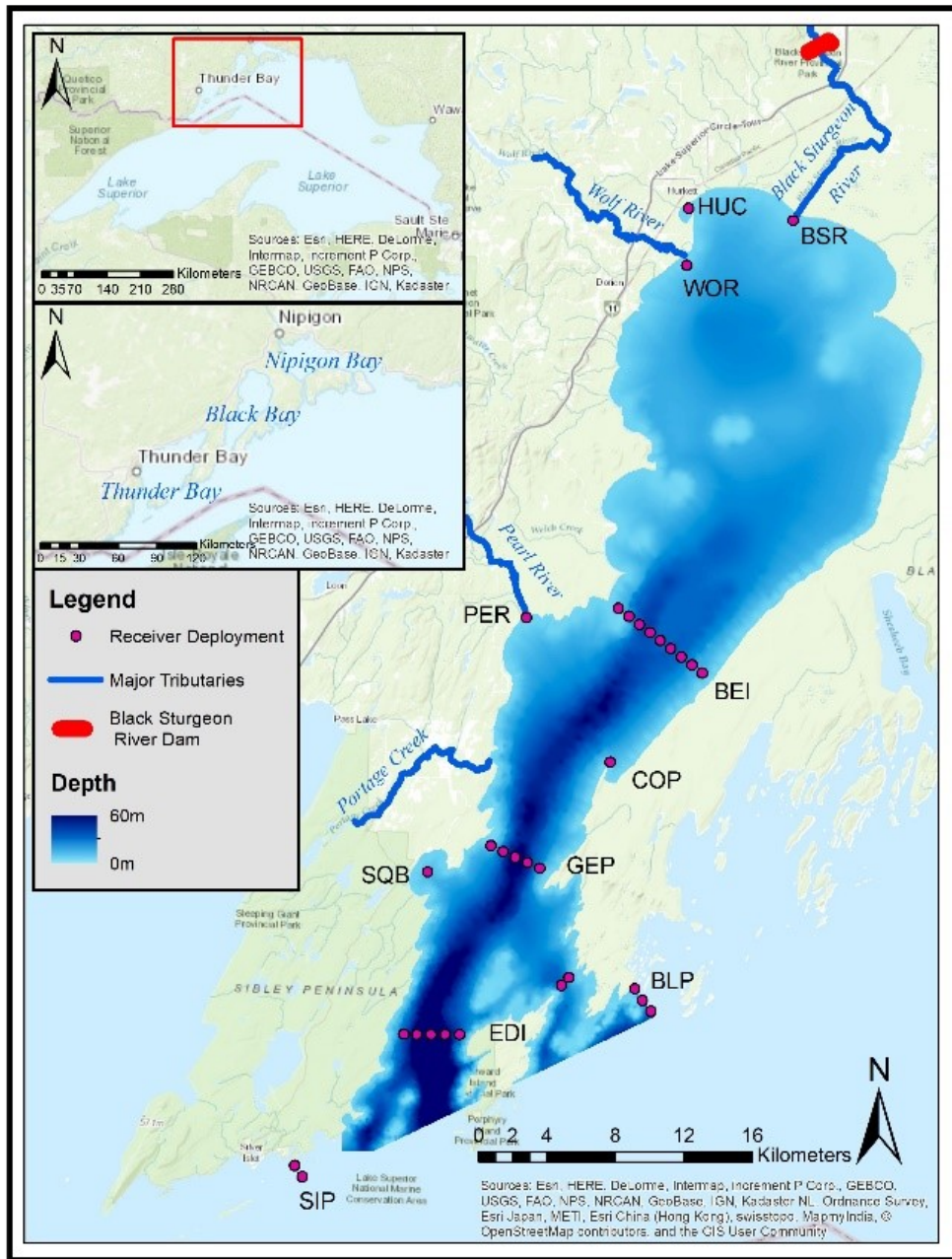
Figure 2.2. Black Bay acoustic receiver deployment May 2016-October 2016. GLATOS abbreviations shown (HUC-Hurkett Cove, BSR-Black Sturgeon River, WOR-Wolf River, BEI-Bent Island, PER-Pearl River, COP-Copper Point, GEP-George Point, EDI-Edward Island, BLP-Black Bay Peninsula, SIP-Sibley Peninsula).
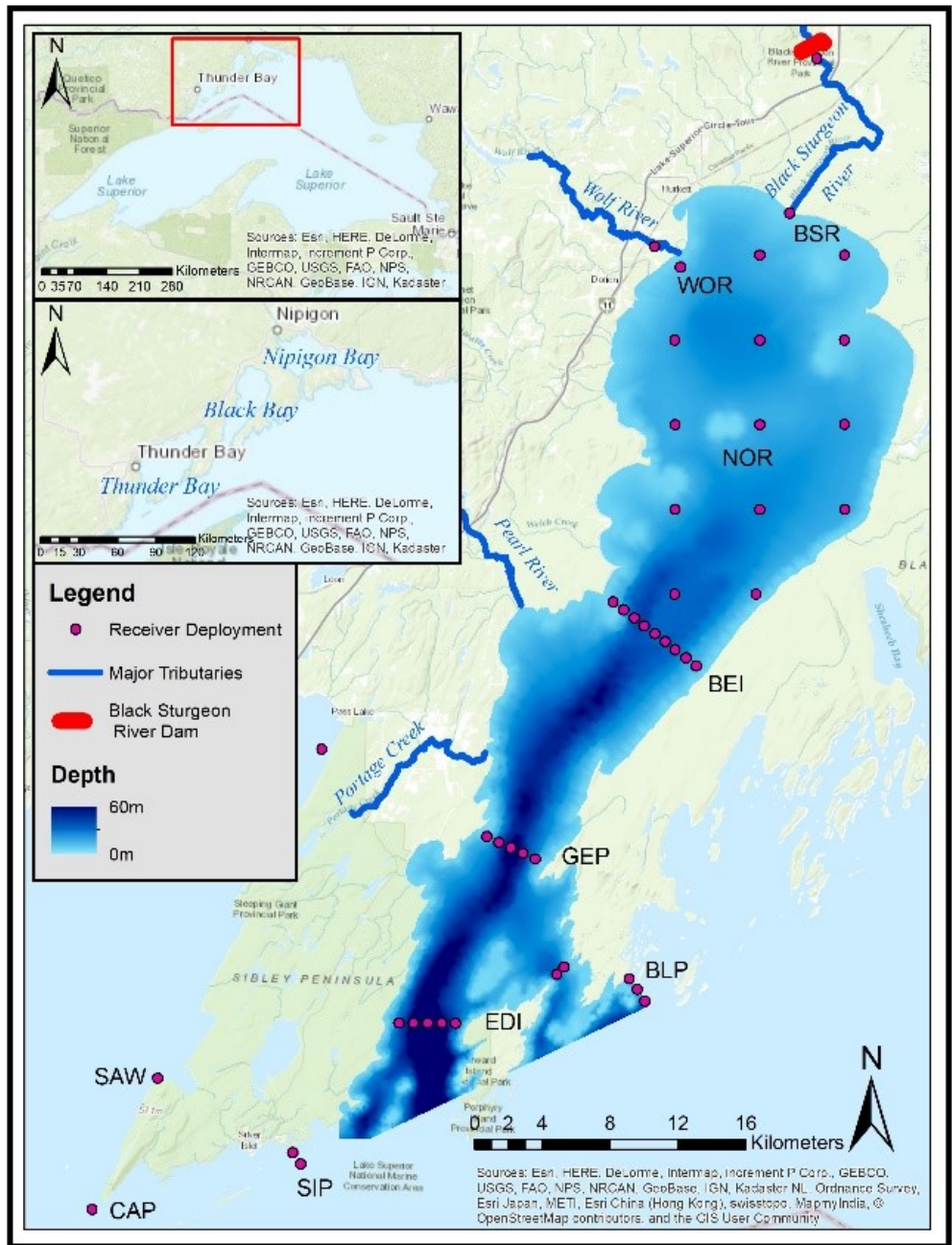
Figure 2.3. Black Bay acoustic receiver deployment May 2017-October 2017. GLATOS abbreviations shown (BSR-Black Sturgeon River, WOR-Wolf River, NOR-North Grid, BEI-Bent Island, GEP-George Point, EDI-Edward Island, BLP-Black Bay Peninsula, SIP-Sibley Peninsula, CAP-Thunder Cape, SAW-Sawyer Bay).
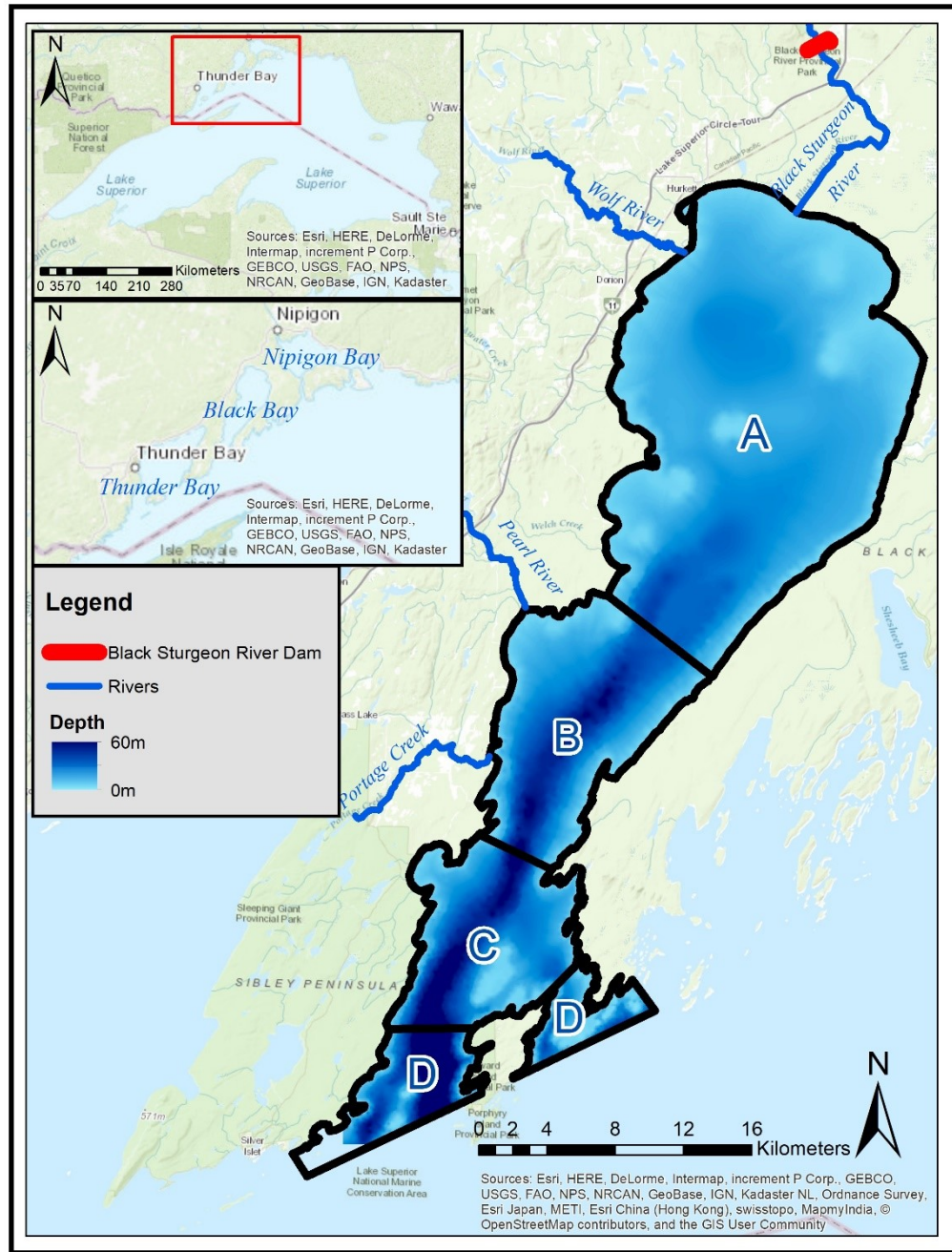
Figure 2.4. Delineation of states defined in the multistate mark-recapture model for the Black Bay study system.
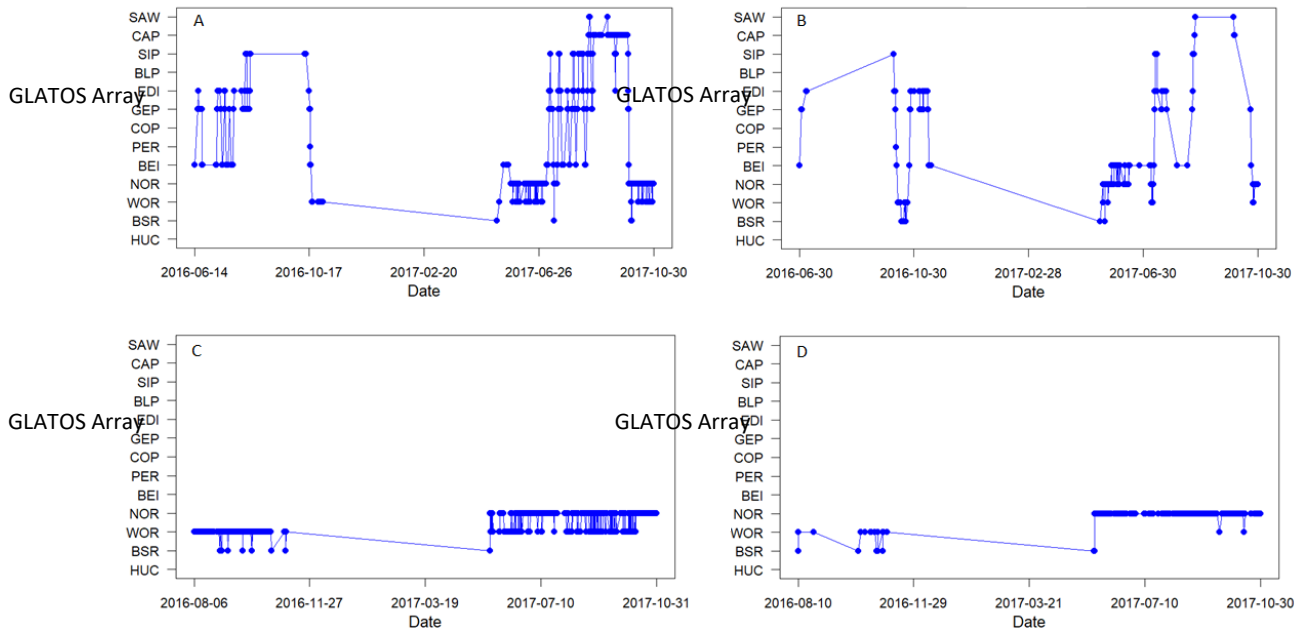
Figure 2.5. Abacus plots of individual Walleye fitted with acoustic transmitters showing detections at GLATOS Arrays (HUC-Hurkett Cove, BSR-Black Sturgeon River, WOR-Wolf River, NOR-North Grid, BEI-Bent Island, PER-Pearl River, COP-Copper Point, GEP-George Point, EDI-Edward Island, BLP-Black Bay Peninsula, SIP-Sibley Peninsula, CAP-Thunder Cape, SAW-Sawyer Bay. Plots shown for A) high frequency movements by migratory fish, B) direct movements by migratory fish, C) high frequency movements by resident fish, and D) direct movements by resident fish.
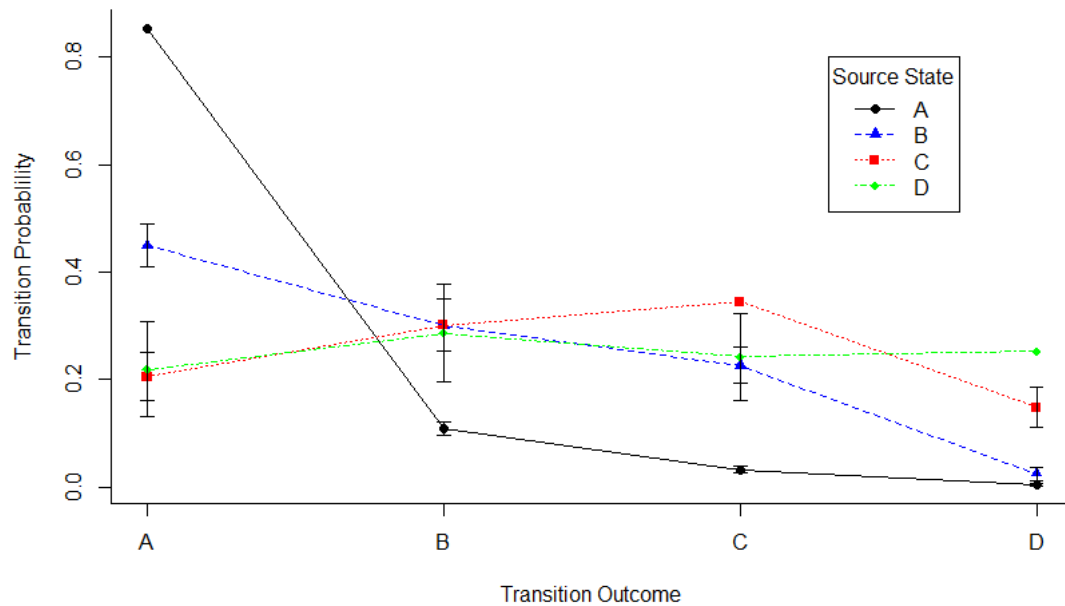
Figure 2.6. Walleye monthly transition probability between states for the area within and immediately outside of Black Bay, Lake Superior (A: North of Bent Island, B: Bent Island to George Point, C: George Point to Edward Island, D: Edward Island to peninsular gates; May 2016-October 2017). Standard error bars shown where calculated. Note: Probabilities of remaining in the same state were determined from subtraction of transitions to other states from 1, and therefore do not have error bars.
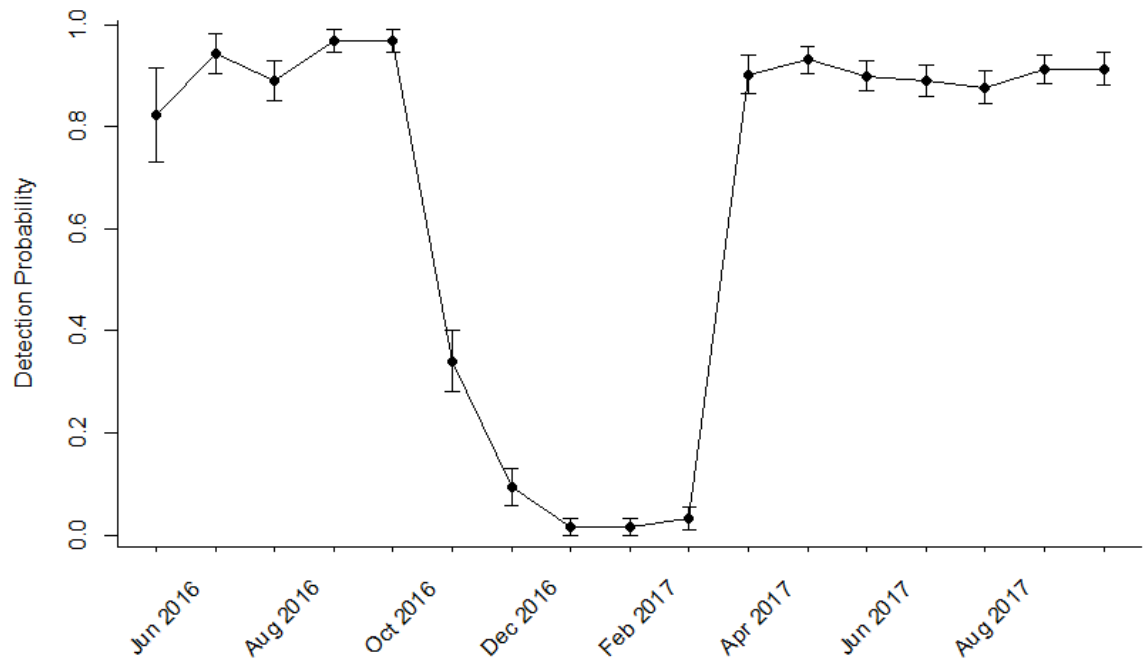
Figure 2.7. Monthly detection probabilities for acoustically tagged Walleye throughout the Black Bay study area (May 2016-October 2017).

