Causes and Consequences of Population Changes in Black Bay Steelhead, Lake Superior

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ABSTRACT

Understanding species interactions is an important component of fisheries resource management. Like the other Great Lakes, Lake Superior's fish species composition (and therefore interactions among species) has been changing for many decades. One of the largest changes in fish species composition in Lake Superior has taken place in Black Bay, with an increase in Walleye abundance since 2002 and a decrease in Steelhead abundance since 2008. However, changes in species interactions associated with this new species composition in Black Bay are unknown. I examined the potential interactions between Walleye and Steelhead in Black Bay using stable isotope analysis and life history theory. My results suggest a complex set of interactions both in stream and lake environments that may act to suppress current Steelhead populations. Specifically, I found shifts in Steelhead smolting strategies within Black Bay not observed elsewhere in Lake Superior that are consistent with size-specific increased juvenile mortality, possibly due to predation on smolts in Black Bay. Niche overlap analysis from stable isotope results showed evidence of some competition between Walleye and adult Steelhead as well as possible predation of smolts by mature Walleye in Black Bay. Furthermore, long-term analysis of Steelhead parr stable isotopes suggests significant changes in Steelhead resource use in the stream environment, possibly resulting from competition with Brook Trout

Key Words: δ^{13}C, δ^{15}N, density-dependence, fishing, North Shore, Portage Creek.

LAY SUMMARY

Steelhead populations along the North Shore of Lake Superior are a popular sport fish and have been monitored on a yearly basis since the early 1990's. During this time, most of the monitored populations have been either stable or increasing since harvest regulations were changed in the late 1990's, with the exception of Black Bay, which has seen its Steelhead population decline by approximately 90% since 2007. I used life history theory and stable isotope analysis to better understand the causes behind the Black Bay Steelhead population decline. My results indicated that there are most likely multiple factors contributing to the decline of Steelhead populations in Black Bay. These include: competition between adult and juvenile Steelhead with Walleye in the lake environment, competition between Brook Trout and juvenile Steelhead in the stream environment, and potential predation of juvenile Steelhead in the lake environment by either Walleye or other predatory fish.

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Rainbow trout (*Oncorhynchus mykiss*) scale samples were provided by the Ontario Ministry of Natural Resources and Forestry, Northwest Biodiversity and Monitoring Unit, Science and Research Branch. As well as the Upper Great Lakes Management Unit – Lake Superior.

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In memory to my fishing buddy Norm Stieh.

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GENERAL INTRODUCTION

The understanding of species interactions, specifically predation and competition, are widely-studied topics in of ecology (Bailey *et al.* 1989, Lima 1998). Predation and competition can have multiple effects on a population, such as changes in population size, natural mortality, growth, fecundity, and size and age at maturation (Sparholt 1994). Predation can affect the prey population by both killing and consuming prey, and by modifying prey behaviours to avoid predation (Mittelbach 1988). Research has shown that there are predicted prey responses when a certain group of individuals is selected against (Reznick *et al.* 1990, Hutchings 1993, Darimont *et al.* 2009). Predator avoidance by prey is also an inherently selective process (Reznick *et al.* 1990). Competition between species often results from advantages in limiting resource use between competitors, and this competitive advantage may also change depending on environmental conditions (Tilman 2007). The removal of certain individuals by predation or competition is often age and size-specific which can generate rapid phenotypic or genotypic changes in morphology and life history (Scharf *et al.* 2000, Darimont *et al.* 2009).

Life history traits can be used to evaluate the changes in a population adapting to environmental change (Coulson *et al.* 2010). Life history traits include fundamental ecological variables such as generation time, fitness, population size and structure, heritability, and genotypic and phenotypic variability (Coulson *et al.* 2010). Life history theory allows us to better understand the patterns and processes that drive species distributions and contribute to species adaptations (Mims *et al.* 2012). Moreover, life

history theory allows us to make predictions regarding how species should adapt to certain selective pressures.

Another method used to evaluate both impacts of environmental change and species interactions is stable isotope analysis of Carbon ($\delta^{13}C$) and Nitrogen ($\delta^{15}N$). Stable isotopes are often used to provide a time-integrated measure of food-web relationships based on energy flow (Vander Zanden *et al.* 1997). Stable nitrogen isotopes of $\delta^{15}N$ become enriched by 3-4‰ between successive trophic levels, thereby allowing for a measure of consumer trophic position (Vander Zanden *et al.* 1999, Post 2002). Stable carbon isotopes of $\delta^{13}C$ show very little trophic level enrichment between predator and prey and are therefore especially useful as indicators of energy sources between distinct carbon pathways (Vander Zanden *et al.* 1999, Vander Zanden *et al.* 2001). In aquatic systems, $\delta^{13}C$ allows for the differentiation between two isotopically distinct sources of potential energy, for example, either from the littoral zone or the pelagic zone. Littoral (near shore) production comes from algae and detritus whereas pelagic (offshore) production comes from phytoplankton (Post 2002). Because the littoral zone tends to be enriched more than the pelagic zone, organisms with less negative $\delta^{13}C$ tend to be more associated with nearshore feeding (Vander Zanden *et al.* 1999, Post 2002). Although stable isotopes of $\delta^{15}N$ and $\delta^{13}C$ provide useful tools for estimating trophic position and carbon source, the isotopic signature of nitrogen and carbon for a consumer is not enough to accurately estimate the trophic position and carbon source without an isotopic baseline (Vander Zanden *et al.* 2001, Post 2002). An isotopic baseline is used to control for variation in $\delta^{15}N$ and $\delta^{13}C$ among different environments. Variability in $\delta^{15}N$ and $\delta^{13}C$ baselines come from differences in the available $\delta^{15}N$ and $\delta^{13}C$ uptake for organisms at

the bottom of each portion the food web (Post 2002). In aquatic systems, stable isotopes can vary between systems and within systems. As such, creating an appropriate isotopic baseline is often one of the most challenging tasks when trying to assess the trophic position of an organism within a food web (Post 2002). Another challenge associated with stable isotope analysis is tissue turnover rates. Tissue turnover rate is the time lag before the isotopic value of the tissue is reflective of a new food source following a change in consumption (Sakano *et al.* 2005). This can present issues when trying to evaluate diets in fish as many species alter their consumption of prey items either in response to seasonality or migration (Sakano *et al.* 2005).

Identifying the ecological niche of a population is an important concept when trying to evaluate species interactions and community structure (Syväranta *et al.* 2013). The ecological niche was previously considered to be all the resources exploited by a population which could be represented by an *n*-dimensional hypervolume (Hutchinson 1957). Unfortunately, this volume is impossible to quantify (Syväranta *et al.* 2013). More recently, stable isotope ratios of δ^{15}N and δ^{13}C have been used to quantifiably measure niche space by assessing the resource use (δ^{13}C) and trophic position (δ^{15}N) for the populations in question (Bearhop *et al.* 2004, Jackson *et al.* 2011, Syväranta *et al.* 2013). Occupied niche spaces determined via stable isotope analysis imply resource use and can often shift in response to changes in competition as well as prey type and abundance (Bearhop *et al.* 2004). For example, competition for niche space among species is often reduced on islands because of species impoverishment. As a result, species that live on islands typically have a larger niche area compared to members of the same species that live on the mainland and are forced to compete for resources to a

greater degree (Bearhop *et al.* 2004). Potential competition for resources can be determined when species occupy the same niche spaces, displaying niche overlap (Swanson *et al.* 2015). Niche overlap is calculated by the probability of one species being found in the niche region in multivariate space of another species (Swanson *et al.* 2015).

One fish species that has exhibited rapid phenotypic changes in response to new or changing environments are migratory Rainbow Trout (*Oncorhynchus mykiss,* hereafter "Steelhead"). In their native habitat, Steelhead are iteroparous, anadromous Pacific salmonids that display exceptional diversity in life history traits. Because of their popularity among fisherman, Steelhead were initially stocked into the Great Lakes from the west coast in the late 1800's, with continued stocking efforts throughout the 1900's (Bronte *et al.* 2003). Adult Steelhead migrate from open waters into their natal stream to spawn. After spawning, Steelhead migrate back into open waters. Once the eggs hatch, juvenile Steelhead (termed 'parr') will live in the stream generally for 1-3 years at which point they will migrate into the lake. This process is called smolting (Shapovalov *et al.* 1954). They will generally spend an additional 1-3 years in the open water environment as sexually immature smolts, before reaching maturation and migrating up their natal stream to spawn. Once spent, they will migrate back into the lake until the following spawning migration. The Steelhead life cycle exhibits exceptional variability in both the parr and smolt life stages, both of which influence their age at maturation. The ability to spend a variable amount of time in both the stream and lake environment may provide an adaptive capacity for Steelhead to withstand ecosystem changes or size-selective pressures (Kruger *et al.* 1993).

Life history theory intuitively predicts that larger or faster growing individuals in a cohort have an advantage over smaller individuals as they have a greater tolerance for environmental extremes and a decreased vulnerability to predators relative to smaller conspecifics (Reznick *et al.* 1990, Hutchings 1993, Sogard 1997). An example of selection for larger body size in Steelhead smolts as an adaptation to changing environments can be seen through increase in the stream residency time as parr after the construction of hydroelectric dams along the west coast (McCormick 2009). Dams frequently impede fish migration, change flow dynamics, and cause a loss of habitat (McCormick 2009), and interfere with the downstream and upstream migration of anadromous fish while also influencing the water velocity and temperature (Keefer *et al.* 2004). These changes have all been observed to impact of the life histories of the fish that use those rivers and tributaries (Evans *et al.* 2004, Hodge *et al.* 2016). More modern dams are constructed with fish ladders which permit fish migration both up and downstream (Boggs *et al.* 2004). However, even when fish are able to spawn above a dam, the smolting age is often increased as the older (and larger) smolts have a better chance at migrating over the dam successfully (Raymond 1979) and evading predators that tend to congregate downstream of the dam (Raymond 1988, McCormick *et al.*2009, Marschall *et al.* 2011).

Life history theory also predicts responses of juvenile salmonids to predation (He *et al.* 1990, Jepsen *et al.* 1998, Metcalfe *et al.* 1998). For example, size-selective predation on juvenile Steelhead by Walleye (*Sander vitreus*) has been observed in the upper Columbia River (Baldwin *et al.* 2003). Once the Steelhead reached a certain size, they were either too large for the Walleye to eat, or too fast for them to catch (Baldwin *et*

al. 2003). Similar results were also found in Wyoming, where predation on stocked Rainbow Trout by Walleye. In both examples, managers stocked juvenile Steelhead at larger sizes to avoid the size-selective predation window (Yule *et al.* 2000, Baldwin *et al.* 2003).

Black Bay once supported one of the largest Walleye populations, and the largest Walleye commercial fishery in Lake Superior (Furlong *et al.* 2006). However, over-exploitation and/or the loss of spawning habitat in a major spawning tributary caused the Black Bay Walleye population to collapse in 1968 (Geiling *et al.* 1996, Furlong *et al.* 2006). Since then, there have been various rehabilitation efforts to try to restore Black Bay Walleye to historic numbers (Berglund 2016). This included the closure of the commercial Walleye fishery (1969), imposing recreational Walleye harvesting limits which closed the northern portion of Black Bay to recreational harvest (1999), transferring adult fish from other locations into Black Bay (1972, 1998-2000), and stocking of Walleye fry into Black Bay (2003-2005; Furlong *et al.* 2006, Wilson *et al.* 2007, Berglund 2016). Findings from microsatellite DNA analyses indicated that Walleye restoration efforts in Black Bay have worked (Wilson *et al.* 2007), and results from the Ontario Ministry of Natural Resources and Forestry (OMNRF) Fall Walleye Index Netting (FWIN) program also indicated that Walleye abundance has increased in Black Bay since 2002 (Berglund 2016).

Since 1991, Steelhead monitoring has been undertaken by the OMNRF in partnership with the North Shore Steelhead Association (NSSA) to gather information about the health of various Steelhead populations found along the North Shore of Lake Superior (George 1994). One of the first streams that was targeted by the NSSA and

OMNRF as a priority stream to collect data from was Portage Creek, located in Black Bay, Lake Superior. Prior to the inception of the sampling program (1991), Portage Creek Steelhead were heavily over exploited by anglers (George 1994). To obtain as much information as possible about the exploited Steelhead population, a mark-recapture study that included scale sampling and individual tagging of all Portage Creek Steelhead began in 1991. This information this was used to generate population estimates, monitor stray rates, and to validate ages of the population. In 1994, access to the lower reaches of Portage Creek became private, effectively eliminating all in-stream fishing exploitation. Based on population estimates generated by the mark-recapture program, the exclusion of angler exploitation allowed the population of adult Steelhead in Portage Creek to go from approximately 600 adults (1994) to over 2000 adults (2004). However, since 2007 the population of returning adults has declined precipitously to approximately 144 adults (as of 2018), fewer than were observed during a period of high angler exploitation (Figure 1.1). This reflects a general trend that has been seen across all the main streams in Black Bay (Coldwater Creek, Wolf River, and the Black Sturgeon River) as indicated by anecdotal evidence of poor angler success in those streams (NSSA, personal communications).

Little research has been conducted thus far on the trophic ecology of Steelhead from Lake Superior. One study analyzed the entire food web of the West arm of Lake Superior, which included both Walleye and Steelhead (Keough 1996). There, Walleye showed higher δ^{15}N levels (δ^{15}N= 9.11‰) indicating a higher trophic position relative to Steelhead (δ^{15}N=8.25‰). In contrast, Walleye and Steelhead had similar δ^{13}C values indicating similar sources of energy or mixing across littoral and pelagic habitats.

Walleye young of the year (YOY) also demonstrated the highest δ^{15}N levels out of any YOY species, suggesting that they become reliant on a piscivorous diet very quickly compared to other YOY species (Keough 1996). Based on their results, they also concluded that Steelhead in Lake Superior had a δ^{15}N ratio signature consistent with a primarily invertebrate diet (Keough 1996). From this previous research and patterns of Steelhead declines coincided with Walleye recovery in Black Bay, Lake Superior, it is plausible to hypothesize that juvenile Steelhead could be a potential prey item for adult Walleye.

OBJECTIVES

The objective of the proposed study was to better understand the causes and consequences of observed declines in the Portage Creek Steelhead population and corresponding shifts in Steelhead life history within Black Bay (using Portage Creek as an index for other Black Bay streams). I used Steelhead life history data collected from around the Lake Superior basin to provide a broader geographical context for long-term life history changes observed in Portage Creek associated with population changes. I then used life history theory to make predictions regarding the maturation schedules of Portage Creek Steelhead during time periods of different selective pressures (i.e. adult mortality, density dependence, and juvenile mortality). Adult mortality estimates along with female fecundity estimates were used to determine which life history strategies observed in Portage Creek maximize fitness and reproductive potential.

I also used stable isotope analysis to evaluate competitive versus consumptive interactions between Steelhead and Walleye in Black Bay. If Walleye were competing with Steelhead, I expected to see a large amount of niche overlap between species.

Additionally, I used isotope analysis to evaluate whether Steelhead were a common prey item of Walleye in Black Bay. If Walleye were eating juvenile Steelhead, I expected to see that they would have similar $\delta^{13}C$ values but Walleye would have elevated $\delta^{15}N$ levels (approximately 3‰) when compared to juvenile Steelhead (Vander Zanden *et al.* 1997, Post 2002, Schmidt *et al.* 2009). Finally, I examined the isotopic values for both adult and parr Steelhead from Portage Creek annually from 1991-2018 to determine if there have been any temporal changes in Steelhead feeding ecology associated with population changes.

Integrating food web dynamics with life history theory can provide a better understanding of how shifts in community composition over time in Black Bay have influenced species interactions which may ultimately be responsible for the changes in Steelhead population size within Black bay.