Figure 2.8. Maximum outbound extent of gate detections for Walleye tagged in Black Bay and detected in both 2016 and 2017.
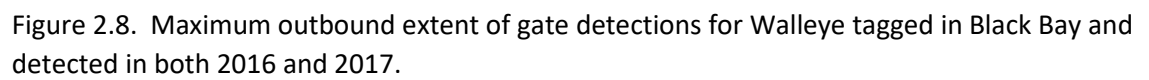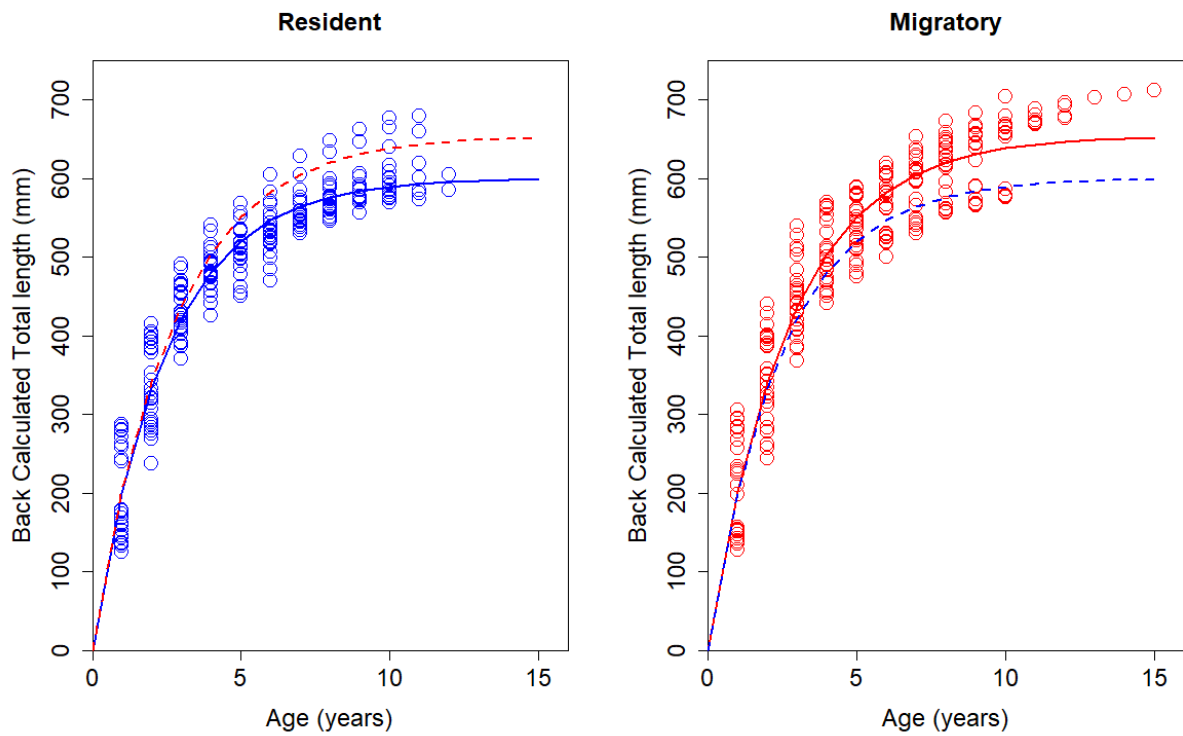
Figure 2.9. Growth trajectories of resident and migratory Walleye tagged in Black Bay, Lake Superior. Von-Bertalanffy growth curves are fit to length at age, back calculated using the Fraser-Lee method (Red: Migratory Walleye, Blue: Resident Walleye; Solid lines represent growth curves of data points, dashed lines represent growth curves of opposite movement strategy).
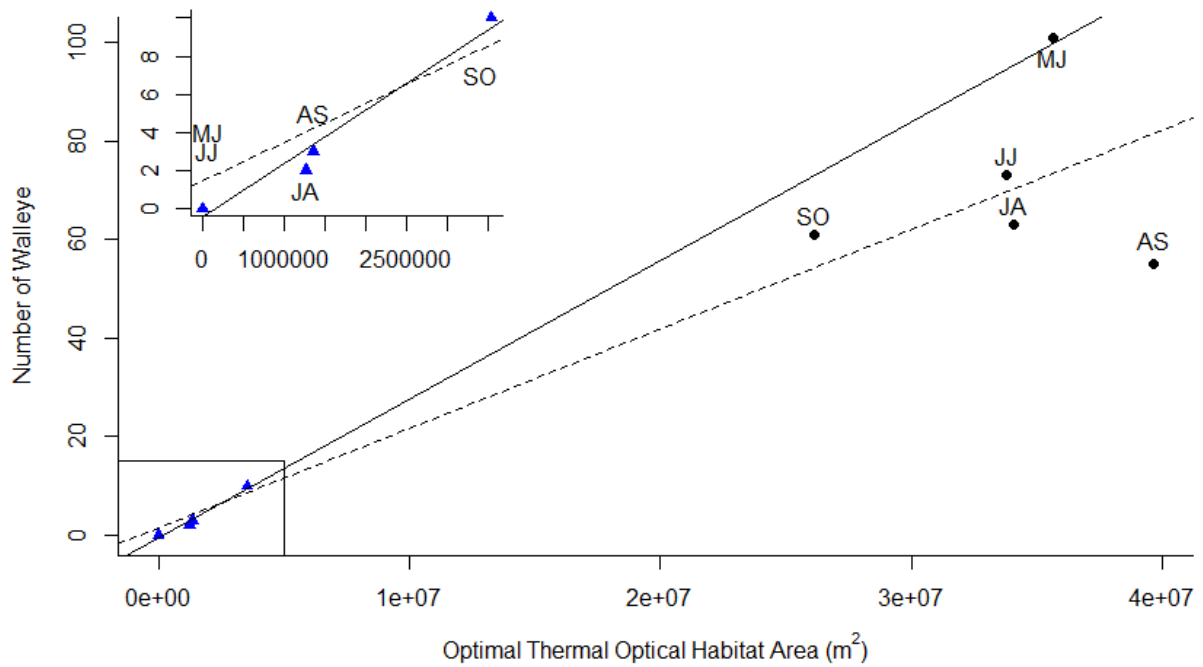
Figure 2.10. Relationship of monthly Walleye occupancy with respect to available TOHA in two regions of the Black Bay study system. Blue triangles represent data from the southernmost state, and black circles represent data from the northernmost state. The solid line shows the significant relationship for the southernmost state, extended through the data for the northernmost state. The dashed trend line shows the relationship for all data combined. Inset shows data for the southernmost state found within the box at the bottom left of the main plot. Monthly time periods of data points shown, with MJ and JJ both falling on (0,0) for the southernmost state (Abbreviations represent time periods during the study: MJ, May 15-June 14, JJ, June 15-July 14, JA, July 15-August 14, AS, August 15-September 14, SO, September 15-October 14).

3. Can prey availability and identity explain variable movement patterns in Black Bay Walleye (*Sander vitreus*)?

3.1 Abstract

The distribution of resources across the landscape can have important implications for animal movement. Spatial differences in available resources may lead to partial migration within a population. Walleye from Black Bay undergo a partial migration from the productive waters of the bay, to the oligotrophic waters of the main basin of Lake Superior. In this study I used stable isotope analysis of tissues taken from migratory and resident acoustically tagged Walleye to assess differences in forage use. Further, I assessed stable isotopes of prey species available to migratory and resident Walleye to determine the forage use by these Walleye. Finally, I used prey density estimates within and outside of Black Bay to determine if prey availability differed between the regions accessed by migratory and resident Walleye. Neither δ^{15}N nor δ^{13}C varied significantly between migratory and resident Walleye. Values of Walleye δ^{13}C fell between those of Yellow Perch (*Perca flavescens*), which are most abundant in the north end of Black Bay, and Rainbow Smelt (*Osmerus mordax*), which are most common in the south end of Black Bay. Recent estimates of prey density did not differ within and outside of Black Bay, although historically the main basin of Lake Superior held a greater density of coregonids, suggesting that current migration patterns may be a consequence of historical selection pressures.

3.2 Introduction

Fish movement patterns, as well as the drivers of these movement patterns, can vary widely within a population, and management of these fish can benefit from a better understanding of the reasons behind movement strategies. While some fish may be highly migratory, travelling great distances within a single year or their entire lifetime, others are far more sedentary, remaining resident to a single home range for most of their life (Mueller & Fagan 2008; Roshier & Reid 2003). These movement strategies are the by-product of an evolutionary history tailored towards maximum reproductive success (Brönmark et al. 2014). The distribution of resources across the landscape, such as forage, predation risk, and breeding areas, often greatly influence selection for a particular movement strategy (Brönmark et al. 2014; Hayden et al. 2014; Mueller & Fagan 2008). When resources are homogenously dispersed, residency typically becomes beneficial, whereas resources that transition across the landscape in a periodically predictable way often lead to migration (Mueller & Fagan 2008). The more mobile movement strategies are selected for when the benefits of acquiring the resources spread over a larger area outweigh the costs of relocating to the new regions (Roff 1988).