CHAPTER I

Life History variation in Steelhead along the North Shore of Lake Superior

ABSTRACT

Steelhead have been naturalized in the Great Lakes since their introduction in the late 1800's. To better understand why certain life history strategies are selected for given a particular set of ecological conditions, I compared local adaptations from Steelhead from eight tributaries along Lake Superior's North Shore and compared them to life history changes in a population that has experienced significant ecological change. The life histories exhibited by adult Steelhead in most tributaries were consistent across space and time, with most tributaries demonstrating a 2-year smolting strategy (2 years residing in the stream prior to migrating to Lake Superior), except in Portage Creek where adult Steelhead historically demonstrated a 1-year smolting strategy. However, since Portage Creek population densities have declined since 2007, observed life histories there have shifted from a 1-year to a 2-year old smolting strategy approximately 2 generations (8 years) after the population showed signs of decline. This outcome is predicted by life history theory under a scenario of increased size-selective juvenile mortality. Though the dominant life history displayed by Portage Creek Steelhead is now similar to other North Shore Steelhead populations, their population size remains uncharacteristically low. I hypothesize that this shift towards older/larger smolts is in response to ecological changes (i.e. increases in predator abundance) in the Black Bay fish community (which Portage Creek flows into).

Keywords: competition, fecundity, life history characteristics, maturation, predation, size-selective mortality, Walleye.

INTRODUCTION

The life history traits presented by organisms provide insight into the selective constraints they experience (Michod 1979) and are continuously evolving (Heibo 2003). Life histories represent the set of age-specific rates of reproduction and likelihood of survival associated with an individual (Law *et al.* 1989). These life history traits are driven by trade-offs which select for traits that are most likely to benefit the organism given its set of selective constraints; for instance, a common trade-off observed in nature is between fecundity and somatic growth (Roff *et al.* 2006). As such, the diversity of life histories observed change — and are driven by — key ecological exchanges and processes such as species interactions (i.e. predation and competition), population density, individual growth rates, reproductive potential and mortality. Natural selection dictates that life histories that are more successful in a particular environment will be selected for in order to best maximize an individual's chances of reproduction in that environment (De Roos *et al.* 2003).

In fish populations, variations in life history strategies may provide adaptive capacity to withstand different stressors such as fishing, competition, and predation. One selective pressure that has the potential to shape life histories is fishing mortality (Dunlop *et al.* 2015). Fishing can induce life history changes to fish populations when certain individuals have either the ability to avoid harvest or to produce more viable offspring than others (Thériault *et al.* 2008). This can be seen along the west coast of North America where the fishing of Pacific salmonids is causing evolutionary changes to several life history traits such as body size, timing of migration, and age of maturation, depending on the method of fishing (Hard *et al.* 2008). These changes in mortality levels

at certain sizes caused by fishing are able to dictate the selection for life history strategies that involve trade-offs between performance early versus late in life (Reznick 1993, Law 2000, Hard *et al.* 2008). An example of this would be the influence of angling removing the largest mature individuals from a population, which selects for smaller smolting size, younger age at maturity and slower growth. The effects of this type of fishery-induced evolution are widespread among salmonids as they are exploited at various life stages and in various environments.

Another factor that can impact the survival of salmonids is density dependence (Grant *et al.* 2005). Density dependence can affect the growth rate and body size of parr salmonids, as increasing densities often result in decreased growth rates and body sizes (Grant *et al.* 2005). In streams, density dependence is commonly observed due to territoriality of parr salmonids (Grant *et al.* 1990, Marschall *et al.* 1995, Grant *et al.* 2005). Therefore, with finite space, the territoriality of parr will limit the maximum population density in streams as individuals that do not have a territory will either die or be forced to emigrate (smolt) out of the stream (Grant *et al.* 1990, Keeley 2001). The size of parr territories as well as how vigorously they defend them depends on various factors such as stream conditions, population abundance and fish size. The physical structure of a stream can also have a significant impact on parr carrying capacity; pools can sustain a greater number of parr than either runs or riffles of equal volume (Grant *et al.* 1990). This means that streams with a higher frequency of pools have the ability to have a higher maximum population density than streams that are mostly runs or riffles.

A third pressure that can lead to predictable changes in population dynamics and life history responses in fish is size-selective mortality caused from predation (He *et al.*

1990, Jepsen *et al.* 1998, Metcalfe *et al.* 1998). For example, size-selective mortality has been shown to drive evolutionary changes in guppy (*Poecillia reticulata*) populations (Reznick *et al.* 1990). Guppies were transplanted from an area of the Aripo River that contained cichlids (*Crenicichia alta*), which prey upon large, sexually mature guppies, to another site on the river which contained killifish (*Rivulus hartii*), which prey upon small, immature guppies. Over the course of 11 years, the size-specific predation on guppies caused significant evolutionary changes to their life history characteristics, primarily the timing of when they became sexually mature; when large guppies were selectively predated upon by the cichlids, the guppies evolved to mature at an earlier age, have higher reproductive effort, and have more and smaller offspring per brood (Reznick *et al.* 1990). The opposite was observed when the smaller guppies were selectively eaten by killifish (Reznick *et al.* 1990). Although the major conclusion from this experiment was that selection on particular life stages (i.e. mature vs immature) drove the evolutionary changes seen on life history, it is more likely to be a result of size-based selection (van Wijk *et al.* 2013). Therefore, some previous life history theory predictions, for instance, that reduced juvenile survival will select for later maturation and decreased reproductive effort (Reznick *et al.* 1990, Hutchings 1993), have been refined towards a size-based selection rather than a maturation stage selection as the understanding of life history theory continues to develop. Therefore, instead of selection on a particular life stage (i.e. immaturity), emphasis should be placed on particular size-classes when making life history predictions caused by predation.

The objective of this research was to see if Steelhead life histories changed with population size, and if the potential observed changes in life histories can be explained by

life history theory, and what impact these shifts in life history may have on the population going forward. In most fisheries, larger and faster growing individuals are harvested more frequently than smaller, slower growing fish (Ricker 1981). For Steelhead, the larger and faster growing individuals are usually those that reach maturation at a later age (Martyniuk *et al.* 2003, Satterthwaite *et al.* 2009). These later maturing fish are likely more vulnerable to size-selective harvest as they will likely reach a greater size than those that mature quickly. Therefore, during a historical period of exploitation, I predict that Steelhead reached maturity at younger ages (Law *et al.* 1989) as these fish were less likely to be harvested than the larger late-maturing fish and more likely to pass on their early maturation genes (Ricker 1981). During a period of release from size-selective harvest, I predict that Steelhead reached maturation at a slightly older age, which is typical of salmonid biology when natural conditions prevail (Ricker 1981). Lastly, during a period of potential juvenile predation or competition, I predict that Steelhead reached maturity at an older age in order to escape predator gape limitation in the open water environment (Ward *et al.* 1989). I used multivariate analysis to compare Steelhead life history characteristics over time and among regional populations. Finally, I evaluated which life histories have the greatest potential to maximize their reproductive output by estimating lifetime fecundity for dominant life history strategies observed in the population.

METHODS

Study Systems

The Steelhead examined for this research live part of their lives in Lake Superior, and another part of their lives in a tributary connected to Lake Superior. Lake Superior

has relatively low biological productivity compared to the other Great Lakes due to lower water temperatures, lower levels of organic pollution, a narrower littoral zone, and lower levels of dissolved minerals (Hornes *et al.* 2003). The tributaries of Lake Superior are also relatively unproductive and often exhibit steep gradients and impassable barriers which limit upstream migration for fish (Hornes *et al.* 2003). The study systems examined focus on the tributaries along the North Shore of Lake Superior, primarily those found within Thunder Bay, Black Bay, and Nipigon Bay. With added emphasis placed on Portage Creek, Black Bay.

Black Bay was also included in my analysis as I examined the catch data from the Fall Walleye Index Netting (FWIN) program from 2002-2014 to describe changes to the fish community within the bay which helped to provide context for some of the changes seen in Black Bay Steelhead populations.

<u>Life History Determination</u>

Steelhead scales were pressed on acetate slides which were then examined with a microfiche reader to identify life history traits from growth patterns on scales. Growth patterns on the scales are represented by both annuli and circul; circuli are growth rings on a scale that appear as the fish grows. During periods of slow growth, such as the winter months, circuli become clustered together and may even overlap, creating an annulus. Annuli are deposited at regular annual intervals during the cold winter months. By conveying information on fish age, scales were used to determine key life history traits such as the number of years any sampled fish has spent as a parr in the stream, the number of years spent in Lake Superior as a smolt, an estimate of age at maturity (e.g., age during a fish's maiden return to the stream), and age at capture. These key life history

traits were determined for each fish in the present study. Annuli that were representative of in-stream parr growth are relatively closer together and the circuli are very crowded, appearing near the origin of the scale (Davis *et al.* 1985). The lake portion of the scale was easily identifiable as the annuli and circuli become more spread apart. These visible distinctions between in-stream and lake annuli enabled the determination of the number of years spent in Lake Superior (both as juvenile smolts and sexually mature adults) and the number of years spent in the stream as parr for each individual fish. Analysis of patterns in growth annuli of scales suggested that Steelhead spawn annually after they have reached maturity. Since the inception of the co-operative angler project in 1991, all the ageing across all streams surveyed has been performed by the same reader, standardizing the process. Ages determined from scales were validated through recaptures of tagged Steelhead in subsequent years from the Neebing River, the McIntyre River, the Mackenzie River and Portage Creek. In addition, the fork length and sex of the fish at capture were recorded for each fish. Length at maturity in this study was determined by the total fork length (mm) of maiden spawning Steelhead.

In total, 17 different life histories were identified and occurred at least one time in either male or female Steelhead along the North Shore, corresponding to a unique combination of a number of years spent in the stream as parr, and the number of years spent in the lake as smolt. However, only the most common six life history categories were selected for further analysis (Table 1.1). The six most common life histories were selected because these life histories encompass all the prominent life histories present from each stream sampled (Table 1.2). Life histories that are represented in a high proportion of the individuals from one stream may be less frequent (or even absent) in

another stream. Therefore, to reduce the likelihood of missing any important life history

strategies, I included all prominent life histories from each stream. Also, multivariate

techniques are often sensitive to the inclusion of rare categories (Legendre *et al.* 2012);

therefore, the removal of rare categories reduced biases due to rare groups. Prominent life

histories were categorized separately for males and females. All analyses relating to life-

history traits and abundance were conducted using R (R core team 2017).

<center>Multivariate and Temporal Analysis</center>

Multivariate analysis is a commonly used approach in evaluating data with

multiple response variables across populations (Fenty 2004). This approach permits the

evaluation of both temporal changes within streams and differences among streams using

multiple commonly expressed life histories. To assess whether Portage Creek Steelhead

life history abundances have changed over time, and how they compare to contemporary

Steelhead life history abundances from streams along the North Shore, I applied Principal

Coordinate Analysis (PCoA) using chord distance. Unlike other distance measures such

as Bray-Curtis, chord distance is a true distance metric. Chord distance has a maximum

value of $\sqrt{2}$ when sites (a given year and/or stream) have no dependent variables (life

history characteristics) in common and a minimum value of 0 when sites share the same

proportions of dependent variables. This is different from Bray-Curtis dissimilarity which

only includes raw count data rather than proportional data (Legendre *et al.* 2012). The

chord distance measure is the Euclidean distance calculated after scaling the site vectors

to a length of 1 (i.e. vector normalization). To normalize life history vectors, the

frequency of each life history strategy from a given site must be divided by the square-

root sums of squared abundances for samples from that site. After vector normalization,

the Euclidean distance is equal to the length of a chord jointing two points within a segment of a sphere with a radius of 1 (Legendre *et al.* 2012). Therefore, the chord distance is the Euclidean distance between samples with normalized life history data. This is beneficial as double-zeros (i.e. a particular life history strategy absent at two sites) do not influence the chord distance, because it is an asymmetric distance; an asymmetric distance ignores any double-zeroes and only focuses on double-presences in the data when calculating dissimilarities (Legendre *et al.* 2012). Using other distance measures can cause problems when trying to draw ecological conclusions about different sites as there are various reasons why the species may be absent from either site, and it is impossible to tell which reason is more correct. Chord distance being an asymmetrical distance is an important attribute in the analysis as there are several double-zeros present in the current data set (Table A1 – A10).

Chord distance measures were calculated separately for each sex from the 2018 collection year across all sites surveyed along the Lake Superior North Shore (Table 1.2). Chord distances were also calculated for each sex from 1993 and 2007 from Portage Creek for comparison to 2018 data. The additional years from Portage Creek (1993 and 2007) were representative of different time periods that exhibited a different set of environmental conditions and were included in the analysis to determine whether there has been a change in life history abundances as the population has fluctuated in response to different environmental factors. The 1993 data represented the period of high adult mortality caused by angling during the spawning migration (George 1994). This era of exploitation ended after the Steelhead migration in 1993 when the lower reaches of Portage Creek became inaccessible to anglers due to the land becoming private property

(Jon George, personal communications). The 2007 data was included in the analysis because it represented the time when Portage Creek was near its peak population size as well as the year prior to the beginning of population declines. The 2018 Portage Creek data was representative of the contemporary Steelhead life histories during the current period of relatively low adult Steelhead abundance in Black Bay. The 2018 data also provided a contextual reference for Portage Creek relative to the other streams analyzed from along the North Shore.

Temporal trends in life history strategies and population abundance were also examined for the McIntyre River for comparison. Much like Portage Creek, the McIntyre River was also heavily exploited for many years until new regulations came into effect in 1999 which essentially made it a catch-and-release fishery (e.g., legal harvest size set intentionally high at 690mm), and helped to increase the adult population size. This temporal analysis of the McIntyre River was done in order to help provide context to Portage Creek by showing how another Lake Superior tributary with a long-term data set has gone through similar ecological processes in the past (i.e. over-exploitation followed by a virtual closure of the fishery).

To determine if potential life history strategy changes observed in Portage Creek were systematic of all Black Bay tributaries, I also examined the proportion of age-1 and age-2 smolts from more recent data collected in the Wolf River and Coldwater Creek. However, due to limited sample size in recent years and considerable variation in historic sample sizes, the comparison examining the number of age-1 and age-2 smolts from the Wolf River and Coldwater Creek were summed together to determine the smolting frequencies (%) of age-1 and age-2 smolts. Temporal trends in smolting frequencies from

the Wolf River and Coldwater Creek were compared to the temporal trends evaluated from Portage Creek.

Age at Maturation determination

Age at maturation is a commonly used metric to evaluate stressors in fisheries because a reduced age at maturity is strongly correlated with a smaller body size, which inevitably leads to lower fecundity and may lead to lower total biomass (Trippel 1995, Law 2000, Kuparinen *et al.* 2007). The frequency (%) of age at maturation was determined for both sexes and across all sites and years examined in the multivariate analysis (Table 1.2). Only the ages at maturation for the six prominent life history strategies (Table 1.1) were included.

Portage Creek von Bertalanffy Growth Models

A von Bertalanffy (VB) growth equation was used to describe the somatic growth of Portage Creek Steelhead among the six identified prominent life history traits (Table 1.1). Both sexes were analyzed separately because Steelhead are known to be sexually dimorphic (Evenson *et al.* 1985). Although the VB growth equation is a commonly used method of illustrating somatic growth in organisms that display indeterminate growth, it has been challenged in its efficacy in modeling immature growth as the traditional VB curve only uses a single equation (Day *et al.* 1997, Lester *et al.* 2004). The problem associated with only using one equation is that it may not account for the changes in energy allocation associated with reaching maturity (Lester *et al.* 2004). Like most fish, when Steelhead are immature, most of their energy is allocated towards somatic growth, but once they reach maturity, most of their energy is likely allocated to gonad

development rather than somatic growth (Lester *et al.* 2004). I assumed that as

demonstrated in other fish species (i.e. Walleye; Lester *et al.* 2004) Steelhead will grow

linearly while they are immature (Nævdal *et al.* 1997). Parr (stream growth) and smolt

(lake growth) life stages were analyzed separately to account for differences in growth

between these two different life stages, and were assumed to conform to linear growth.

Therefore, a triphasic VB growth curve was used to illustrate the growth of Portage

Creek Steelhead to best take advantage of available data and estimate growth patterns

that conform best with the current understanding of growth in fishes (Lester *et al.* 2004).

The three segments of Steelhead growth in the VB models are as follows: parr-smolt

(linear), smolt-maturation (linear), and post-maturation (curvilinear).

To determine length and age data for the parr portion of the Steelhead life stage

for all years, electrofishing surveys were conducted on Portage Creek during the summer

of 2003 and 2018. Parr were classified as either young of the year (YOY) or yearling.

The average length for both YOY and yearlings were calculated separately. For Steelhead

that displayed the life history characteristic of having spent only 1 year as a parr, the

average YOY length represented their growth for age-1 via a linear line from the origin to

the average YOY length at age-1 as determined from electroshocking surveys. For

Steelhead that displayed the life history characteristic of having spent 2 years as a parr,

the average yearling length represented their growth for age-1 and 2 via a linear fit from

the origin across both years 1 and 2 (from electroshocking surveys). Immature lake

growth during the smolt phase was calculated from the slope of the line representing the

linear interval between the average size-at-age for newly smolted parr and the average

maiden spawning size for each life history category and for both sexes.

The growth of mature Steelhead was defined via the VB growth equation used by Beverton (1954):

$$E[L|t] = L_\infty(1 - e^{-K(t-t_0)}),$$

where $E[L|t]$ is the expected or average length at time (or age), L_∞ is the asymptotic average length, K is the Brody growth rate coefficient and t_0 represents the time (or age) when the average length was zero.

Kruskal-Wallis tests were applied to the Portage Creek Steelhead growth models across all years to determine if there were any differences in length at maturation for similar life histories strategies between sexes, as well as between different life histories for the same sex. Dunn's tests ($\alpha = 0.05$) were performed post-hoc to determine which growth models differed significantly.

<u>Adult female Steelhead mortality estimates</u>

Mortality rates for prominent life history categories of female Steelhead from Portage Creek were calculated to assess which set of life history characteristics provided the greatest survivorship for adult female Steelhead. To estimate instantaneous adult mortality (Z), catch curves were created by estimating the natural logarithm of the number of observations in each age class for each of the major Steelhead life histories. A regression line was fit to the descending arm of these data where the slope of the regression represented Z. Instantaneous mortality can easily be converted to annual mortality (A) where:

$$A = 1 - e^{-Z}$$

Because there were relatively few observations of Steelhead older than 8 years old,

mortality estimates were calculated from when Steelhead within each life history first

reached maturation until age 8, or until the final observation prior to age 8 which

represented the 95th age percentile in the mortality estimates. This was done to avoid any

potential biases associated with accelerated mortality beyond age 8 and potential

differences in longevity among life histories.

The instantaneous mortality rate and the annual average mortality rates were

assumed to be solely a result of natural mortality as fishing mortality (harvest) has not

taken place on Portage Creek since 1993.

Fecundity estimates

The fecundity of Portage Creek Steelhead was estimated using an equation from

Dubois *et al.* 1989 which examined Steelhead fecundity from Western Lake Superior

over a range of years. The equation they recommended to use for estimating Lake

Superior Steelhead fecundity was:

$$\log_{10} y = -1.46 + 1.85 \log_{10} x,$$

where *y* is the number of eggs and *x* is the total length of the fish in millimeters. This

equation assumes a constant relationship between Steelhead length and egg production

throughout an individual's life. Fork lengths were multiplied by 1.046 to convert to total

length (Dubois *et al.* 1989).

To remove any potential bias in the results due to very old fish, only mature

female Steelhead that fell within the 95th percentile of ages were included in fecundity

estimates. The average length-at-age for each age class for all prominent life histories

was calculated to determine the average number of eggs that a Steelhead would produce throughout its lifetime. To determine which life history strategies have the greatest lifetime fitness, the estimated number of eggs at length from the Dubois *et al.* equation across all ages that fell within the 95th age percentile for each prominent life history strategy were summed.

RESULTS

Since 2008, the Portage Creek adult Steelhead population has decreased every year, except for 2014 which increased slight in population size compared to the 2013 population estimate (Figure 1.1). Prominent life history categories examined included unique combinations of 1 or 2 years spent in the stream as parr, and 1, 2 or 3 years spent in Lake Superior as smolt (Table 1.1).

Principal Coordinate Analysis (PCoA) using chord distance explained 47.8% of the variation in prominent life history strategies on the first axis, and 34.3% of the variation on the second axis (Figure 1.2). PCoA indicated that Portage Creek Steelhead life histories have changed over time; during the exploitation era of Portage Creek in 1993, males are closely associated with LH1.2, while females are closely related to LH1.3 (separate along axis 2). In 2018, both sexes appear to have delayed smolting; males became more closely associated with LH2.2 while females are associated with LH2.3 (Figure 1.2). In addition, the PCoA results also suggested that contemporary Portage Creek Steelhead life histories were similar to Steelhead life histories from various other streams along the North Shore (Figure 1.2), which were dominated by 2-year smolting strategies (LH2.1, LH2.2 and LH2.3).

Males and females displayed different life histories and separated across all streams/years on axis 2, but within each stream along axis 1 (Figure 1.2). Generally, males tend to spend 1-2 years in the lake prior to maturation whereas females tend to spend 2-3 years in the lake prior to maturation. Life histories also usually appear to be separated along axis 2 with LH1.1, LH1.2, LH2.1 and LH2.2 are associate mostly with males, while females are more closely associated with LH1.3 and LH2.3, spending an additional 1-2 years as a smolt in Lake Superior prior to first reproduction.

The results suggested that early maturation continued in Portage Creek Steelhead even after exploitation ceased in 1994; Portage Creek males most frequently displayed LH1.2 from 1993 until 2007 whereas females reduced the number of years in the lake from 3 to 2 indicating earlier maturation by one year following the removal of exploitation (Figure 1.2). As such, in 2007 when the Portage Creek Steelhead population was near its peak, LH1.2 appeared to be the most dominant life history exhibited for both sexes (Figure 1.2).

Between 2007 and 2018, when the adult population decreased from approximately 1800 to around 144 adult Steelhead (Figure 1.1), there appeared to be a significant shift away from early age at maturation for both sexes. The contemporary data for Portage Creek showed that both males and females were more commonly delaying smolting by one year by spending an additional year in the stream as parr (Figure 1.2).

The temporal trends in the proportion of age-1 and age-2 smolts for Portage Creek (Figures 1.3 and 1.4) compared to the McIntyre River (Figure 1.5 and 1.6) showed that Portage Creek has exhibited major changes in predominant smolting age along with a reduction in adult Steelhead population size not seen in the McIntyre River. Portage

Creek has seen a decrease in adult Steelhead population size over the last 10 years whereas the McIntyre River population has increased over that time. From 1991-2016, the majority of adult Steelhead returning to Portage Creek to spawn were exhibiting age-1 smolting characteristics; however, this changed in 2017 and 2018 as age-2 smolting characteristics became more common (Figures 1.3 and 1.4). Conversely, the McIntyre River has continuously demonstrated that age-2 smolting characteristics are a more common smolting strategy, across all population densities.

Temporal analysis regarding the proportion of age-1 and age-2 smolts from other Black Bay tributaries showed similar results to Portage Creek. The Wolf River and Coldwater Creek showed that historically, most returning adults were displaying age-1 smolting characteristics (Figures 1.7 and 1.8). However, more recent data showed that both of those tributaries shifted to adults that displayed age-2 smolting characteristics (Figures 1.7 and 1.8). The difference between the shift in smolting between Portage Creek and the other Black Bay tributaires appeared to be the time of the shift. The Wolf River and Coldwater Creek shifted to mostly age-2 smolts earlier relative to the shift that occurred in Portage Creek in 2017. Although the timing is different, these results show that the shift from age-1 to age-2 smolting characteristics happened throughout the major tributaries of Black Bay. Currently, in these three major Black Bay tributaries, 28-30% of adult Steelhead are displaying age-1 smolting characteristics while the remaining 70-72% of adults are displaying age-2 smolting characterictics.

Age at maturation

The contemporary age at maturation of Portage Creek Steelhead was delayed relative to the historic age at maturation (Table 1.3). In 1993, male Steelhead in Portage

Creek typically matured at age 3 while females matured at ages 3 or 4. In 2007, both sexes predominantly matured at age 3. However, in 2018, males usually reached maturation at 3 or 4 year of age, while females reached maturation at 4 or 5 years old. A trend that can be seen across all sites is that the most common age at maturation for males generally occurs one year prior to the most common age at maturation for females (Table 1.3). The exception to this is 2007 Portage Creek which indicated that both sexes were reaching maturation at age 3 (Table 1.3).

Changes in von Bertalanffy growth

Overall, Steelhead growth varied between life histories for both sexes (Figures 1.9 and 1.10). Based on stream electroshocking data, parr that smolted at age-2 averaged 70 mm of growth per year (total length or 140 mm during smoltification) whereas parr that smolted at age-1 averaged 61 mm in length during smoltification.

Lake growth (mm per year) was negatively related to the number of years spent as a smolt; however, despite the reduced annual lake growth (mm per year), life history strategies that demonstrated having spent additional years as smolts reached greater lengths at maturation relative to life histories that spent fewer years as smolts (Tables 1.6 and 1.7). LH1.1 females had a much greater asymptotic length (857 mm) than any other life history category; however, this is likely an artifact of fitting the model to a small sample size (n=18) that is poorly represented by individuals at asymptotic size, indicative of an infrequent life history strategy. Therefore, the predicted asymptotic length for LH1.1 females should be interpreted with caution. LH2.2 males displayed an asymptotic length that does not conform to the pattern of increased asymptotic length that would be expected with an increased amount of time spent as a smolt; LH2.2 males reached a

smaller asymptotic length then LH2.1 males even though they spent an extra year as a smolt relative to LH2.1. Similarly, for females, LH2.2 reached a greater asymptotic length than LH2.3 even though LH2.3 spent three years as a smolt whereas LH2.2 only spent two years as a smolt.

A Kruskal-Wallis test detected a difference between the mean ranks of length at maturation between at least one of the life history categories for both males ($x^2 = 1568.2$, df = 5, p <0.05) and females ($x^2 = 776.68$, df = 5, p <0.05). Dunn's post-hoc test was used to determine which life history categories have significantly different average lengths at maturation for both sexes. For males, LH1.3 and LH2.3 displayed similar average lengths at maturation ($p > 0.05$), while all other life history strategies showed significantly different average lengths at maturation for males ($p < 0.05$; Table 1.4). For females, LH1.1 and LH2.1 have similar average lengths at maturation as do LH1.3 and LH2.3 ($p > 0.05$; Table 1.4). The remaining life history strategies all demonstrated significantly different average lengths at maturation for females (Table 1.4).

Results from the Kruskal-Wallis test indicated that there were significant size differences for the average length at maturation for the male – female comparisons of similar life history strategies (Table 1.5). Dunn's post-hoc test showed that LH1.1, LH1.3 and LH2.1 all exhibited significantly different average lengths at maturation ($p < 0.05$). LH1.1 and LH2.1 females matured at a greater length than LH1.1 and LH2.1 males, respectively, whereas LH1.3 males matured at a significantly larger size than LH1.3 females. LH1.2, LH2.2 and LH2.3 showed insignificant differences ($p > 0.05$) in length at maturation between males and females (Table 1.5).

Adult female Steelhead mortality

Adult female Steelhead that smolted at age-2 had a lower annual average mortality rate than those that smolted at age-1 (Figure 1.11). For female Steelhead that smolted at age-1, annual average mortality of adults increased slightly as individuals delayed maturation (LH1.1 A=34.0%, LH1.2 A=34.3%, LH1.3 A=38.4%; Table 1.5). For female Steelhead that smolted at age-2, annual average mortality of adults was greatest amongst those who spent 2 years as smolts (LH2.2 A=33.0%), and lowest amongst those who spent 3 years as smolts (LH2.3 A=24.6%; Table 1.6). Females that displayed LH2.1 have an average annual mortality rate of A=30.6% (Table 1.6).

Fecundity

Lifetime fecundity of female Steelhead generally decreased as they delayed maturation (Figure 1.12). The exception to this was LH1.1 which reaches maturation at age-2, but also had the lowest estimated lifetime fecundity of any of the prominent life history strategies examined (Figure 1.12). Except for LH1.1, life histories that smolted at age-1 were more fecund than those that smolted at age-2. Additionally, life histories that spent additional years as smolts and fewer years as parr tended to be slightly more fecund relative to those that spent fewer years as smolts and additional years as parr if they both reach maturation at the same age. Overall, the life history with the greatest estimated lifetime fecundity was LH1.2 which produced an average of 30772 eggs throughout its lifetime (Table 1.6).

DISCUSSION

I found evidence of a shift in optimal life history strategies in Portage Creek Steelhead and across tributaries in Black Bay associated with changes in environmental conditions to a set of strategies more similar to other populations along the North Shore of Lake Superior following a population decline since 2007. Furthermore, these changes appear to be due to a consequence of changes in size-dependent mortality in Black Bay. The observed shift in optimal life history strategies was from early smolting and maturation, consisted with a strategy expected under a scenario of high adult mortality, towards delayed smolting and delayed age at maturation, consistent with a strategy resulting from increased mortality of small juveniles (smolts).

Age at maturation for Portage Creek Steelhead has been increasing over the past 10 years which is consistent with increased mortality on smaller juvenile Steelhead (Reznick *et al.* 1990, Hutchings 1993, Reznick 1993). Steelhead in other parts of Lake Superior (Minnesota and Wisconsin) smolt most commonly at age-1, followed by age-2 and lastly age-3 (Hassinger *et al.* 1974, Peterson 2015, Peterson *et al.* 2015, Peterson *et al.* 2016). However, this is assessed by determining the frequency at which age Steelhead parr migrate into Lake Superior from their natal stream by using juvenile fish traps located near the mouth of the stream (Peterson 2015, Peterson *et al.* 2015, Peterson *et al.* 2016). When evaluating returning fish (similar to what was done in the current study), these same studies suggested that the majority of returning adult Steelhead exhibit age-2 smolting characteristics (Hassinger *et al.* 1974, Peterson 2015, Peterson *et al.* 2015, Peterson *et al.* 2016), consistent with the results along the North Shore of Lake Superior reported here. Collectively, these results indicate that although most Steelhead only spend

one year in the stream, this life history strategy is not as successful for reproduction as a delayed smolting strategy, as only a small fraction of age-1 smolts reach maturation and spawn. If both biotic and abiotic factors were selecting for Steelhead to smolt after one year in the stream, other biotic and abiotic pressures were selecting against age-1 smolts once they have migrated into Lake Superior.

Data collected from Black Bay showed that there has been a significant change to the fish community since the mid 2000's. Some changes in the fish community of Black Bay can be seen by the resurgence of Walleye as well as increases in Yellow Perch (*Perca flavescens*) and Northern Pike (*Esox Lucius*) densities (Table 1.9; Berglund 2016). This increase in the percid and esocid communities suggest that predation on smolts is a potentially important selection pressure present in 2018 that was likely not as significant in the other time periods (1993 or 2007). Based on predictions from life history theory, this predation pressure (size-selective mortality on small juveniles) could also be contributing to the observed shifts to later smolting observed in Portage Creek Steelhead between the earlier time periods (1993 and 2007) and 2018. For example, Northern Pike have been found to be the cause of over half the predation of Atlantic salmon (*Salmo salar*) smolts in certain streams in Norway (Jepsen *et al.* 1998) and was determined to be a size-selective phenomenon: once the smolts reached a certain size, they were either too large or too fast to be eaten (Jepsen *et al.* 1998). Steelhead survival has also been positively correlated with smolt size (Ward *et al.* 1988); this can be seen in Black Bay where the majority of adult Steelhead are currently displaying an age-2 smolting strategy, which is associated with a larger body size. The sum of evidence presented here (increase in potential predator abundance, delayed maturation and larger

smolting size) suggests that predation may be an important factor in influencing the dominant life history strategies present in Black Bay Steelhead, and may have ultimately contributed to observed Steelhead population declines.