The spatial extent of the Great Lakes, along with their large variability in habitat, results in a large degree of diversity in both species composition and food web structure (Sierszen et al. 2014). Often this variation is linked to differences in depth, such as the greater abundance of *Diporiea* in shallow, nearshore sites than deeper offshore sites (Scharold et al. 2004). This in turn creates spatial differences in species presence at higher trophic levels, which can affect the diets of top predators such as Walleye. Yellow Perch and Rainbow Smelt are common in shallow, warmer environments, while coregonids tend to inhabit deeper, colder waters (Gorman et al. 2012; Mercado-Silva et al. 2006; Parker et al. 2012). The overall contribution of these prey species to the diet of Walleye can vary both spatially and temporally (Pothoven et al. 2016).

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Rainbow Smelt are often preyed upon early in the summer, while coregonids make up a greater proportion of the late summer diet (Pothoven et al. 2016). Yellow Perch, on the other hand, tend to be a common food source throughout the year (Pothoven et al. 2016).

Due to their value in commercial, recreational, and subsistence fisheries, Walleye have become one of the most intensely studied fish in the Great Lakes (Landsman et al. 2011). This has led to the discovery of the potential for long distance migration in this species, such as their 350km migration through Lake Huron (Hayden et al. 2014). Walleye are a piscivorous top predator found throughout the Great Lakes, which can exhibit a great degree of flexibility in their forage species use based on available prey (Herbst et al. 2016; Pothoven et al. 2016). Young Walleye typically feed on zooplankton and aquatic insects, and eventually undergo an ontogenetic shift to feeding on other fish as adults (Herbst et al. 2016). The most common food source for adult Walleye is yellow Perch (*Perca flavescens*), as the two species commonly overlap in habitat preferences (Pothoven et al. 2016). As generalists, however, Walleye will readily shift their diets to what forage species become available, such as invertebrates, Rainbow Smelt (*Osmerus mordax*) and coregonids (Pothoven et al. 2016).

Stable isotopes are a commonly used tool in the field of ecology for the identification of food web structure and connectivity (Hobson et al. 1999; Perkins et al. 2014). Stable isotope analysis provides a broader window into diet composition than point in time stomach content analysis, due to the relatively slow tissue turnover time when compared to gut content turnover (Hesslein et al. 1993). In lake ecosystems, carbon-13 ($\delta^{13}C$) isotopes have proven particularly useful in delineating isotopically distinct energy pathways, such as between benthic and pelagic energy channels (Harrison et al. 2016; Hobson et al. 1999). Because enrichment is small or insignificant from prey to consumer up the food chain, $\delta^{13}C$ can be used to delineate energy pathways (Perkins et al. 2014; Vander Zanden & Rasmussen 2001). By contrast, nitrogen-15

(δ^{15}N) shows significant enrichment when increasing in trophic level, typically by 3.4‰, making

it an ideal tool for identifying the trophic position of a consumer (Post 2002; Vander Zanden &

Rasmussen 2001).

While lethal sampling of fish is typically used to assess the stable isotopes found within

their tissue, research that involves populations of concern, or the subsequent release of

individuals for further study (e.g. acoustic telemetry), necessitate the use of non-lethal sampling

techniques (Fincel et al. 2012). Provided a relationship can be generated between the isotopic

signature of non-lethally sampled tissue, and white muscle (typically used in lethal sampling),

these non-lethal techniques can be used to compare individuals within and between

populations (Fincel et al. 2012). In an acoustic telemetry study, this allows researchers to

identify forage species used by tagged fish with non-lethally sampled tissue such as dorsal

spines, and compare them to differences in movement and space use.

Understanding the forage use of a fish population utilizing different movement

strategies can provide insight into the connectivity of the habitats in which they are found. This

is particularly true where populations of fish, such as Walleye, exhibit partial migration between

two distinct habitat types. Black Bay, Lake Superior represents a unique habitat compared to

the deep, cold, and clear main lake. Because Black Bay is much shallower, more turbid, and

warmer than the main basin of Lake Superior, the habitat is much more productive (Furlong et

al. 2006; Myers et al. 2009). This higher productivity supports significant populations of both

Yellow Perch and Rainbow Smelt (Furlong et al. 2006; Myers et al. 2009). While Black Bay once

supported a strong commercial fishery for Cisco, the abundance of this species significantly

declined in the 1980s, and has yet to recover to allow for a substantial fishery (Ebener et al.

2008). By contrast, nearby Thunder Bay, which represents a much more oligotrophic habitat,

has seen a recovery in its Cisco population, while holding a much more moderate population of smelt (Ebener et al. 2008; Myers et al. 2009).

Recently, the use of acoustic telemetry has tracked an annual migration of some Walleye out of Black Bay, many of which travel through the main body of Lake Superior, along the Sibley Peninsula, towards nearby Thunder Bay (Chapter 2). Migration from the warmer, more turbid waters within Black Bay to the colder, clearer waters found outside may suggest that migratory Walleye are using different resources than those that reside within the bay for the entire year. Presumably, this might lead to a greater overall energy acquisition by migrating fish, which may explain the greater average and asymptotic size of migratory Walleye when compared to the residents (Chapter 2).

Objectives

My study makes use of stable isotope analyses of samples collected from Black Bay Walleye fitted with acoustic tags, as well as putative prey species from within and immediately outside of Black Bay, to test the hypotheses that migratory and resident Walleye forage from different energy pathways and reside at different trophic levels. Population trends of Rainbow Smelt and Coregonids were also assessed within and immediately outside of Black Bay to test the hypothesis that prey density differs between these regions to determine if prey availability differs between migratory and resident Walleye.

3.3 Methods

Fish capture, tagging, and biological sampling

During the spring and summer of 2016, 94 adult Walleye were captured from 4 locations in the Black Bay study system (Figure 3.1), and fitted with acoustic transmitters following

procedures approved by the Canadian Council on Animal Care (Chapter 2; Lakehead University

AUP #05 2017). During tagging, measurements of fish length were taken, and the first three

dorsal spines were removed for ageing and stable isotope analysis. An additional 27 Walleye

were captured throughout Black Bay during the fall of 2016 in the MNRF Fall Walleye Index

Netting (FWIN) survey and lethally sampled for both dorsal spine tissue and skinless white

muscle tissue to develop a relationship between spine isotopic signatures and white muscle

isotopic signatures. Smelt, coregonids, and Yellow Perch were also captured from Black Bay and

nearby areas outside of Black Bay along the Sibley Peninsula (Figure 3.1) through both FWIN

survey gill nets and spring bottom trawls conducted by the United States Geological Survey

(USGS) vessel Kiyi with a 39 foot Yankee bottom trawl chain foot rope (Data provided by Mark

Vinson, USGS). Skinless white muscle tissue was removed from putative prey fish for stable

isotope analysis.

Movement

Walleye movement strategies were assigned to 62 acoustically tagged fish detected in

both 2016 and 2017 based on the maximum gate distance travelled from the mouth of the Black

Sturgeon River at the north end of Black Bay (Chapter 2). Walleye in Black Bay showed a

remarkable degree of consistency in migration patterns between years (Chapter 2) however, 3

fish did not follow consistent patterns of migration or residency, and were removed from the

current analysis. An additional 3 Walleye were removed from the analysis because the epoxy

used to prepare the dorsal spine for aging prevented access to tissue for stable isotope analysis.

Acoustically tagged Walleye were divided into two groups to assess connectivity between

habitat within Black Bay, and that outside of the mouth of the bay: (1) Walleye that passed the

George Point (GEP) gate and reached the Edward Island (EDI) gate were assigned to the

migratory group (n=28), and Walleye that were not detected further outside of Black Bay than the George Point (GEP) gate were assigned to the resident group (n=28).

Diet

Forage use and trophic positioning of resident and migratory Black Bay Walleye were determined through the analysis of $\delta^{13}C$ and $\delta^{15}N$ from dorsal spine tissue taken from acoustically tagged fish. Linear models comparing FWIN Walleye spine isotopic signatures and white muscle signatures showed no relationship for either $\delta^{13}C$ ($F_{1,25}$=1.45, R^2=0.02, p=0.24) or $\delta^{15}N$ ($F_{1,25}$=2.78, R^2=0.06, p=0.11). Paired t-tests were therefore used to determine if a difference existed between white muscle $\delta^{13}C$ and $\delta^{15}N$ in Walleye from spine signatures. $\delta^{15}N$ was not significantly different between muscle and spine tissue (t=1.87, df=26, p=0.07), so no $\delta^{15}N$ correction was applied to the acoustically tagged Walleye spine tissue. Spine tissue, however, was found to be significantly enriched in ^{13}C by 3.06‰ when compared to white muscle (t=-10.62, df=26, p<0.0001). As such, spine $\delta^{13}C$ was corrected in acoustically tagged Walleye to be representative of white muscle values for comparison to putative prey isotopic signatures. In order to determine if seasonal differences existed in the isotopic signatures of Walleye spine tissue, $\delta^{13}C$ and $\delta^{15}N$ signatures were compared for acoustically tagged Walleye (captured May to July), and Walleye captured in the FWIN program (September to October) using Welch two-sample t-tests. Relationships of length to $\delta^{13}C$ and $\delta^{15}N$ signatures were also tested for acoustically tagged Walleye spines in both the migratory and resident groups with linear regressions, to assess potential changes in diet as the fish grow. Both the $\delta^{13}C$ and $\delta^{15}N$ compositions of the migratory and resident Walleye were compared using Welch two sample t-tests. The $\delta^{13}C$ and $\delta^{15}N$ signatures of every prey group (Black Bay Yellow Perch, Black Bay smelt, Black Bay coregonids, main lake smelt, main lake coregonids) were compared using single factor ANOVAs, to determine if differences existed between potential diet items available to

resident and migratory Walleye. Where significant differences were found, a Tukey's Honest

Significant Difference post-hoc test was used to identify where these differences occurred.