Since 2002, there has been an increase in the range of sizes, average age and abundance of both Northern Pike and Walleye in Black Bay (Berglund 2016). Both Northern Pike and Walleye are piscivorous and have negatively impacted Steelhead populations through predation in other systems (McMahon *et al.* 1996). When the Steelhead population was being exploited prior to 1994, the majority of life histories being expressed in Portage Creek smolted at age-1. These results suggest that whatever is currently selecting for a high abundance of life histories that smolt at age-2 was not a factor during the era of exploitation in Portage Creek. Juvenile predation of Steelhead likely would not have been an important selective pressure when adult Steelhead were being harvested in high numbers (as indicated by 1993 Portage Creek data) as there was still an active Yellow Perch commercial fishery on the lake (Bronte *et al.* 2003, Berglund 2016), suppressing both Perch and Walleye abundances in Black Bay. However, predation of juvenile Steelhead may have started to become an important selective pressure once the Perch fishery was closed (2003), the recreational Walleye fishery closed in the northern portion of Black Bay (2008) along with stocking measures to assist with Walleye recovery within Black Bay (1998-2000, 2003-2005; Berglund 2016).

Prey selection by Walleye is dictated by prey morphology (Einfalt *et al.* 1997). Studies have shown that juvenile Walleye (200mm total length) can eat prey that are up to 39% of their own total body length, provided that the prey are not deep bodied and are soft rayed (Einfalt *et al.* 1997). Like all salmonids, Steelhead are soft rayed and the

juveniles possess a cylindrical body shape (Bisson *et al.* 1988). When Steelhead smolt at age-1, they can reach a length of approximately 80mm long (Addison 2007), very close to the maximum prey size for juvenile Walleye that are 200mm long (Einfalt *et al.* 1997). Based on FWIN survey data, the average length for male Walleye in Black Bay was 410mm and the average female length is 454mm (Berglund 2016). Although the FWIN nets selectively capture larger Walleye, the results of these surveys indicated that there were many large Walleye present in Black Bay that could easily prey upon age-1 Steelhead smolts. When Steelhead smolt at age-2, they can obtain a maximum length of around 160mm (Addison 2007) and are likely large enough to be able to avoid being predated upon by smaller Walleye but not larger Walleye. Using the predator to prey ratio of 39% (Einfalt *et al.* 1997), 96% of the Walleye in Black Bay exceed 205mm and would be capable of consuming age-1 Steelhead smolts (80mm), whereas only 62% of Walleye in Black Bay exceed 410mm, which would make them capable of consuming age-2 smolts (160mm). Portage Creek Steelhead that smolt at age-2 are protected by the stream environment when they are age 1+; thus, by smolting at age-2 they can potentially reduce predation risk compared to that which they would have experienced in the lake if they had smolted at age-1.

Historical patterns in early smolting life history strategies were consistent with patterns expected to result from high adult mortality resulting from over-exploitation of mature fish. When Portage Creek was being heavily exploited in 1993, a large portion of female Steelhead were exhibiting LH1.2. This life history showed that female Steelhead were reaching maturation at age-3 which is earlier relative to contemporary data from streams along the North Shore (which show that females typically reach maturation at

age 4). These results agree with life history theory, which predicts that low adult survival as a result of heavy angling pressure would select for earlier age at maturation (Reznick *et al.* 1990, Hutchings 1993). During periods of high fishing mortality, it is expected that Steelhead would maximize their potential lifetime fecundity by reaching maturity at an early age (due to high adult mortality). Harvesting of many fish stocks, both freshwater and marine, are associated with evolution towards earlier maturation (Law *et al.* 1989). Given the high rate of exploitation experienced by the Portage Creek population prior to 1993 (George 1994), the generally early maturation (and smolting) is consistent with trends observed in other stocks undergoing fisheries-induced evolution (Hard *et al.* 2008).

My analysis indicated that the tendency for delayed smoltification and older maturation occurs in other North Shore stream populations as well as in the contemporary Portage Creek population. Interestingly, fishing and harvesting is permitted to the general public across all sites, except Portage Creek. However, there are currently strict possession limits on Steelhead across all sites (maximum bag limit of 1 Steelhead without size restriction), as well as size restrictions on the McIntyre and Neebing Rivers (maximum bag limit of 1 Steelhead over 690mm; OMNR 2006) which have essentially reduced harvest to zero. Prior to 1996, there was a possession limit of 5 Steelhead, without size restrictions across all streams. In 1996, the limit changed to 2 fish with one allowed to be less than and one allowed to be greater than 500mm (Boston 1998). In 1999, the regulations were changed to the current limits.

Once exploitation was removed as a selective pressure from Portage Creek in 1994 and adult mortality declined, the population increased from approximately 600

Steelhead to over 2000 Steelhead in 2004. From 1994 to 2007, there was a slight shift towards more prominent LH1.2 abundances for both sexes, as well as a shift away from any life history strategy that exhibited age-2 smolting (LH2.1, LH2.2 and LH2.3). Therefore, even with the reduction in adult harvest, Portage Creek Steelhead were still maturing at an early age, contrary to my predictions. Once harvest was eliminated, I expected to see an increase in the age at maturation as larger, older fish are more fecund on a per year basis compared to younger, smaller fish.

A theory for why Steelhead continued smolting at age-1 and continued to reach maturation rapidly once exploitation stopped, contrary to my predictions, is due to density-dependence of parr. Density-dependence could contribute to the historically higher tendency for age-1 versus age-2 smolts in Portage Creek during the period of high Steelhead abundance. Juvenile Steelhead numbers have been shown to fluctuate as a result of density dependence (Ward *et al.* 1993, Keeley 2001). When limited resources are not partitioned among individuals equally, individuals that are not getting enough food or that have limited space may choose to emigrate (undergo smoltification) out of the stream (Keeley 2001). My results along with previous studies have shown that age-2 smolts are between 140-160mm in size whereas age-1 smolts are approximately 60-80mm in size (Addison 2007); therefore, there are increased productivity and space requirements placed on the stream when Steelhead smolt at age-2 instead of age-1. If parr were being forced out of the stream at age-1 because of density dependence during the periods of high adult Steelheads abundances, the expectation would be to exhibit LH1.2 based off the mortality and fecundity estimates. LH1.2 had the greatest lifetime fecundity and low average annual mortality for Steelhead that smolt at age-1. This is corroborated

by my results which showed that during the period of density dependence in Portage

Creek Steelhead exhibited LH1.2 in relatively high frequency (Table 1.3).

Interspecific competition between Steelhead parr and Brook Trout may also be

having a negative impact on the Steelhead population in Portage Creek. Since Brook

Trout sampling in Portage Creek began in 2014, there has been an order of magnitude

increase in the number of Brook Trout captured (Table 1.8). The increase in Brook Trout

abundance will likely result in greater interspecific competition between Steelhead parr

and Brook Trout as they share similar diets (Rose 1986) and have shown to occupy

similar in stream habitats (Rose 1986, Bear *et al.* 2007). The mean length at capture

results for Brook Trout also indicated that Brook Trout size is decreasing as densities

increase which also supports increased density dependence with time (Table 1.8). This

increase in interspecific competition may be detrimental to Steelhead parr as the Brook

Trout sampled in Portage Creek are much larger than both the largest age-1 parr (80mm)

and age-2 parr (160mm; Table 1.8). Size is an important factor in determining dominance

in both adult and juvenile interspecific competition between salmonids as larger

individuals have the capability to out-compete smaller individuals for territory and food

resources (Fausch *et al.* 1981).

Approximately 10 years following the start of the Steelhead population decline in

Portage Creek, Steelhead life history strategies have shifted away from younger smolting

age and earlier maturity to older smolting and delayed maturity. Similar trends have been

seen elsewhere in Black Bay; historically, adult Steelhead in both the Wolf River and

Coldwater Creek used to exhibit life histories that smolted at age-1. However, since 2013,

both streams have shifted towards adult Steelhead displaying predominantly age-2

smolting characteristics (Figures 1.7 and 1.8). This demonstrates that whatever is causing the changes in smolting ages to shift from age-1 to age-2 in Portage Creek is likely happening in all the Black Bay tributaries.

In conclusion, Portage Creek and Black Bay in general have been subjected to several environmental changes and selective pressures over the past few decades which have impacted the life history strategies and characteristics of its Steelhead. This study suggests that high rates of exploitation of adults, density-dependence of in stream juveniles, and predation on juveniles have all likely affected the life history strategies expressed by Portage Creek Steelhead over the past 3 decades. However, despite the similarities in life history strategies, Portage Creek is at its lowest adult population ever recorded while many other streams along the North Shore of Lake Superior are near their highest observed population sizes.

FIGURES
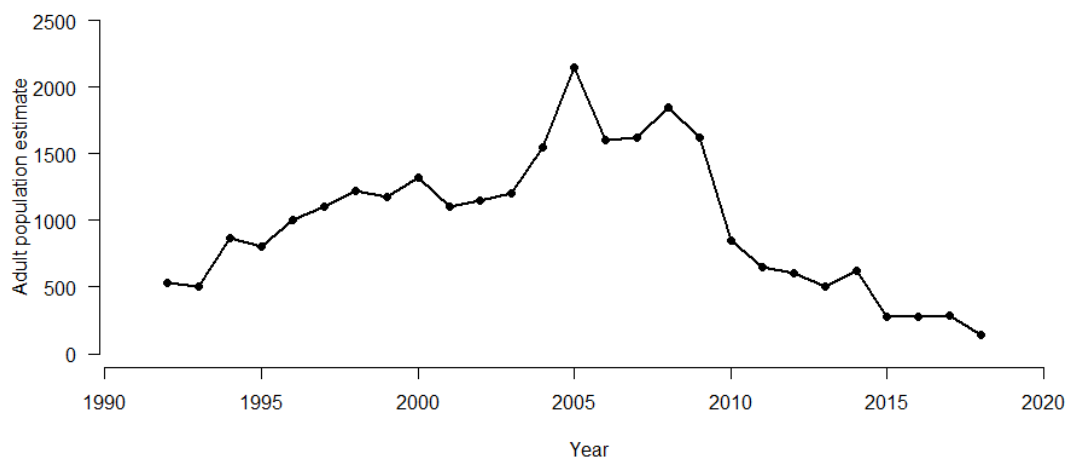
Figure 1.1. Adult Steelhead population estimate for Portage Creek from 1991-2018.
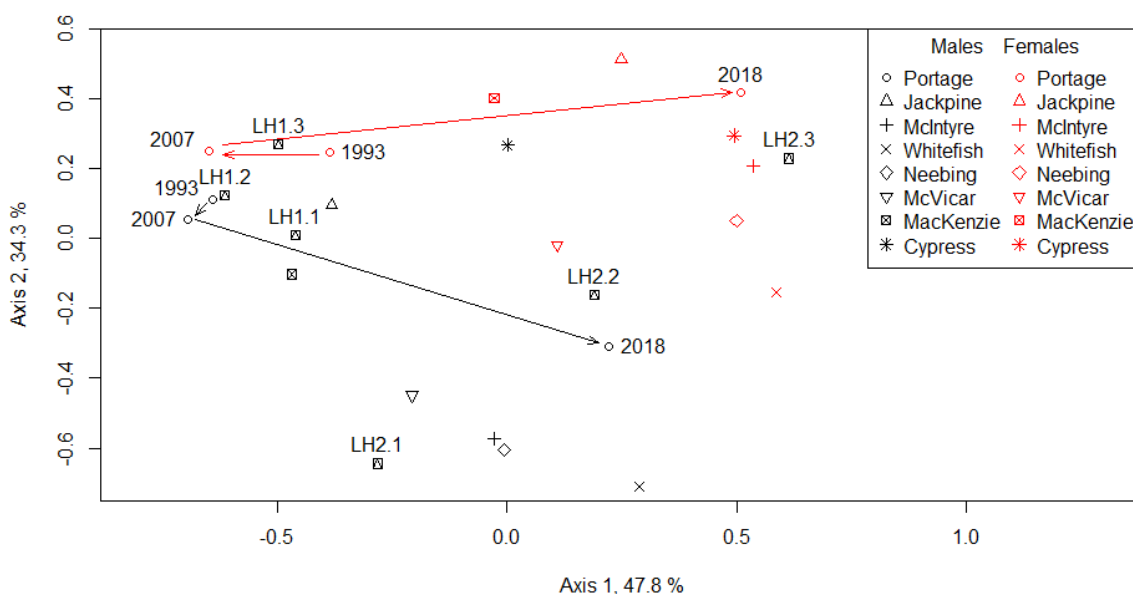
Figure 1.2. Site scores from Principal coordinates Analysis (PCoA) of chord distance comparing the relative similarities of life histories of male and female Steelhead from Portage Creek, the Jackpine River, McIntyre River, Whitefish River, Neebing River, McVicar Creek, MacKenzie River and the Cypress River; North Shore, Lake Superior. Each data point represents a single sampling event (2018) for each sex at each location. Included is Portage Creek historical data (1993 and 2007) which represents different selective pressures that were present on the stream which affected the population size. For Portage Creek, 1993 represents the time period when fishing mortality occurs for migrating adults, 2007 represents a period of high in-stream population density of juveniles, while 2018 represents a time period of potentially higher juvenile (smolt) mortality in the lake.
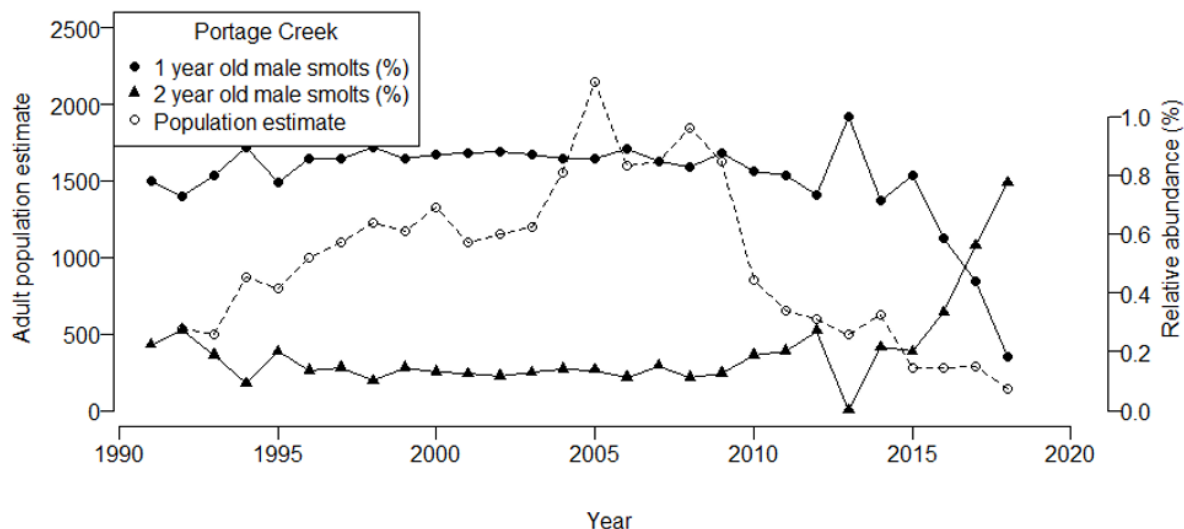
Figure 1.3. Population estimate for adult Steelhead in Portage Creek (hollow circles) along with the relative abundance of Portage Creek male Steelhead that returned to spawn after smolting at age-1 (black circles) and age-2 (black triangles). Population estimates and smolting abundances were measured from 1991-2018.
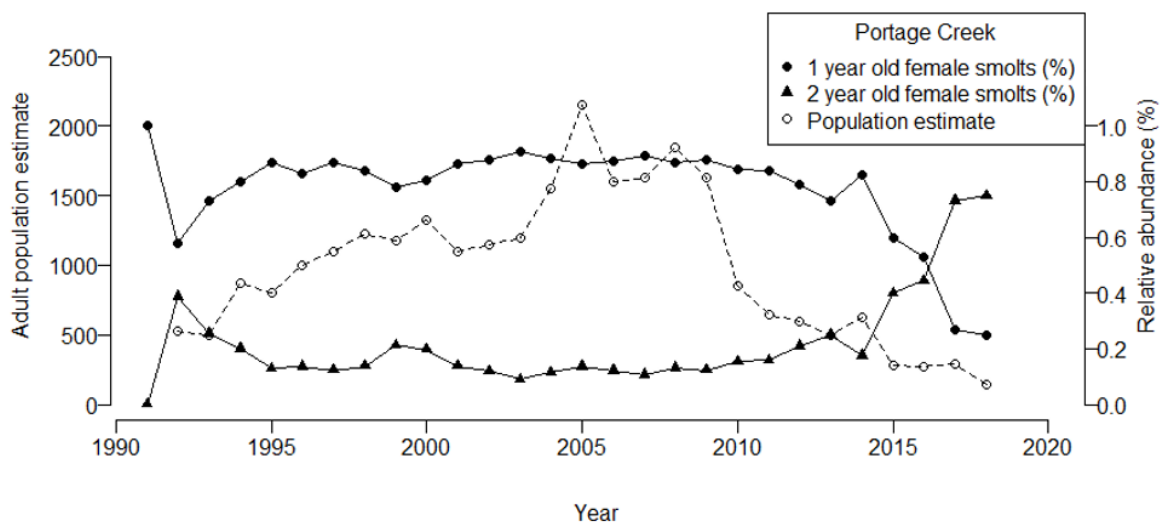
Figure 1.4. Population estimate for adult Steelhead in Portage Creek (hollow circles) along with the relative abundance of Portage Creek female Steelhead that returned to spawn after smolting at age-1 (black circles) and age-2 (black triangles). Population estimates and smolting abundances were measured from 1991-2018.
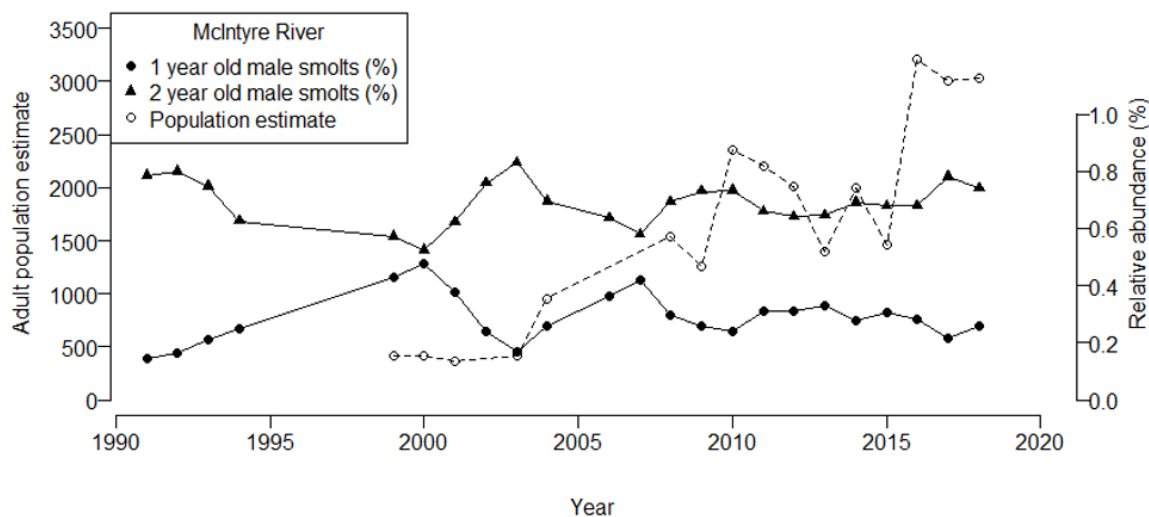
Figure 1.5. Population estimate for adult Steelhead in the McIntyre River (hollow circles) along with the relative abundance of McIntyre River male Steelhead that returned to spawn after smolting at age-1 (black circles) and age-2 (black triangles). Population estimates for 1999-2001 and 2003-2004 were generated using a counting fence located at the top of the fish ladder located at Lake Tamblyn. Estimates from 2008-2018 were generated using a Peterson Population Estimate. Smolting abundances were measured from 1991-1994 and 1999-2018.
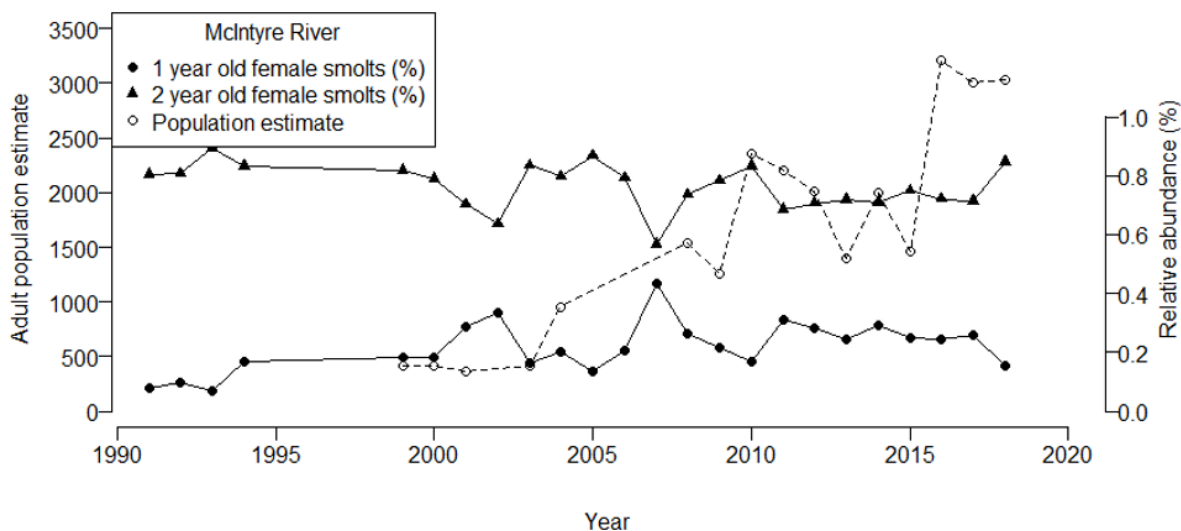
Figure 1.6. Population estimate for adult Steelhead (hollow circles) in the McIntyre River along with the relative abundance of McIntyre River female Steelhead that returned to spawn after smolting at age-1 (black circles) and age-2 (black triangles). Population estimates for 1999-2001 and 2003-2004 were generated using a counting fence located at the top of the fish ladder located at Lake Tamblyn. Estimates from 2008-2018 were generated using a Peterson Population Estimate. Smolting abundances were measured from 1991-1994 and 1999-2018.
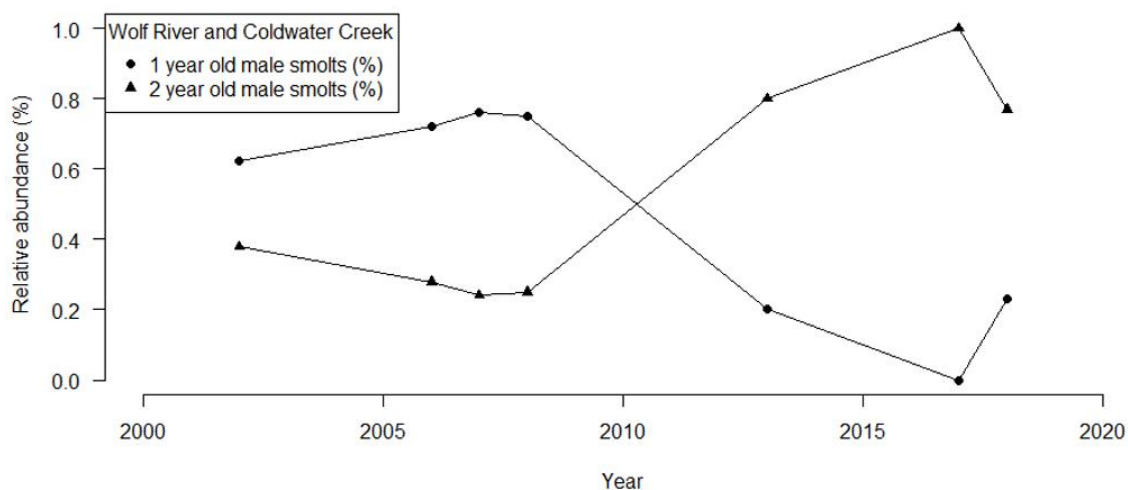
Figure 1.7. Relative abundance (%) of Wolf River and Coldwater Creek male Steelhead that returned to spawn after smolting at age-1 (black circles) and age-2 (black triangles).
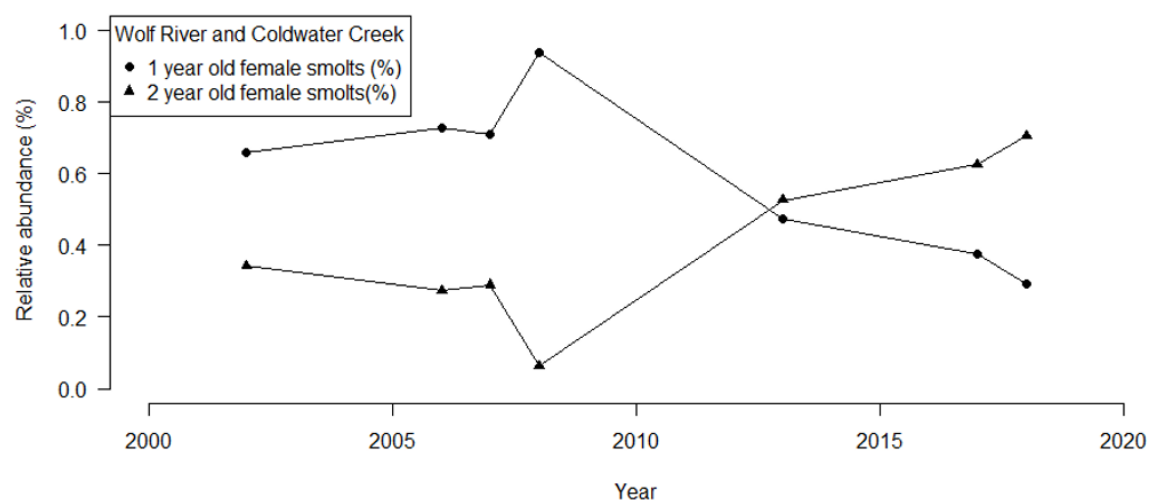
Figure 1.8. Relative abundance (%) of Wolf River and Coldwater Creek female Steelhead that returned to spawn after smolting at age-1 (black circles) and age-2 (black triangles).
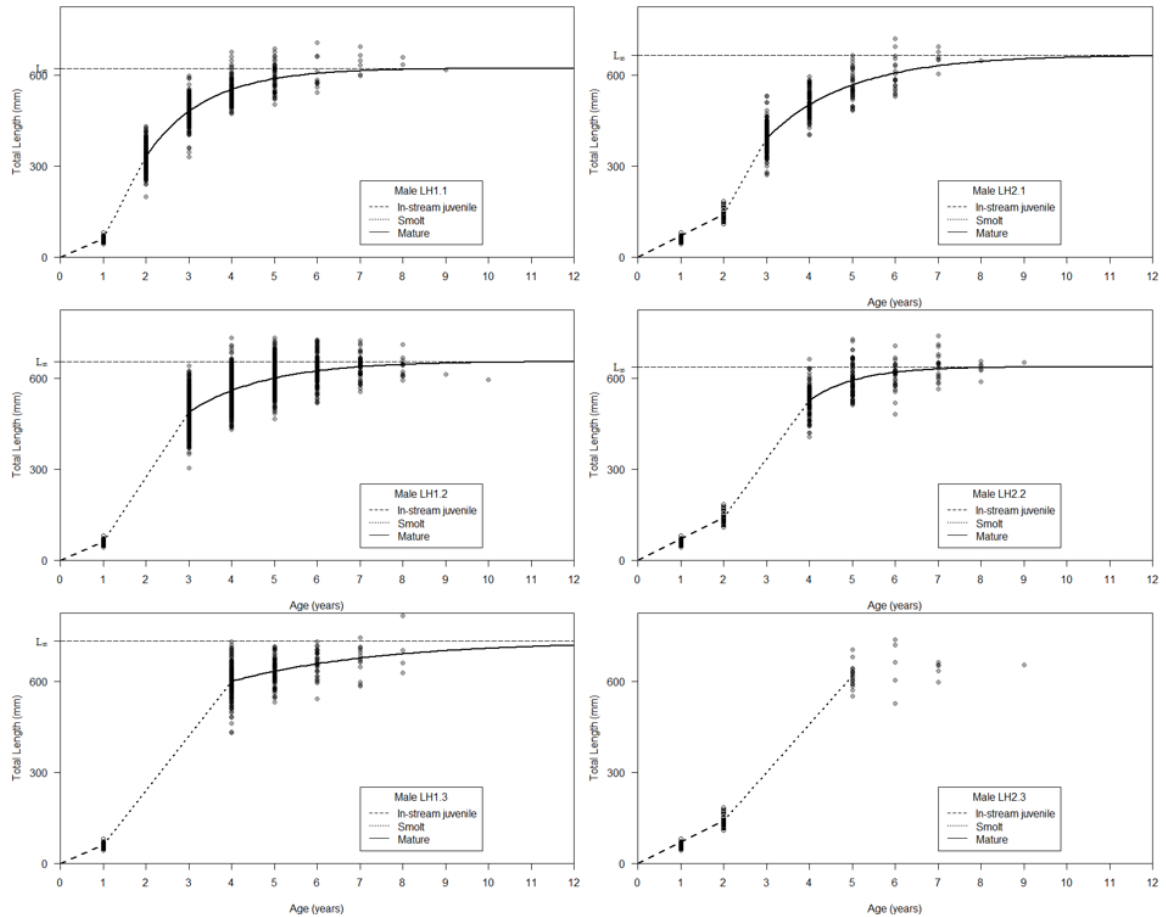
Figure 1.9. Triphasic von Bertalanffy growth models for prominent male Steelhead life history categories from Portage Creek. Data collected from all years of sampling Portage Creek Steelhead were included in the VB curves (1991-2018). The thick dashed line represents the stream growth (parr life stage), the thin dashed line represents the in-lake growth (smolt stage), and the solid line represents the growth once mature. The horizontal dashed line that extends the length of the x-axis is the average asymptotic length (mm) of that life history. Note: LH2.3 (bottom right) does not have a line representing the mature growth as there was insufficient size variance within the different ages.
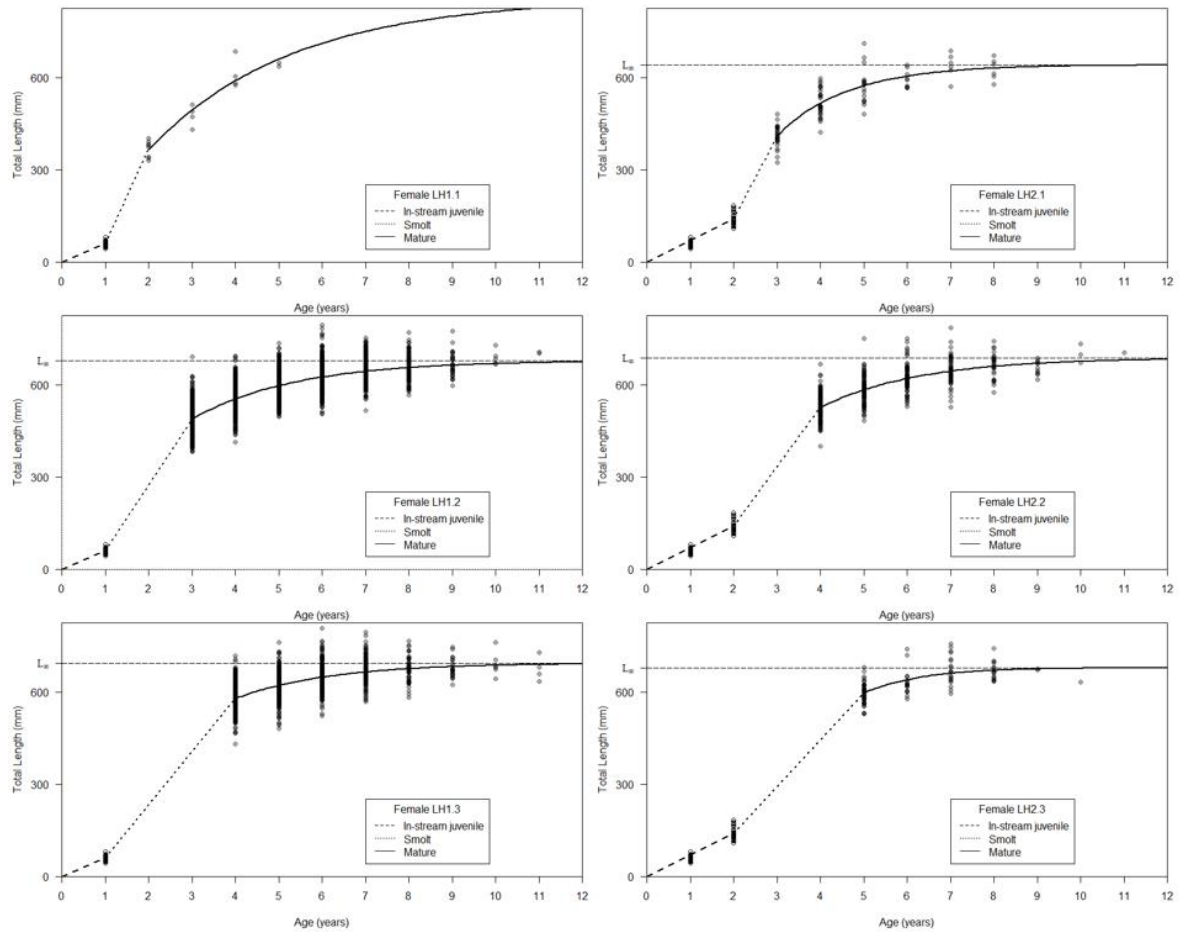
Figure 1.10. Triphasic von Bertalanffy growth models for prominent female Steelhead life history categories from Portage Creek. Data collected from all years of sampling Portage Creek Steelhead were included in the VB curves (1991-2018). The thick dashed line represents the stream growth (parr life stage), the thin dashed line represents the in-lake growth (smolt stage), and the solid line represents the growth once mature. The horizontal dashed line that extends the length of the x-axis is the average asymptotic length (mm) of that life history. Note: the asymptotic length for LH1.1 (top left) should be interpreted cautiously as there is a lack of sample size for this life history causing an increase in the predicted asymptotic length.
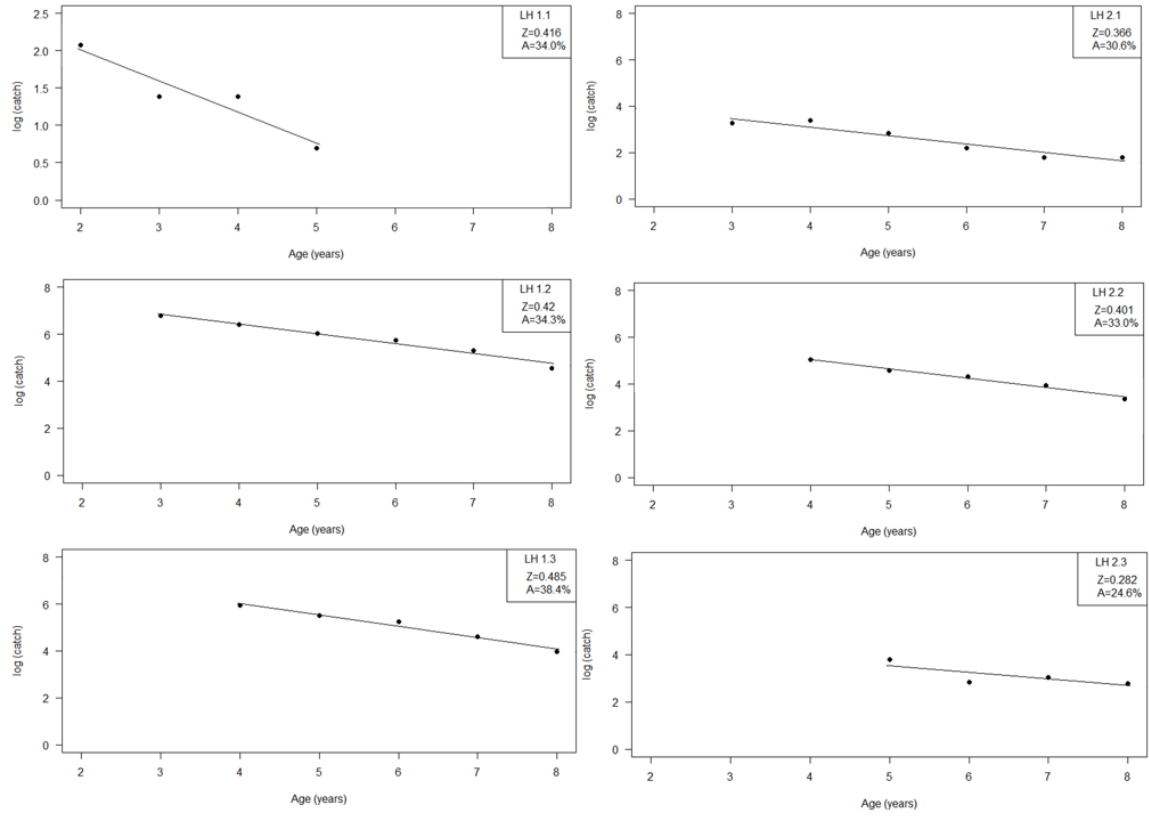
Figure 1.11. Catch curves estimating both instantaneous mortality (*Z*) and annual mortality rate (*A*) of female Portage Creek Steelhead up to age 8 (if applicable) that exhibit prominent life history characteristics.
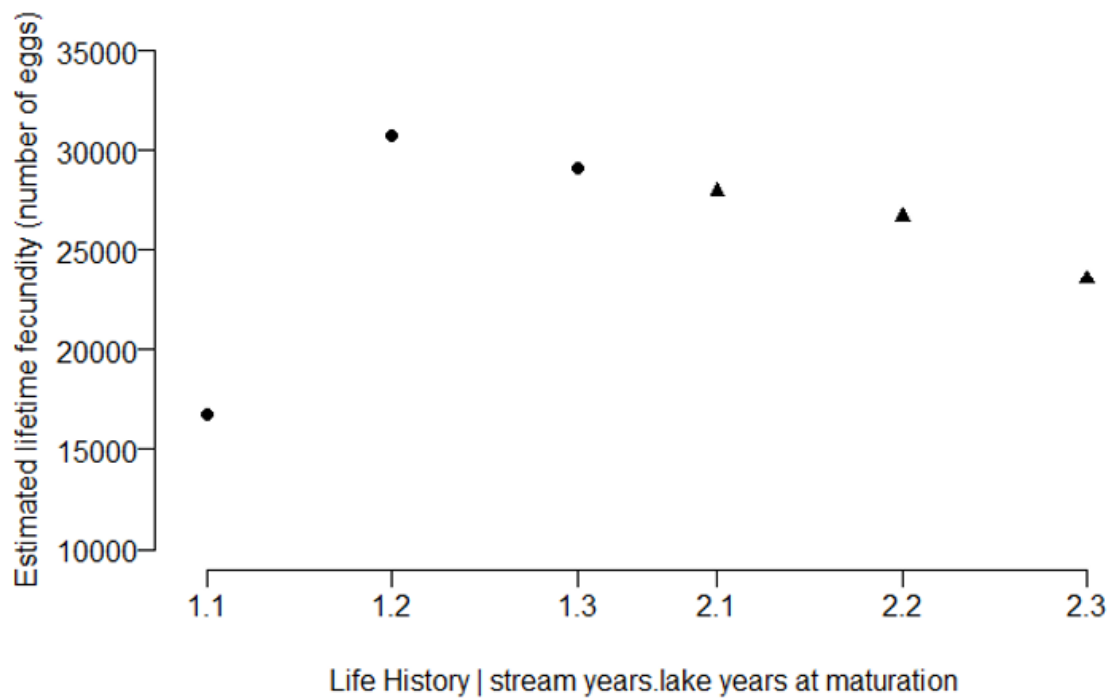
Figure 1.12. Estimated lifetime fecundity (number of eggs) of female Portage Creek Steelhead for each prominent life history category using ages that fell within the 95th percentile for their respective life history category.