All stable isotope samples were prepared in tin cups, weighed, and sent to Isotope

Tracer Technologies (Waterloo, Ontario, Canada) for analysis on a Finnigan Mat DeltaPlus

Isotope Ratio Mass Spectrometer (IRMS) with ConFlo III Interface (Bremen, Germany) coupled

with a CE instruments EA 1110 CHN (Italy). δ^{13}C was determined based on the standard Vienna

Pee Dee Belemnite and δ^{15}N was determined based on the standard of air. Analytical error

associated with the determination of δ^{13}C and δ^{15}N was determined by the laboratory to be

0.2‰ and 0.3‰, respectively. Paired t-tests were run on periodic repeated samples of fish

tissues in order to confirm sample error in the current study.

Prey Density

Annual smelt and Coregonid biomass density measurements were determined for both

Black Bay and the region around the Sibley Peninsula, based on the average biomass collected

from a series of trawls carried out by the USGS in each bay. Contemporary smelt densities in

Black Bay and the Sibley Peninsula, determined by dividing the total biomass from trawls by the

hectares swept, were compared for the years of 2010-2016 using a paired t-test. Because smelt

density estimates were not available within Black Bay during 2012, this year was excluded from

the analysis. This was repeated for densities of coregonids found in the two regions for these

years. Data on prey densities for 2010 to 2016 were used because prey densities during this

period appear relatively stable following a general decline since the 1980s (Figure 3.2, Figure

3.3), and so represent the most current population levels. Comparisons of prey densities

between Black Bay and the Sibley Peninsula were also carried out using paired t-tests for the

years of 1989-1996 for both smelt and coregonids. This provided historical comparisons of prey

availability between the two regions with a similar temporal window to the analysis of recent

population densities.

3.4 Results

Acoustically tagged Walleye ages ranged from 5 to 16 years (mean=9.6 years) and

lengths ranged from 471 mm to 782 mm (mean=612 mm). Length did not have a significant

effect on either $\delta^{13}C$ ($F_{1,26}$=0.72, R^2=-0.01, p=0.40) or $\delta^{15}N$ ($F_{1,26}$=0.29, R^2=-0.03, p=0.59) in the

resident group of acoustically tagged Walleye. Likewise, in the migratory acoustically tagged

Walleye $\delta^{13}C$ did not vary significantly with length ($F_{1,26}$=4.10, R^2=0.10, p=0.053), nor did $\delta^{15}N$

($F_{1,26}$=2.48, R^2=0.05, p=0.13). Neither $\delta^{15}N$ nor $\delta^{13}C$ significantly differed between Walleye

captured in the spring and summer acoustic tagging program, and Walleye captured in the FWIN

program ($\delta^{15}N$: t=-1.40, df=48.66, p=0.17; $\delta^{13}C$: t=-0.12, df=35.31, p=0.91). Welch two sample t-

tests found no significant differences between resident and migratory Walleye with respect to

$\delta^{15}N$ (t=-0.80, df=40.83, p=0.43) or $\delta^{13}C$ (t=-0.84, df=52.89, p=0.41).

An ANOVA of prey $\delta^{15}N$ showed significant differences between groups ($F_{4,52}$=9.25,

p<0.0001). A Tukey's honest significant difference post hoc test showed that Yellow Perch

captured in Black Bay had significantly depleted $\delta^{15}N$ signatures compared to smelt captured in

Black Bay, as well as those captured along the Sibley Peninsula (Figure 3.4). In addition, Black

Bay Yellow Perch were significantly depleted in $\delta^{15}N$ compared to coregonids captured along the

Sibley Peninsula (Figure 3.4). No other comparisons of groups were significantly different with

respect to $\delta^{15}N$. An ANOVA of prey $\delta^{13}C$ also showed significant differences between groups

($F_{4,52}$=85.56, p<0.0001). A Tukey's honest significant difference post hoc showed that

differences existed between all group pairs except three. Black Bay smelt did not significantly

differ from smelt captured along the Sibley Peninsula, or from coregonids captured in Black Bay

(Figure 3.4). Coregonids captured in along the Sibley Peninsula, likewise, were not significantly

different from smelt captured in along the Sibley Peninsula (Figure 3.4).

Paired t-tests of repeated tissues analyzed for stable isotopes indicated mean values

comparable to reported analytical error, with no significant difference among paired samples for

either δ^{13}C (mean of differences=0.028‰, *t*=-0.17, *df*=24, *p*=0.87) or δ^{15}N (mean of differences=-

0.15‰, *t*=-0.42, *df*=24, *p*=0.68).

Smelt density was not significantly different between Black Bay and the Lake Superior

waters along the Sibley Peninsula during the period of 2010-2016 (*t*=1.38, *df*=5, *p*=0.23; Figure

3.2). Coregonid density, likewise, was not significantly different between Black Bay and the

Sibley Peninsula from 2010-2016 (*t*=2.52, *df*=5, *p*=0.053; Figure 3.3). The significance of this

difference was borderline, though, with Black Bay having on average 0.74 kg/ha fewer

coregonids than the Sibley Peninsula during this period. While smelt density did not differ

between Black Bay and the Sibley Peninsula between 1989 and 1996 (*t*=1.27, *df*=6, *p*=0.25;

Figure 3.2), the coregonid density was 3.8 times higher along the Sibley Peninsula than within

Black Bay during the period of 1989-1996 (Mean of differences=2.65 kg/ha, *t*=3.81, *df*=6,

p=0.009; Figure 3.3).

3.5 Discussion

Stable isotope analysis suggests that Black Bay Walleye do not differentiate in their

forage use, despite the distinct movement strategies and habitats used by the migratory and

resident fish. Since coregonids are highly energy dense (Pothoven et al. 2016), one might expect

them to contribute more significantly to the diets of the larger migratory Walleye than the

smaller residents. They do not, however, contribute to the isotopic signature of migrators to a

greater degree than residents. While the δ^{13}C of Sibley coregonids in this study was the most

depleted of any prey group, migratory Walleye have a very similar δ^{13}C signature to the resident

Walleye, and do not reflect this depletion. This is surprising since the migratory Walleye tend to

grow larger than their resident counterparts (Chapter 2), even though the migrators presumably

consume more energy travelling to habitat outside of Black Bay. Because coregonids are far

more energy dense than the other prey species largely available in the study region (Pothoven

et al. 2016), one could expect them to offset the energy costs of migrating out of Black Bay.

Walleye in lakes with Lake Herring (*Coregonus artedi*) regularly make use of this large, high

energy food source, resulting higher growth rates than those in lakes that lack Herring

(Henderson et al. 2004).

The main basin of Lake Superior outside of Black Bay contains a similar density of

coregonids to Black Bay, despite the fact that the commercial fishery for coregonids on Black

Bay has not recovered since its decline in the 1980s (Ebener et al. 2008). The statistical

significance of this difference was borderline (p=0.053), however, and historically Black Bay

coregonid stocks were significantly lower than those found immediately outside of the bay.

While Walleye may not currently encounter a higher density of coregonids between the two

regions, this difference in abundance may have instigated migratory behavior in a subset of the

population in the past.

The larger size attained by Walleye that migrate out of Black Bay compared to those

that remain within the bay (Chapter 2) suggests that migration likely has some energetic benefit.

Reduced foraging has been observed in male Percids compared to females, which results in

smaller size (Rennie et al. 2008). This is believed to be a behavioral trait that leads to lower

predation of males (Rennie et al. 2008). Female Walleye from Black Bay may have greater

tendency to migrate than males (Chapter 2), which could be a result of risking greater travel

distances in order to acquire food. Males on the other hand, could be remaining within the

turbid waters of Black Bay, thereby reducing their risk of predation as juveniles, and maintaining this movement strategy throughout life. Partial migration of Walleye has been observed in other Great Lakes, resulting in connections with distinct habitat types (Hayden et al. 2014; Strange & Stepien 2007).

If female Walleye are indeed migrating out of Black Bay based on an historical difference in coregonid abundance, one may not always expect the isotopic signature to be evident in tissue developed during somatic growth, such as dorsal spines. Walleye somatic growth tends to occur largely in the spring and summer, while the development of ovaries in females tends to ramp up from August until October (Henderson et al. 1996). Detections of Walleye outside of Black Bay peaked during the period of August-October in both 2016 and 2017 (Chapter 2). The allocation of energy to ovarian development rather than somatic growth during this period may prevent isotopic signatures from coregonids accessed outside of Black Bay from contributing to the isotopic signatures of Walleye dorsal spine tissue.