TABLES

Table 1.1. Six most prominent life histories present Portage Creek, the Jackpine River, McIntyre River, Whitefish River, Neebing River, McVicar Creek, MacKenzie River, Blind Creek, Wolf River and the Cypress River.

Life History	Number of years spent in the stream	Number of lake years at first spawn	Age at maturation (years)
1.1	1	1	2
1.2	1	2	3
1.3	1	3	4
2.1	2	1	3
2.2	2	2	4
2.3	2	3	5

Table 1.2. List of streams to analyze life history characteristics for 2018. Selected streams are based off having sample sizes >30 Steelhead per stream in 2018. All samples were gathered by the Portage Creek and co-operative angler programs.

Stream	Sample size
Whitefish River	105
Neebing River	131
McIntyre River	206
McVicar Creek	189
MacKenzie River	78
Portage Creek	35
Jackpine River	73
Cypress River	48

Table 1.3. Frequency (%) of age at maturation (years) for Steelhead for both sexes across all study sites and years of interest. The most common ages at maturation are bolded for both sexes across all sites and years examined. Multiple ages at maturation are bolded if the two most frequent ages at maturation for a given site and sex are within 5% of each other.

Site	Sex	Age at maturity (years) frequency (%)			
		2	3	4	5
Portage 1993	M	6	**73**	21	0
	F	2	**47**	**51**	0
Portage 2007	M	13	**79**	8	0
	F	0	**71**	28	1
Portage 2018	M	0	**48**	**43**	10
	F	0	8	**50**	42
Whitefish	M	0	**62**	35	3
	F	0	23	**54**	23
Neebing	M	2	**71**	21	6
	F	0	10	**76**	14
McIntyre	M	2	**70**	23	7
	F	0	14	**44**	**42**
McVicar	M	5	**71**	18	6
	F	3	29	**41**	26
MacKenzie	M	11	**64**	23	2
	F	0	34	**41**	25
Jackpine	M	9	**51**	30	9
	F	0	17	**50**	33
Cypress	M	0	**37**	**42**	21
	F	0	16	**40**	**44**

Table 1.4. Summary of the Dunn's test results comparing the average length at maturation (mm) among male and female Steelhead that exhibit prominent life history strategies from Portage Creek. Life histories strategies that demonstrate having insignificantly different ($p > 0.05$) average lengths at maturation are bolded.

Life history strategy Comparison	adjusted p-values for male-male comparisons	adjusted p-values for female-female comparisons
LH1.1 - LH1.2	< 0.05	< 0.05
LH1.1 - LH1.3	< 0.05	< 0.05
LH1.2 - LH1.3	< 0.05	< 0.05
LH1.1 - LH2.1	< 0.05	**> 0.05**
LH1.2 - LH2.1	< 0.05	< 0.05
LH1.3 - LH2.1	< 0.05	< 0.05
LH1.1 - LH2.2	< 0.05	< 0.05
LH1.2 - LH2.2	< 0.05	< 0.05
LH1.3 - LH2.2	< 0.05	< 0.05
LH2.1 - LH2.2	< 0.05	< 0.05
LH1.1 - LH2.3	< 0.05	< 0.05
LH1.2 - LH2.3	< 0.05	< 0.05
LH1.3 - LH2.3	**> 0.05**	**> 0.05**
LH2.1 - LH2.3	< 0.05	< 0.05
LH2.2 - LH2.3	< 0.05	< 0.05

Table 1.5. Summary of the Dunn's test results comparing the average length at maturation (mm) between male and female Steelhead that exhibit prominent life history strategies from Portage Creek. Significantly different *p*-values (*p* > 0.05) are bolded when females display a significantly larger length than males, and bolded and italicized when males display a significantly larger length than females.

LH	Sex	Average length at maturation (mm)	adjusted *p*-values for male-female differences (95% confidence)
1.1	Male	333	**0.007**
	Female	367	
1.2	Male	487	0.9
	Female	488	
1.3	Male	600	***<0.0001***
	Female	579	
2.1	Male	391	**0.01**
	Female	409	
2.2	Male	526	0.9
	Female	526	
2.3	Male	618	0.06
	Female	597	

Table 1.6. Summary of the age at maturation, average length at maturity (mm), average asymptotic length (mm), average stream growth as parr (mm per year), average immature lake growth as smolt (mm per year), average lifetime fecundity (number of eggs), and average annual mortality rate (%) for all prominent life history traits of female Portage Creek Steelhead.

Life History	Age at maturation (years)	Length at maturation (mm)	L_∞ (mm)	Stream growth (mm per year)	Smolt growth (mm per year)	Lifetime fecundity (number of eggs)	Annual mortality rate (%)
LH1.1	2	367	857	61	306	16745	34.0
LH1.2	3	488	678	61	213	30772	34.3
LH1.3	4	579	694	61	173	29142	38.4
LH2.1	3	409	641	70	269	27931	30.6
LH2.2	4	526	687	70	193	26659	33.0
LH2.3	5	597	678	70	152	23567	24.6

Table 1.7. Summary of the age at maturation, average length at maturity (mm), average asymptotic length (mm), average stream growth as parr (mm per year), and average immature lake growth as smolt (mm per year) for all prominent life history traits of male Portage Creek Steelhead.

Life History	Age at maturation (years)	Length at maturation (mm)	L_∞ (mm)	Stream growth (mm per year)	Smolt growth (mm per year)
LH1.1	2	333	621	61	271
LH1.2	3	487	641	61	213
LH1.3	4	600	731	61	179
LH2.1	3	391	664	70	251
LH2.2	4	526	637	70	194
LH2.3	5	618	664	70	159

Table 1.8. Catch summary for Brook Trout angled during the Portage Creek Steelhead sampling period (2014-2018).

Year	Number of Brook Trout caught	Average Length (mm)
2014	14	282
2015	31	299
2016	72	286
2017	50	259
2018	120	261

Table 1.9. Total catch summary of potential Steelhead predators and competitors from Fall Walleye Index Netting, Black Bay, 2002-2014. Data from Berglund, 2016.

Species	2002	2008	2010	2012	2013	2014
Walleye	13	212	106	193	143	111
Northern Pike	2	17	17	35	44	49
Smallmouth bass	1	24	3	18	6	5

CHAPTER II

Trophic Ecology of Black Bay Steelhead

ABSTRACT

Several changes in the fish community of Lake Superior over the last 30 years have likely influenced species interactions, including, increased Walleye and decreased Steelhead abundances in Black Bay. Here, I used stable isotopes of $\delta^{15}N$ and $\delta^{13}C$ to evaluate potential predator-prey interactions and competition between both immature and mature Walleye and Steelhead in Black Bay, Lake Superior. Results from niche width estimates showed no overlap or evidence of predation between mature Walleye and Steelhead parr, some overlap between Steelhead smolts with both mature (32.0%) and immature (30.2%) Walleye, along with the potential for predation of smolts by mature Walleye, and a lesser amount of overlap between adult Steelhead with both mature Walleye (20.0%) and immature Walleye (18.2%). Niche width areas were also found to be greater for adult Steelhead compared to Walleye, indicating that mature Steelhead utilize a wider range of environments and prey items in the lake relative to the other fish species examined. Temporal analysis of $\delta^{15}N$ and $\delta^{13}C$ for adult Steelhead showed relatively stable trends over time, while parr Steelhead demonstrated a positive shift towards $\delta^{13}C$ enrichment, suggesting a consistent change in forage items. This shift may be a result of competition with Brook Trout, which have increased in density over a similar timeframe as the observed changes in parr $\delta^{13}C$. I conclude based on these results that increased competitor densities (Walleye, Brook Trout) have resulted in increased competitive interactions with immature Steelhead life stages, are likely contributing factors influencing the currently low Steelhead abundance in Black Bay tributaries.

Keywords: benthic, littoral, pelagic, Portage Creek, standard ellipse area, trophic niche space.

INTRODUCTION

Food web structure is important in regulating ecological patterns and processes (Vander Zanden *et al.* 1999). The understanding of food web structure in fisheries allows for the better management of natural resources by providing insights into species interactions that impact species of recreational and commercial interest (Blanke *et al.* 2017). For instance, the estimation of an organism's trophic position is a significant factor in food web ecology when trying to understand trophic connections and interactions (Swanson *et al.* 2015, Blanke *et al.* 2017). A common approach to estimating an organism's trophic position is by using stable isotope analysis (SIA) of nitrogen (δ^{15}N), whereas carbon (δ^{13}C) can provide information on resource partitioning assuming isotopic end members are known and distinct.

Stable isotope analysis can be used to evaluate the trophic connections of a species following ecosystem changes such as density changes of another species, or with species introductions. Species introductions commonly result in substantial deviations in resource partitioning of native species (Vander Zanden *et al.* 1999). For instance, the introduction of littoral Smallmouth Bass (*Micropterus dolomieu*) and Rock Bass (*Ambloplites rupestris*) in central Ontario lakes reduced the trophic position and importance of littoral resources of Lake Trout (*Salvelinus namaycush*) due to competition with invasive bass (Vander Zanden *et al.* 1999). Species invasions can also result in fewer prey-fish species and lower prey-fish abundance, leading to further competitive interactions and changes in resource partitioning in native species (Vander Zanden *et al.* 1999).

Similarly, an increase in the abundance of a previously suppressed species can have similar implications on food web connections with other species occupying these same ecosystems. One potential example is the re-establishment of Walleye (*Sander vitreus*) populations in Black Bay, Lake Superior. Black Bay Walleye abundance increased during the mid 2000's (Table 2.8; Berglund 2016), at a time when the Portage Creek Steelhead (*Oncorhynchus mykiss*) population was near it's peak (Figure 1.1). However, since 2007, the Steelhead population in Portage Creek has declined by over 90% while Walleye abundance has remained constant since 2008 after its initial increase in abundance. Similarly, Brook Trout abundance in Portage Creek has also increased since 2014 (Table 1.8). An analysis of data from Portage Creek, Black Bay suggests that population declines are associated with poor survival of juvenile Steelhead from the smolt stage (migration from Portage Creek to Black Bay) to first time spawners, as well as increased levels of competition between Steelhead parr and Brook Trout in Portage Creek (Chapter I). Thus, the decline in returning adult Steelhead may be a result of reduced juvenile survival which is associated with increases in the Walleye population in Black Bay after 2002 as well as increased Brook Trout (*Salvelinus fontinalis*) densities in Portage creek. These observations suggest a possible negative interaction between Walleye with Steelhead, either through competition or predation once Steelhead smolts leave the stream environment.

The objective of this study was to evaluate changes in Steelhead trophic ecology relative to potential competitors or predators to help interpret declines in Black Bay Steelhead populations over the past decade. This was achieved by using SIA of $\delta^{15}N$ and $\delta^{13}C$ to evaluate the potential changes in the food web position of immature and mature

Steelhead from Portage Creek relative to Walleye, and to identify any temporal changes in Steelhead isotopic values (and therefore food web change) that may have occurred between 1991-2018. I tested the hypothesis that there has been either direct predation or competition between Steelhead and Walleye in Black Bay using a stable isotope approach. I used scales from Portage Creek Steelhead and Black Bay Walleye to evaluate either trophic overlap or direct predation. If Walleye and Steelhead are competing for the same resources, they should occupy similar niche spaces (Swanson *et al.* 2015). I used the isotopic signatures of adult Steelhead that just completed their first year as smolts to estimate smolt isotopic values. If Walleye are consuming Steelhead smolts, I expected to see similar δ^{13}C values between species indicating that they forage in similar areas, but elevated δ^{15}N for Walleye relative to the δ^{15}N of juvenile Steelhead (approximately 3‰ per successive trophic level; Vander Zanden *et al.* 1997, Post 2002, Schmidt *et al.* 2009). Baseline isotopic samples of potential prey species for mature Steelhead, parr Steelhead and Walleye were analyzed for contextual reference. In addition, I also evaluated whether there were any significant changes over time in both parr and adult Steelhead isotopic signatures from 1991-2018 to determine if Steelhead trophic ecology has changed in response to ecosystem changes.

METHODS

Scale Preparation for Stable Isotope Analysis (SIA)

Steelhead displaying a prominent life history strategy (Table 1.1) from Portage Creek were selected for isotope analysis. A life history was defined as prominent if it was present in >1% of the total abundance of mature fish for each sex over all time periods. A

maximum of four Steelhead were randomly selected from each of the six prominent life history categories for each year that scale samples were made available (1991-2003, 2005-2018). Scales were the primary tissue used in the analyses, as they provide a nonlethal approach to SIA that can be used as a substitute for muscle tissue (Kelly *et al.* 2006) and allowed the use of archival samples.

The lake phase and stream phase of individual Steelhead scales were separated using biopsy punches and surgical scissors to individually evaluate the trophic position of each life stage. The circuli on Steelhead scales are continuous rings that go around the scale; when they get close together, they form an annulus (Davis *et al.* 1985). Annuli allow for the determination of life history parameters such as number of years spent in the stream as parr, number of years spent in the lake as smolt, age at maturation, and age at capture. Annuli that are representative of in-stream parr growth are closer together and the circuli are very crowded, appearing near the origin of the scale (Davis *et al.* 1985). The lake portion of the scale was easily identifiable as the annuli and circuli became more spread apart. These visible distinctions between annuli enabled the determination of the years of lake and stream phase of each scale. To extract a portion of the scale that was representative of the lake life phase of each fish, pie-shaped wedges of scale that showed signs of representing lake growth (larger spaces between circuli and annuli) were cut from the outermost part of the scale towards the origin. The portion of scale representing stream growth was identified under a microscope centred on the origin of the scale and removed using a biopsy punch. For Steelhead that spent a single year in Portage Creek before smolting, a 0.5 mm biopsy punch was used to remove the stream portion of the scale. A 1.0 mm biopsy punch was used on scales of Steelhead that spent two years in the

stream before smolting. A duplicate sample was taken ever twentieth sample for quality control and quality assurance purposes. Scale samples were placed in 3.5 x 5 mm tin capsules and weighted using a Sartorius Microbalance to ensure that the sample weighted between 0.25-0.45 g.

<div align="center">Baseline Determination</div>

Isotopic baselines were established for both stream and lake environments. Benthic invertebrate samples from the stream environment were collected from two sections on Portage Creek using the kick and sweep technique during the summer. The first section was upstream from a series of rapids which can act as a bottleneck for migrating fish under low water flows (Jon George, personal communications), and the second section was downstream of the rapids. Sites were sampled on both sides of the rapids to help determine if there were any differences in trophic position of benthic invertebrates or parr Steelhead between sites. All benthic invertebrates were identified to their respective order and dried in an oven for 24 hours at 60 ºC. Once removed from the oven they were ground to a fine powder using a mortar and pestle and weighed (0.25-0.45 g) in tin cups and sent for isotopic analysis.

For the lake environment, common nearshore and offshore prey fish species from Lake Superior were used to create a nearshore and offshore baseline. Yellow Perch are commonly associated with coastal regions and wetlands around Lake Superior (Brazner *et al.* 2004), whereas Lake Herring prefer the pelagic regions of the lake (Hrabik *et al.* 2006). Therefore, Yellow Perch (*Perca flavescens*) and Lake Herring (*Coregonus artedi*) were used to represent nearshore and offshore baselines in Black Bay respectively. Scales

were used to establish δ^{15}N and δ^{13}C baseline values for Yellow Perch and Lake Herring as no other tissue samples were available.

Scale samples of Yellow Perch and Lake Herring were obtained through the Fall Walleye Index Netting (FWIN) program conducted in Black Bay in 2002 and 2010. The FWIN program was initiated in 2002, which was during a time when the Walleye abundance was relatively low in Black Bay (Berglund 2016), and the Portage Creek Steelhead population was approximately 1200 individuals and trending towards an increasing population (Figure 1.1). The 2010 baseline represented a time in Black Bay when the Walleye abundance had increased (Berglund 2016) while the Portage Creek Steelhead population was approximately 800 individuals and trending towards a decrease in population size (Figure 1.1). These two years were also the only years when samples of Steelhead, Walleye, Yellow perch and Lake Herring were all collected. Five samples of Yellow Perch and Lake Herring from 2002 and 2010 were included in the baseline analysis for Black Bay.

Stable isotope abundance is expressed in delta (δ) notation, with relative variations of stable isotope ratios expressed in per mil (‰) relative to international standards for both carbon (Vienna Pee Dee Belemnite) and nitrogen (atmospheric N_2) where:

$$\delta^{15}N \text{ or } \delta^{13}C = ([R_{sample} / R_{standard}] - 1) \times 1000$$

where R is the ratio of the heavy to light isotope, $^{15}N/^{14}N$ or $^{13}C/^{12}C$. All samples were analyzed at Isotope Tracer Technologies Inc., in Waterloo, Ontario, Canada, on a Delta Plus Isotope Ration Mass Spectrometer (IRMS). The isotope laboratory reported

analytical error of C and N determinations at ±0.15‰ and ±0.3‰ respectively. Paired *t*-test results indicated no significant difference between the duplicate samples (n=27) of $\delta^{13}C$ (paired *t*-test, $T_{26} = 1.51$, $p = 0.14$) or $\delta^{15}N$ (paired *t*-test, $T_{26} = 0.39$, $p = 0.70$) for adult Steelhead. For parr Steelhead duplicate samples (n=21), a paired *t*-test showed no significant difference in $\delta^{13}C$ (paired *t*-test, $T_{20} = -1.99$, $p = 0.06$), but did show a significant difference in $\delta^{15}N$ (paired *t*-test, $T_{20} = 2.62$, $p = 0.01$) with an average difference of 0.2‰ between duplicate samples. However, this value is still below reported instrumentation precision by the analytical laboratory and insignificant biologically.

<p align="center">Correction factor – scale centre corrections</p>

Three different correction factors were applied for SIA results of Steelhead scales. The first correction applied was a scale centre correction, followed by a scale – tissue correction, and lastly, for all temporal analyses, a Suess correction.

Centres of scales required a mathematical correction in order to isolate deposition of collagen during the parr stage. Though the centre of the scale is initially representative of deposition during the parr stage, yearly incremental layers of added collagen to fish scales build up vertically over the centre portion of the scale which are more representative of adult feeding rather than from past feeding as parr (Hutchinson *et al.* 2006). Therefore, a correction factor was applied to the biopsy punched central portion of the Steelhead scales to account for the additional vertical growth of the scales that increases with the age of the fish and to provide an estimate of parr isotopic signatures.

To show how the stable isotope signature of a scale centre representative of the parr life stage changed with age, I used a model to predict how the isotopic ratios should change with age compared to the known parr isotopic ratios from 2018. This model assumed that: i) at the end of age 1, the isotopic ratio (I_1/I_2) of the scale centre is equal to A/B, where A and B are the concentrations per unit scale volume of the two isotopes for a given element (either C or N); ii) at the end of each age, an additional layer is deposited over the scale centre; iii) at the end of age n, the scale centre consisted of n layers, the ratio in the first layer is A/B, and in all other layers it is C/D, where C and D are the concentrations per unit scale volume of the two isotopes; (iv) the thickness of each layer (α) is equal, and the area of the sample that is taken from each layer (β) is also equal as the biopsy punch of scale centres is fixed; therefore the sample volume from each layer is identical and equal to V, where V = α * β. Therefore, at age n (age at which the scale is collected), the isotopic ratio (I_1/I_2) in the scale centre is:

$$\text{Equation 2.1)} \qquad \frac{A*V + (n\text{-}1) * C*V}{B*V + (n\text{-}1) * D*V}$$

which can be rearranged to:

$$\text{Equation 2.2)} \qquad \frac{A/B + (n\text{-}1) * C/B}{1 + (n\text{-}1) * D/B}$$

A and B values are fixed from the 2018 parr isotopic values while C and D values are the observed adult isotopic values for individual Steelhead. The predicted centre isotopic ratio I_1/I_2 (in ‰) was then used to determine estimated centre values for parr by subtracting the observed centre values from the predicted centre values from equation 2.2; finally, this difference was added to the mean 2018 parr isotopic signatures (obtained via electroshocking Portage Creek) to determine the estimated isotopic signature. This is

because adult isotopic values were already accounted for in equation 2.2, and therefore

any difference between equation 2.2 and the observed values should have resulted in the

difference of the estimated parr isotopic ratios relative to the known isotopic ratio from

the 2018 parr. Fish were also categorized by age class to represent the isotopic signature

of a parr at age-1 or age-2 when the fish was that age. This method assumed that the

observed isotopic signatures of the parr from 2018 are representative of all parr isotopic

signatures from Portage Creek for 2018, and that parr isotopic signatures have remained

fixed over time.

<div align="center">Correction Factor – scales to muscle tissue</div>

An additional correction factor was applied to convert scale isotopic values to

tissues. A correction factor was applied for both the parr and in-lake portions of the scales

used for SIA. A total of 18 parr were collected via electroshocking in Portage Creek

during the summer of 2018 by the Ontario Ministry of Natural Resources and Forestry

and carcasses were provided for analysis. Both scales and muscle tissue were removed

from the parr and sent for SIA. Muscle tissues for adult Steelhead were obtained from

sacrificing nine mature fish from along the North Shore. Eight muscle tissue samples

were collected from McVicar Creek, and one was from the Whitefish River. Fish were

collected under Lakehead University animal utilization protocol #1466357. Muscle

tissues were dried in an oven for 24 hours at 60 °C and ground to a powder before being

placed in tin cups and weighed. Muscle tissue was analyzed for $\delta^{15}N$ and $\delta^{13}C$ and

compared against scales from the same fish.

To determine the necessary correction factor for both parr and adult Steelhead, a

paired *t*-test was used to determine the average difference between the $\delta^{13}C$ (‰) and $\delta^{15}N$

(‰) for both muscle tissue and scales. The average difference from statistically

significant *t*-tests was then applied to scales to estimate muscle tissue isotopic values.

Correction factors for scale to muscle tissue for Yellow Perch (Rennie unpubl.), Lake

Herring (Langen in prep.) and Walleye (Fincel *et al.* 20120) were based on literature

values.

<div align="center">Correction factor – Suess correction</div>

The release of anthropogenic source CO_2 into the atmosphere via the burning of

fossil fuels and deforestation has caused a reduction in the amount of atmospheric $\delta^{13}C$

over the past two centuries (Bacastow *et al.* 1996, Verburg 2007). This change in the

abundance of carbon isotopes in the carbon cycle because of anthropogenic activities is

referred to as the Suess effect (Verburg 2007). The Suess effect needs to be included

when interpreting $\delta^{13}C$ in aquatic environments over time (i.e. >10 years) as changes in

atmospheric CO_2 over this time scale will affect aquatic CO_2, therefore affecting $\delta^{13}C$

signatures of aquatic organisms over time. The Suess correction equation used to account

for the depletion of atmospheric $\delta^{13}C$ over time is (Verburg 2007):

$$7.7738118*10^{-16} *Y^6 - 1.2222044*10^{-11} * Y^5$$

$$+ 7.1612441*10^{-8} *Y^4 - 2.1017147*10^{-4} * Y^3$$

$$+ 3.3316112*10^{-1} *Y^2 - 2.73.715025 *Y$$

$$+ 91703.261$$

For the temporal analysis, adult Steelhead were corrected to 1992 levels of CO_2, and parr

corrected to 1985 levels of CO_2 for within group comparisons. For comparisons of niche

spaces between 2002 and 2010, a Suess correction was applied to the 2010 δ^{13}C isotopic

signatures to the 2002 levels of CO_2 for all groups. For comparisons of niche spaces

across all years for all groups, a Suess correction was applied to the δ^{13}C isotopic

signatures to the 1985 levels of CO_2 for all groups.