The mean $\delta^{13}C$ values for both the migratory and resident Walleye fall between those found for both smelt and Yellow Perch, suggesting Black Bay Walleye are largely foraging on both of these species during periods of somatic growth. Previous work using stomach content analysis on Black Bay has found that Walleye primarily feed on smelt (Chiodo 2017), which are abundant within Black Bay, and have patchy abundance around Edward Island immediately outside of Black Bay (Myers et al. 2009). While Walleye are commonly known to feed on Yellow Perch due to habitat overlap, they tend to select for soft bodied fish without spiny rays when available for ease of capture (Einfalt et al. 2012; Herbst et al. 2016; Pothoven et al. 2016). Selection for spiny rayed fish by Walleye does tend to occur in situations where prey abundance is low (Herbst et al. 2016). Walleye predation on Yellow Perch in Lake Huron tends to be highest during the spring and early summer, while later in the year they shift towards softer bodied

species (Pothoven et al. 2016). The temporal window for Walleye stomach sampling by Chiodo (2017) was during the fall, a period when Walleye in Black Bay are most dispersed (Chapter 2) and can access the softer bodied smelt. The Yellow Perch population is significant in Black Bay, with a popular recreational fishery during the winter over the shallow water in the north end of the bay. Since both resident and migratory Walleye in Black Bay tend to concentrate in the north end of the bay during the winter and spring, they may experience greater competition for resources due to higher densities. This may in turn lead them to make use of the abundant Perch population during this time.

The consistency with which smelt are used in both the migratory and resident Walleye diets is perhaps not surprising, given that smelt densities within Black Bay have remained similar to those in main basin of Lake Superior immediately outside of the bay. Walleye that migrate out of Black Bay do not encounter greater densities of smelt than they would in the bay indicating foraging on this species outside of Black Bay is not providing an energetic benefit that will outweigh the cost of migrating to this region. As such, differences in smelt densities within and outside of Black Bay are likely not a driver of differentiation in growth patterns between migratory and resident Black Bay Walleye. Productivity in Walleye is, however, strongly linked to habitat quality (Lester et al. 2004).

The cold and clear water found in the main basin of Lake Superior is not typically thought of as well suited to Walleye, unlike the warmer, turbid water found within Black Bay. Walleye productivity is known to decline rapidly outside of optimal thermal and optical habitat conditions (Chu et al. 2004; Lester et al. 2004). The *tapetum lucidum* in the eyes of Walleye makes them highly effective hunters in low light conditions however, while foraging activity does increase in low light conditions, capture efficiency does not (Einfalt et al. 2012). The colder water temperatures in the main basin could also allow Walleye to feed less often, as a slowed

metabolism could allow a greater proportion of energy to be used for growth. In Lake Huron, Walleye living in Saginaw Bay require 10-18% higher consumption than those migrating to, or living in the main basin of the lake in order to achieve similar growth rates (Pothoven et al. 2016). Like Saginaw Bay, Black Bay represents a unique habitat when compared to the larger lake in which it is found. However, Saginaw Bay is often warmer than the upper thermal limit of Walleye (Hayden et al. 2014), while optimal conditions for Walleye productivity can be found within Black Bay throughout the summer (Chapter 2). This means that other factors are likely contributing to discrepancies in growth rates beyond habitat conditions alone.

The values of δ^{13}C in Yellow Perch from Black Bay are the most enriched of all groups, which is indicative of a littoral food source (Vander Zanden & Rasmussen 1999). Rainbow Smelt, by comparison, have more negative values of δ^{13}C, suggesting that they take part more heavily in the pelagic food chain (Vander Zanden & Rasmussen 1999). Furthermore, Black Bay smelt are indistinguishable from main basin smelt based on their δ^{13}C signatures suggesting that the spatially separated food webs of these groups are interconnected. Both migratory and resident Walleye from Black Bay forage from the littoral and pelagic food webs to the same degree. This suggests that there is a great deal of intermixing between the food webs of Black Bay and the main basin of Lake Superior.

Rainbow Smelt are highly mobile (Harvey & Kitchell 2000) and may themselves migrate between Black Bay and the main basin. This would explain the similarity in δ^{13}C signatures between smelt captured both within the bay, and in the main basin, while also allowing resident Walleye to acquire the δ^{13}C signature from the main basin of Lake Superior. Migration of multiple fish species between Black Bay and nearby regions of Lake Superior may allow for a greater degree of connectivity than previously thought to exist, potentially across multiple trophic levels.

The trophic structure of the Black Bay region food web as determined by δ^{15}N suggests that Rainbow Smelt, coregonids, and both migratory and resident Walleye are on the same trophic level, with Yellow Perch falling only a fraction of a trophic level below. This, however, does not agree with the stomach content analysis by Chiodo (2017), which found that Black Bay Walleye feed heavily on smelt. The fish captured by Chiodo (2017) were all taken in fall, and only represent a snapshot of forage use, which is known to vary seasonally in Walleye (Pothoven et al. 2016). If Walleye in Black Bay vary food sources temporally, they may make greater use of invertebrates during periods when stomach samples have not been collected. Because invertebrates are lower in trophic level, they are depleted in δ^{15}N (Anderson & Cabana 2007), which could contribute to a lower δ^{15}N signature in Black Bay Walleye. Pothoven et al. (2016) found that Walleye in Lake Huron used invertebrates as a food source to a greater degree early in the spring and summer than during the later periods of the summer. They also found that there was a spatial distinction in invertebrate use between Walleye found in Saginaw Bay and those found in the main basin of Lake Huron, where Walleye found within Saginaw Bay incorporated invertebrates into their diet to a greater degree (Pothoven et al. 2016). The δ^{15}N signatures of migratory and resident Walleye from Black Bay do not differ, suggesting that if they do make use of invertebrates, it is not to a different degree. Since both groups of Walleye use the north end of Black Bay during the winter, and particularly during the spring when invertebrates tend to be abundant, they may both heavily feed on invertebrates here during this period.

Seasonal dependence on invertebrates by Walleye has also been observed in smaller inland lakes. Walleye in Oneida Lake, New York fed almost exclusively on invertebrates during May and early June (Forney 1974). Fish did not become a significant part of Walleye diets in this lake until late June, largely consisting of Yellow Perch, and not until the fall did Walleye begin

making any significant use of other fish species as prey (Forney 1974). In a chain of inland lakes

in Michigan, Walleye were found to have large trophic niche sizes, due in large part to the

population's use of a variety of forage species (Herbst et al. 2016). Because individual Walleye

specialize on prey at a variety of different trophic levels, from a variety of habitat types, the

overall populations exhibit a large variance in trophic level (Herbst et al. 2016). The error

surrounding the δ^{15}N and δ^{13}C signatures of Walleye from Black Bay is quite large, particularly in

relation to the prey groups analyzed in this study. This may be due to individual specialization

on a specific food source similar to what was found by Herbst et al. (2016).

Baseline signatures of δ^{15}N can also vary spatially (Harvey & Kitchell 2000), and

integration of these signatures into Walleye could result in confounding trophic positioning of

Walleye relative to prey species. Spatial variation in δ^{15}N can be particularly evident when

assessing space use in differing proximity to a point source of pollution (Harvey & Kitchell 2000),

such as a city like Thunder Bay. Depth can also play a role in spatial variations in baseline δ^{15}N

signatures (Vander Zanden & Rasmussen 1999). In both cases, due to the deeper water, and

closer proximity to Thunder Bay, one would expect the δ^{15}N values of fish partaking in the food

chain outside of Black Bay to be enriched, indicating a higher than true trophic level. Despite

these factors, spatial variability affecting δ^{15}N seems unlikely in this case. Yellow Perch captured

at the north end of Black Bay, in the shallowest water furthest from the city, did show depleted

δ^{15}N compared to some other prey groups. However, prey captured throughout the rest of

Black Bay did not differ in δ^{15}N from those found outside of the bay. In addition to this, there is

no difference in δ^{15}N between the migratory and resident Walleye. In the case of spatial

variability in δ^{15}N, if smelt are mixing between Black Bay and the main basin, then all Walleye

should be higher in trophic level than smelt, which is not the case. Alternatively, if only the

migratory Walleye are mixing between the areas, then they should be more enriched in ^{15}N than

their resident counterparts, as well as all prey species. This again, is not the case. A greater understanding of Black Bay Walleye foraging ecology could benefit from the understanding of baseline δ^{15}N values within the Bay, as well as a greater coverage of potential prey species available to these fish.

This work identifies a connection between two spatially separated, and physically distinct habitats in Lake Superior. Partial migration of Walleye has now been documented throughout the Laurentian Great Lakes, and this work suggests that this mixing results in connections between energy pathways. Furthermore, the mobility of fish that connects food chains may not occur in only the largest, predatory fish, but may also be a result of movement patterns by smaller prey species. This suggests that managing different regions within the Great Lakes as distinct units may not always be appropriate, as fish densities in one area may be linked to those in another. Migratory and resident Walleye were indistinguishable in this study based on δ^{13}C and δ^{15}N. This suggests that one must proceed with caution when assigning spatial differences in food web use by top predators, particularly if prey species are highly mobile, or allocation of energy to tissues varies throughout the year.

In addition to regional mixing of fish populations, this work suggests that forage species use may not be a strong driver of differentiation in somatic growth patterns for Walleye in Black Bay. The causes of these variations in growth should be a subject of future research, such as potential effects of different thermal regimes on metabolism, or differences in prey body size within and outside of Black Bay. While Black Bay Walleye may not show foraging differences based on growth pattern, individuals may still specialize on a particular type of forage, leading to a wide range of δ^{15}N values across the population. This variation within the population could provide a degree of plasticity to changes in forage abundance and species structure, as is occurring across the Great Lakes (Zimmerman & Krueger 2009).

3.6 Figures
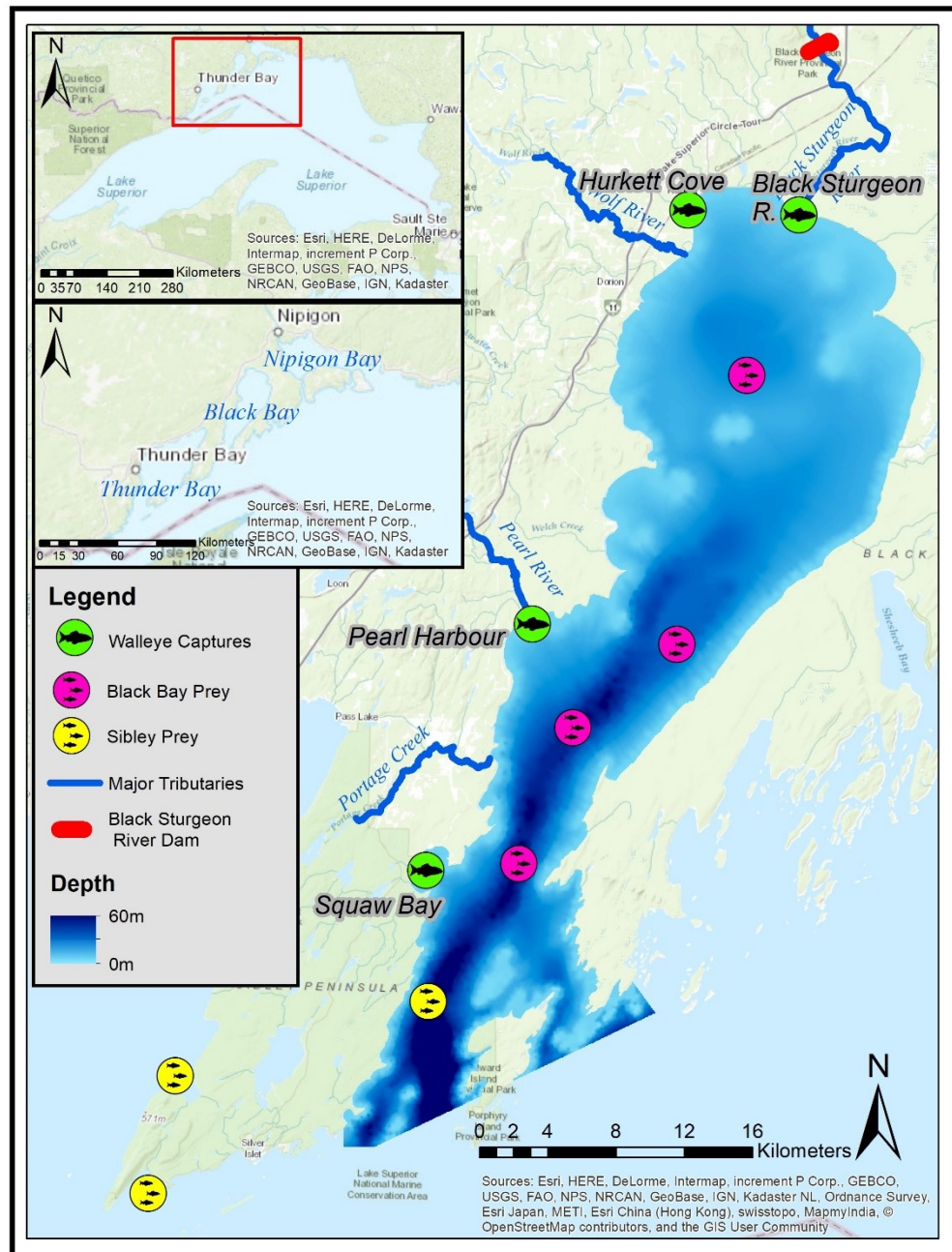
Figure 3.1. Capture locations for Walleye tagged with acoustic transmitters and sampled for stable isotopes in the Black Bay study system (2016), and prey fish captured in the Black Bay study system for stable isotope analysis (2017) and density estimates (1989-2016; Prey density data does not exist for the northernmost capture site).

Figure 3.2. Average annual Rainbow Smelt biomass density in Black Bay, Lake Superior and the Lake Superior waters along the Sibley Peninsula (1989-2016).

Figure 3.3. Average annual Coregonid biomass density in Black Bay, Lake Superior and the Lake Superior waters along the Sibley Peninsula (1989-2016).

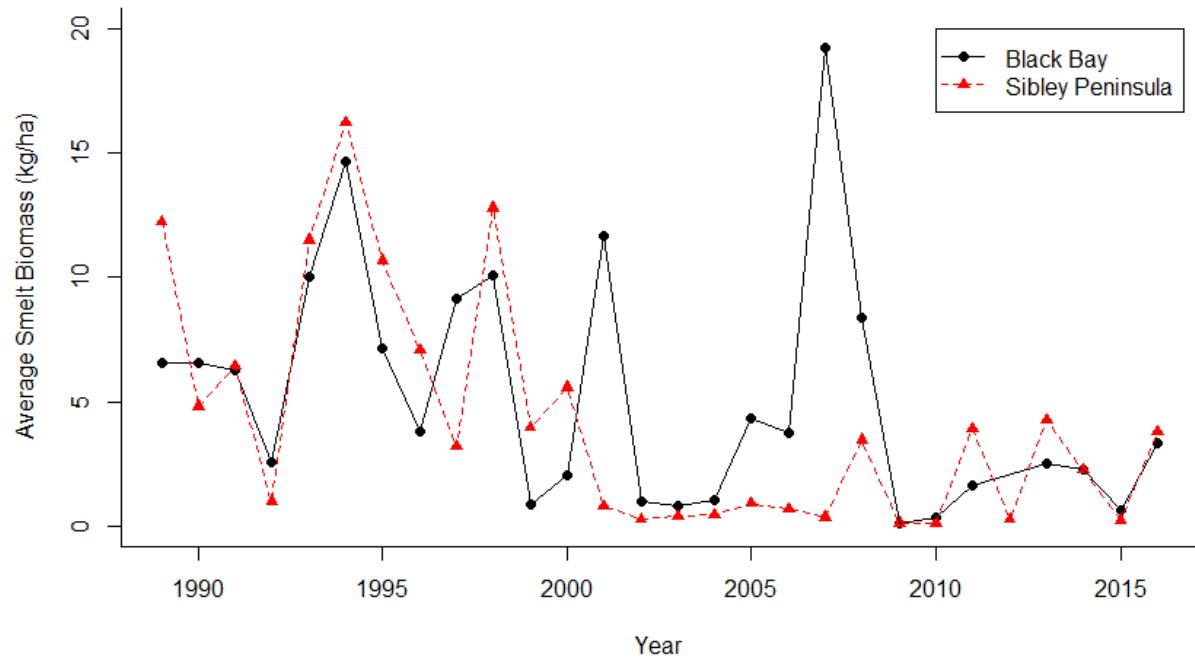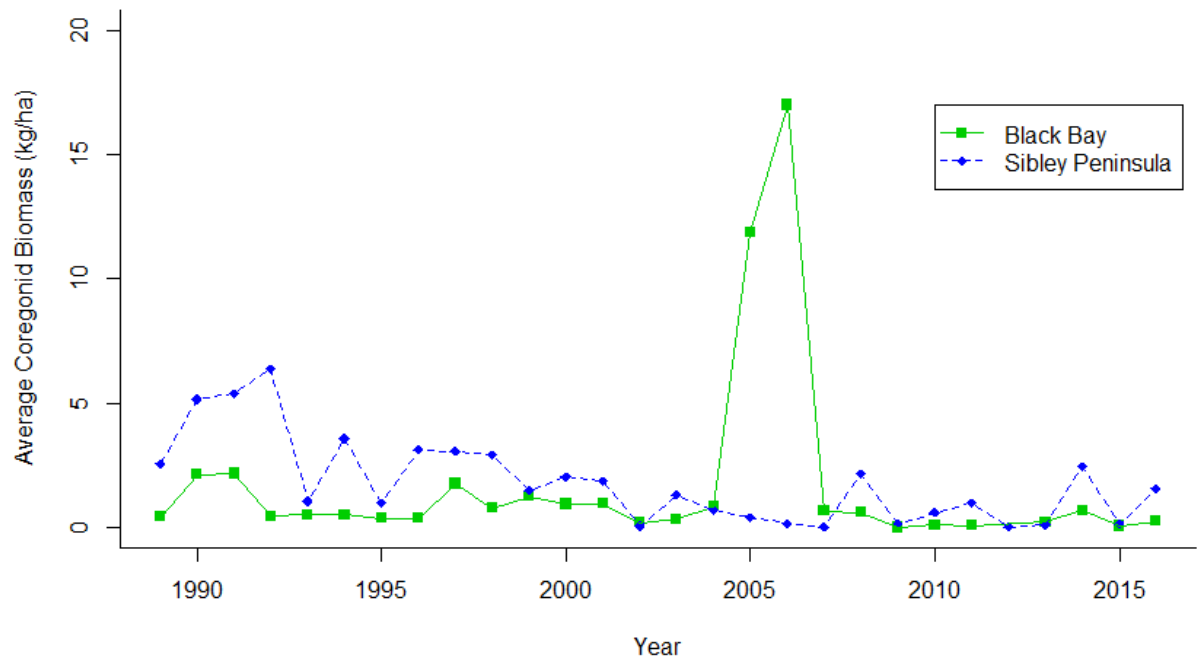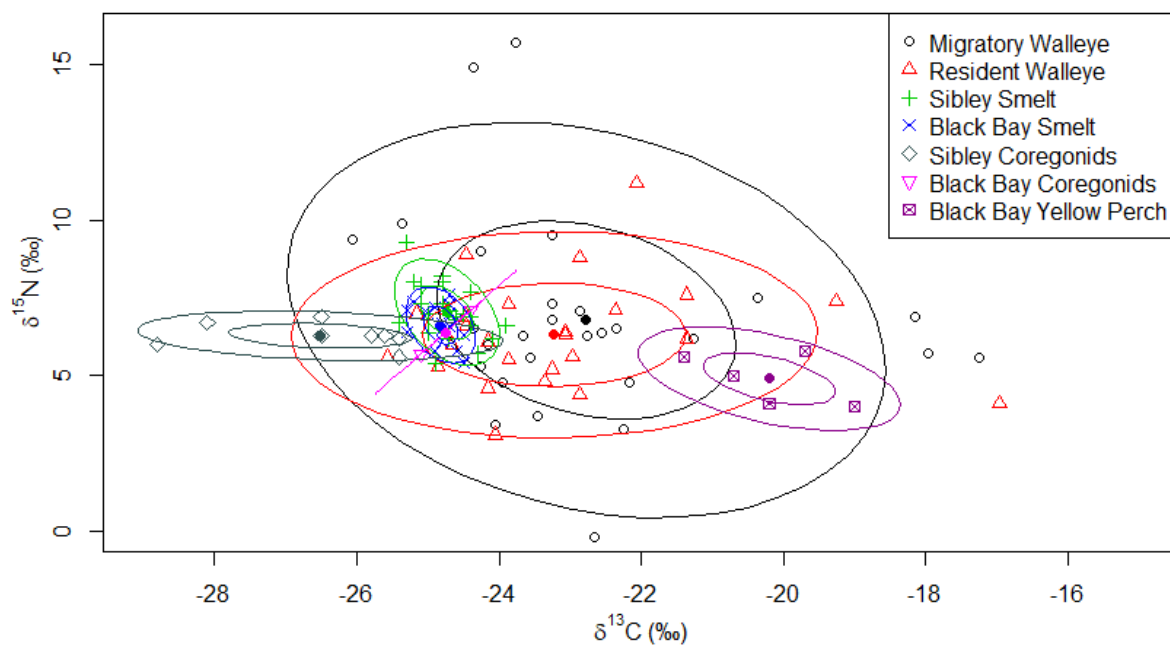Figure 3.4. Isotopic signatures from migratory and resident Black Bay Walleye, as well as available prey groups from within Black Bay and outside of Black Bay along the Sibley Peninsula. Group means are indicated by solid points. 95% and 50% ellipses are shown for each group.

4. Conclusion

Walleye movement through Black Bay and the nearby waters of Lake Superior can be divided into two categories: (1) residents that remain within Black Bay for the entire year, and (2) migrants which leave Black Bay entirely at some point during the year. The distinction of movement strategies used by Black Bay Walleye suggests that there exists a degree of variation within the population, as would be expected with the POLS (Nakayama et al. 2016). While the larger asymptotic maximum length of migratory Walleye compared to residents supports the prediction by the POLS that more mobile strategy will lead to greater growth, the monthly Walleye survival outside of Black Bay does not differ from survival within the bay. This lack of differentiation in survival is contrary to predictions that mobile strategies should lead to reduced survival however, survival was provided as an additional parameter for the entire population through the multi-state mark recapture model, and I was not able to compare survival between migratory and resident groups.

All of the Walleye tagged in my study were adults, and Walleye in Black Bay tend to be larger than those in other nearby waterbodies (Berglund 2014), which means that the risk of natural predation is likely low across the population. Furthermore, there is no active commercial fishery for Walleye on Black Bay and only a small recreational fishery, so current human caused mortality is likely insignificant. The assessment of movement strategies used by Walleye in their juvenile stage, as well as through maturation deserves more study. My study did not include juvenile Walleye which may experience the effects of predation in Black Bay, and remain in shallow turbid embayments, as Juvenile Walleye do in Lake Erie (Pandit et al. 2013). Male Walleye tend to reduce predation risk by living less active lifestyles than females (Rennie et al. 2008), and if this is true of juveniles in Black Bay, then males may retain this life history strategy through life based off of a memory of past predation risk.

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Walleye migrating out of Black Bay following the spring spawn tend to achieve greater asymptotic maximum lengths than those that remain within the bay for the entire year. The differences in growth patterns of migratory and resident fish closely match what one might expect from sexual dimorphic growth, which has been well documented in Percids (Henderson et al. 2003). Here, it appears that female Walleye may have a greater propensity to migrate out of Black Bay than males. Acoustic telemetry on Lake Huron showed a difference in the timing of Walleye migration, with females migrating earlier than males, but in this study the overall distance of migration did not vary with sex (Hayden et al. 2014). Walleye from Black Bay migrate much later than populations from the other Great Lakes (Ferguson & Derksen 1971; Hayden et al. 2014), which may relate to the cold temperatures of Lake Superior outside of Black Bay. If female Walleye do tend to migrate earlier than males, then a shorter growing season in Lake Superior may result in a larger proportion of females actually undertaking this migration than males.

Migratory Walleye did not make any appreciable use of the region outside of Black Bay until some habitat reached their thermal-optical optimum. In the north end of Black Bay, though, there was no apparent relationship between Walleye occupancy and available TOHA. This suggests that rather than driving migration of Walleye out of Black Bay, available TOHA may act as a gatekeeper preventing Walleye from leaving the bay until conditions are favorable.

Because migrating Walleye tend to reach larger sizes than their resident counterparts, there must be some energetic benefit to migration that outweighs the costs of energy lost to undertake this migration (Roff 1988). Surprisingly, migratory and resident Walleye did not significantly differ in their isotopic signatures for either $\delta^{13}C$ or $\delta^{15}N$, indicating that both groups are feeding from the same forage base and reside at the same trophic level (Vander Zanden & Rasmussen 2001). Abundances of smelt and coregonids did not differ between the regions used

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by resident and migratory fish. Historical prey densities did differ between the two regions, however, and may have acted as a driver of a migratory strategy that still remains within the Walleye population. Access to a higher density of coregonids outside of Black Bay may have allowed female Walleye to deposit this energetically dense food source into ovarian development, thereby driving the need for migration by females but not males.

Almost half of the Walleye tagged in this study were detected outside of Black Bay during part of the year, and the decision to migrate or remain resident to Black Bay was highly consistent between years. Many of the Walleye migrating out of Black Bay swam towards nearby Thunder Bay, providing a possibility for the population to overlap with Walleye from Thunder Bay. While the exact locations of Walleye spawning in Black Bay have yet to be identified (with the exception of the Black Sturgeon River; Furlong et al. 2006), all Walleye congregate at the north end of the bay during the winter prior to spawning, and remain in this area through the spring spawning period.

Understanding the geographic extent of a population is important when considering management actions. This is particularly true on the Great Lakes, which cross many geopolitical boundaries, are used by a variety of stakeholders, and are managed by a number of federal, state and provincial agencies, as well as private groups. Black Bay is of particular concern due to the Walleye collapse in the 1960s, and slow subsequent recovery (Berglund 2014). Substantial Walleye migration out of the no fishing sanctuary on the north end of Black Bay during the summer opens a large proportion of the population to potential harvest. This is particularly concerning considering females may travel the greatest distance from the sanctuary, and may spend the greatest amount of time outside of the protected area. However, survival of Walleye in this study was high, and did not differ spatially, suggesting that mortality due to angling did not increase dramatically outside of the sanctuary. In addition to this, Walleye congregate in

the sanctuary on Black Bay during the winter and spring. There is a popular recreational fishery for Yellow Perch in this area during the winter, and the sanctuary may protect incidentally caught Walleye from over exploitation.   Further study of the Black Bay Walleye is required to properly assess the effectiveness of the sanctuary, but the multistate mark recapture modelling framework used in this thesis will allow managers to assess spatial and temporal changes in space use and survival of this population. Use of this framework on Black Bay, as well as other waterbodies, will allow managers to set appropriate harvest limits, and sanctuary boundaries during suitable temporal windows.

A better understanding of how temperature and light conditions affect Walleye movement will also aid in management of this population. This is particularly true in the face of climate change, which will likely affect the spatial distribution of optimal Walleye habitat in Black Bay, and the rest of Lake Superior. Warmer water temperatures may result in longer duration migrations from the fishing sanctuary, resulting in a higher chance of mortality due to fishing. On the other hand, warmer water temperatures in the main basin of Lake Superior could result in more optimal Walleye habitat in this region, leading to an increased carrying capacity for the population as a whole.

Since Black Bay Walleye appear to forage from the same energy base regardless of what movement strategy they employ, the food webs between Black Bay and the region outside of the bay are likely connected. This probably occurs at multiple trophic levels, which should be considered when implementing management strategies across the regions. This will aid managers in predicting the outcome of management actions put in place not only on Black Bay, but also surrounding areas.

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Appendices

Appendix A

Multistate mark-recapture modelling for separated migratory and resident Walleye

To further understand the movement patterns of migratory and resident Black Bay Walleye, I modelled residents and migrants separately with the multistate mark-recapture model. This allowed me to determine if differences existed between the spatial and temporal dependence of the model parameters for these two groups. The top candidate model for migratory Walleye was psi(.)p(t*g)S(g). Transition probabilities were consistent across space and time, indicating that the initial location of a migratory Walleye had no bearing on its direction or magnitude of movement for any month. This is consistent with the near equal transition probabilities from southern states from the original multistate mark-recapture model, which were only inhabited by migratory Walleye, and is likely due to the disparity in direct vs indirect movement patterns exhibited by these Walleye. The probability of detection was both state and time dependent, but values remained near estimates from the original model. Monthly survival was state dependent for migratory fish, but remained above 96% for all states. The top candidate model for resident Walleye was psi(g)p(t*g)S(g). Transition probabilities were highest when remaining within, or travelling towards the northernmost state, indicating that residents preferred to remain largely within the northern portion of Black Bay. The probability of detection varied spatially and temporally, but remained near to values from the original model. Monthly survival was 14% lower in the state within the southern portion of Black Bay (82%) than the state in the northern portion (96%). The boundary between these two states represents the boundary to the recreational fishing sanctuary, which may provide a degree of protection to resident walleye.

Appendix B

Table B.1. Number of acoustically tagged Walleye from each capture location designated as resident and migratory.

Capture Location	Number of Resident	Number of Migratory
Black Sturgeon River	16	13
Hurkett Cove	12	15
Pearl Harbour	1	1
Squaw Bay	0	4