Estimated smolt isotopic signatures

Maiden spawning individuals that have life history strategies that exhibit spending

only 1 year in the lake as smolts (LH1.1 and LH2.1) were used to represent the isotopic

signatures of smolts and were included in the niche overlap analysis. The corrected

isotopic signatures of δ^{13}C and δ^{15}N were compared using a *t*-test between maiden

spawning Steelhead and repeat spawning Steelhead for each prominent life history

strategy.

Niche overlap

Population niche area can be expressed as total area (TA) and can be calculated

from a convex hull which is drawn around the most extreme data points on the isotope bi-

plot (Jackson *et al.* 2012). However, the niche area generated from the convex hull may

be an incomparable measure when samples sizes differ among groups under comparison.

Therefore, the approach I used to estimate niche area was the standard ellipse area (SEA)

as a measure of the mean core population isotope niche. Although the convex hull may

better represent the individual variation of isotope niche width within a group, the SEA

was more robust to differences in sample size among groups (Jackson *et al.* 2012). All

analyses performed to determine isotope niche width were conducted in the SIBER

package (Stable Isotope Bayesian Ellipses in R) in R (Jackson *et al.* 2011). To correct for

limited samples sizes for each group in both years (2002 and 2010), bootstrapping (resampling) was used. When comparing niche width overlaps using SEAs, it has been shown that when sample sizes are <30, the ability to make accurate conclusions becomes very difficult because of biases associated with outliers which have a larger impact on the data set when samples sizes are small (Jackson *et al.* 2011, Syväranta *et al.* 2013). Therefore, 50 samples of individuals per group (species and life stage) were selected with replacement for the niche overlap comparisons between 2002 and 2010. To evaluate competition, niche overlap was determined between Walleye and Steelhead. Groups were made for each species to determine if different life stages impacted the degree of species interactions. Analysis performed by the OMNRF determined that Walleye isotopic signatures did not differ among sexes; however, maturation did, with mature individuals having a significantly greater $\delta^{15}N$ signature and a less depleted $\delta^{13}C$ signature compared to immature Walleye. Therefore, Walleye subsets used to evaluate niche width area were created based on whether a fish was noted as mature or immature at the time of sampling. Similarly, for Steelhead, niche width areas were also calculated for different life stages with parr, age-1 smolt, and adult Steelhead being examined.

To determine niche overlap, specific years were selected to represent different fish community assemblages in Black Bay. In 2002, Walleye abundances in Black Bay were low (Berglund 2016), while Steelhead abundances were relatively high (Figure 1.1). In contrast, 2010 represented a time period where Walleye abundances had increased substantially (Berglund 2016), while the Steelhead abundances had decreased (Figure 1.1).

<u>Variation in isotopic signatures between prominent life histories strategies</u>

To determine in any life history strategies were more vulnerable to possible Walleye predation or competition, a Kruskal-Wallis test was used to evaluate if there were any significant differences in the corrected δ^{15}N and/or δ^{13}C between the six prominent life history strategies for Portage Creek Steelhead across all years. Dunn's tests were performed post-hoc to determine which isotopic signatures differed significantly between life history strategies. Adult and parr Steelhead were analyzed separately. Average δ^{13}C and δ^{15}N were also calculated for each prominent life history strategy for both adult and parr Steelhead.

<u>Temporal isotopic analysis</u>

I examined the corrected δ^{13}C and δ^{15}N signatures among prominent life history strategies for adult Steelhead in Lake Superior and parr Steelhead in Portage Creek to evaluate whether there have been any changes in the feeding ecology of either life stage over time in response to ecosystem changes. To determine the feeding ecology of parr Steelhead, I subtracted the age of the fish (in years) from the year of capture (as mature adults) to estimate the year in which the fish turned age 1. For life histories that remained as parr in Portage Creek for 2 years, the same calculation was used except I added to the year estimate above. This provided the year class in which the fish was born the feeding ecology of parr Steelhead. Changes over time were evaluated using linear regressions.

RESULTS

Correction factor results – scales to muscle tissue

There was a significant difference between tissues and scales for Steelhead parr (δ^{15}N, paired t-test, T_{17} = -2.43, $p < 0.05$; δ^{13}C, paired t-test, T_{17} =5.75, $p < 0.05$). Similar results were found for adult Steelhead (δ^{13}C, paired t-test, T_8 = 15.98, $p < 0.05$; δ^{15}N, paired t-test, T_8 = -6.11, $p = 0.07$). Mean differences between tissue types were calculated and applied to all Steelhead scales representing both parr and adult life stages for both δ^{13}C and δ^{15}N (Table 2.1).

Baseline Results

Samples of benthic invertebrates showed a considerable amount of variation in δ^{15}N and δ^{13}C both between and among taxa (Figure 2.1). Sample location for benthic invertebrates was deemed insignificant as no significant differences between δ^{15}N or δ^{13}C were found when comparing samples that were collected above or below the rapids across all taxa (δ^{15}N: t-test, $T_{6.38} = 0.71$, $p = 0.498$; δ^{13}C: t-test, $T_{4.51} = 2.01$, $p = 0.106$). All Steelhead parr obtained via electroshocking in 2018 were collected below the rapids.

Over both years examined, lake baseline results indicated significantly different δ^{13}C and δ^{15}N between Yellow Perch and Lake Herring in Black Bay (Table 2.2). Yellow Perch foraged in more nearshore environments and were enriched in δ^{13}C relative to Lake Herring (δ^{13}C, paired t-test, $T_9 = 4.33$, $p = 0.001$), and Yellow Perch also had a higher δ^{15}N (trophic position) compared to Lake Herring (δ^{15}N, paired t-test, $T_9 = 2.58$, $p = 0.029$).

Year of collection had a significant influence on δ^{13}C values for Yellow Perch in Black Bay. In 2002, Yellow Perch were 3‰ more negative on average, indicating a greater influence of offshore environments when compared to 2010 (δ^{13}C, paired *t*-test, T_4= -3.18, $p = 0.035$; Table 2.3); however, their trophic position did not change significantly between years (δ^{15}N, paired *t*-test, T_4= 0.807, $p = 0.464$; Table 2.2). Yellow Perch variation in δ^{13}C signatures was greater in 2010 (Standard Deviation=2.25‰) compared to 2002 (SD=0.39‰), suggesting an increase in foraging diversity since 2002 (Table 2.2). There were no significant differences between 2002 and 2010 for Lake Herring in either δ^{15}N or δ^{13}C (δ^{15}N, paired *t*-test, T_4= 0.04, $p = 0.965$; δ^{13}C paired *t*-test, T_4= 1.30, $p = 0.262$).

Estimated smolt isotopic signatures

T-test results indicated that for maiden spawning Steelhead, those that spent one year as a smolt in Lake Superior before reaching maturation had significantly lower δ^{15}N values relative to repeat spawners of the same life history strategy. Both maiden spawning LH1.1 (*t*-test, $T_{46} = -2.8$, $p = 0.008$) and LH2.1 (*t*-test, $T_{64} = -3.8$, $p < 0.05$) Steelhead had lower δ^{15}N compared to repeat spawners of the same life history, regardless of sex. Maiden spawning LH1.1 and LH2.1 Steelhead showed no significant difference in δ^{15}N (*t*-test, $T_{52} = -0.44$, $p = 0.6$) or δ^{13}C (*t*-test, $T_{65} = 0.64$, $p = 0.5$). All other prominent life history strategies showed no significant difference between maiden and repeat spawning isotopic signatures.

Niche overlap

Steelhead parr from Portage Creek in 2018 typically had greater δ^{15}N signatures than benthic invertebrates (Table 2.1), but also had a much smaller δ^{13}C range,

suggesting that the parr are likely mainly foraging on Isopods and Amphipods within Portage Creek (Figure 2.1). Steelhead parr had an average δ^{15}N signature of 10.37 (SD=0.58‰) and an average δ^{13}C signature of -31.53 (SD=0.83‰).

Both δ^{15}N and δ^{13}C varied greatly among individuals of the same group (species and age class) across both years (Figure 2.2). There was zero niche overlap found between estimated Steelhead parr and Walleye isotope ratios, regardless of Walleye life stage (Table 2.4). Steelhead smolts showed the most amount of overlap with Walleye (Figure 2.2) with 32.0% overlap with mature Walleye and 30.2% overlap with immature Walleye (Table 2.4). Results showed that there was some overlap between mature Steelhead in Black Bay and both immature and mature Walleye; adult Steelhead in Black Bay have a niche width overlap of 20.0% with mature Walleye, and 18.2% with immature Walleye.

For all years, adult Steelhead in Black Bay appeared to be generalists, as their SEA occupies the second largest amount of area (second only to Yellow Perch; Figure 2.2), with δ^{13}C ranging from -26.4‰ to -14.6‰ (SD = 1.8‰) and δ^{15}N ranging from 6.6‰ to 10.9‰ (SD = 0.8‰).

Bootstrapped SEA estimates for 2002 and 2010 indicated that mature and immature Walleye trophic ecology were different in both years (Figures 2.3 and 2.4). During 2002, mature Walleye had the largest trophic niche area of all the groups examined, and encompassed the trophic niche area for adult Steelhead (Figure 2.3). Mature Walleye were also elevated in δ^{15}N by 0.9‰ and had similar δ^{13}C relative to smolts. By contrast, there was zero overlap between Walleye and adult or smolt Steelhead in 2010, with the only overlap occurring between mature and immature

Walleye (Figure 2.4). From 2002 to 2010, the average $\delta^{15}N$ for mature Walleye dropped from 8.4 ‰ (SD=0.44‰) to 6.6 ‰ (SD=0.11‰) while the average $\delta^{13}C$ went from -23.5‰ (SD=0.90‰) to -22.7‰ (SD=0.09‰).

<u>Variation in isotopic signatures between prominent life histories strategies</u>

There were significant differences between isotopic signatures of prominent life history strategies for both $\delta^{13}C$ (Kruskal-Wallis test, $x^2 = 31.55$, df = 5, $p <0.05$) and $\delta^{15}N$ ($x^2 = 43.12$, df = 5, $p <0.05$) for adult Steelhead from Portage Creek. Dunn's test indicated which of the life history strategies differed significantly for $\delta^{13}C$ and $\delta^{15}N$ (Table 2.5). Adult Steelhead life history strategies that displayed smolting at age 1 had more enriched $\delta^{13}C$ signatures relative to those that displayed smolting at age 2 (Table 2.7). For adult Steelhead, average $\delta^{15}N$ generally increased with age at maturity (Table 2.7), while $\delta^{13}C$ was more associated with smolting age as adult Steelhead that exhibited smolting at age-2 had more depleted $\delta^{13}C$ signature relative to those that smolted at age-1 (Table 2.7). Similarly, Steelhead parr isotopic signatures were significantly different between prominent life history strategies for both $\delta^{13}C$ ($x^2 = 79.80$, df = 5, $p <0.05$) and $\delta^{15}N$ ($x^2 = 71.75$, df = 5, p <0.05). Once again, a Dunn's test indicated which of the life history strategies differed significantly for each isotope (Table 2.6). Estimated Steelhead parr isotopic signatures were dependent on the number of years spent in the stream; age-1 parr in Portage Creek have lower $\delta^{15}N$ and were more enriched in $\delta^{13}C$ relative to age-2 parr (Table 2.8).

<u>Temporal changes in Steelhead isotopic signatures</u>

Mature Steelhead isotopic signatures collected from Portage Creek were relatively stable over time (Figures 2.5 and 2.6); linear regression indicated that the only LH2.1 δ^{15}N changed significantly ($F_{(1, 23)} = 8.33$, $p = 0.008$), trending towards a lower trophic position over time (Figure 2.6).

Estimated parr isotopic signatures shifted consistently over time in both feeding habits and trophic position (Figures 2.7 and 2.8). Linear regression indicated that LH1.2 ($F_{(1, 21)} = 8.45$, $p = 0.008$) , LH1.3 ($F_{(1, 22)} = 17.11$, $p = 0.0004$), LH2.2 ($F_{(1, 26)} = 11.48$, $p = 0.002$) and LH2.3 ($F_{(1, 22)} = 7.16$, $p = 0.013$) all became more enriched in δ^{13}C over time. Although four of the six prominent life histories showed trends towards becoming more enriched in δ^{13}C over time, all life histories showed considerable annual variation in annual average δ^{13}C signatures (Figure 2.7). The relative trophic positions of parr showed no temporal trends with the exception of LH1.3 ($F_{(1, 22)} = 7.62$, $p = 0.011$) which decreased in δ^{15}N.

DISCUSSION

Across all years examined, I found evidence of limited niche width overlap between Steelhead (adults and smolts) with immature and mature Walleye in Black Bay, but no overlap between Steelhead parr with any other group of fish in Black Bay (Figure 2.2). Results also showed that in 2002, mature Walleye were elevated in δ^{15}N by 0.9‰ relative to Steelhead smolts with similar δ^{13}C. These results suggested that there was potential for some competitive interactions between immature and mature Walleye and smolt and mature Steelhead, as well as the potential for smolt predation by mature Walleye in Black Bay during a period of high smolt abundance. Despite the overlap,

both species seem to generally demonstrate different foraging strategies; Steelhead appear to be more opportunistic as demonstrated by their wide range in $\delta^{13}C$ and $\delta^{15}N$ values across all years, whereas Walleye appear to be more specific in their feeding approach as illustrated by their much smaller $\delta^{15}N$ and $\delta^{13}C$ ranges over all years. These results are similar to previous studies that have examined the feeding habits of Steelhead and have concluded that they eat a wide variety of prey items (Brodeur 1990, Rand *et al.* 1993, Godby *et al.* 2007), many of which are invertebrates (Keough *et al.* 1996, Godby *et al.* 2007). On the contrary, Walleye are mostly piscivorous and seem to occupy more narrow niche widths as they tend to exploit specific prey species to fulfill a large part of their diet (Lyons *et al.* 1987, Keough *et al.* 1996, Vander Zanden *et al.* 1997).

My results did not indicate any signs of adult Walleye interacting with Steelhead parr once they initially smolt out in Black Bay. Estimated Steelhead parr isotope ratios indicated what the feeding ecology and trophic position of the parr were throughout their time in Portage Creek and indicated what their isotopic ratios were once they first smolted relative to other fish in Black Bay. As new Steelhead smolts begin to forage in Lake Superior, their tissues will start to reflect their new feeding habits and will likely be reflected in their isotope ratios over time. Therefore, any conclusions regarding Steelhead parr relative to other groups may not be accurate as the parr ratios are representative of the stream environment rather than the lake environment where all the other groups have been feeding. However, the possibility of Walleye feeding on newly smolted parr cannot be discounted for several reasons. First, as Walleye have densities increased and Steelhead densities have decreased, the likelihood of capturing a Walleye that has consumed a juvenile Steelhead get progressively smaller. Additionally, the tissues used to

determine Walleye isotopic signatures (scales) may not be sensitive enough to reflect the isotopic signatures of prey items (such as newly smolted parr) that likely only comprise a fraction of their overall diet.

Potential competition and predation between Steelhead and Walleye was greatest during a Steelhead's smolt phase. In this study, smolt isotopic signatures were estimated using the isotopic results of maiden spawning Steelhead that exhibit having spent 1 year in the lake environment as a smolt. Results showed that maiden spawning Steelhead that exhibit life history strategies that spend 1 year in the lake environment prior to reaching maturation (LH1.1 and LH2.1) had a significantly lower δ^{15}N signature relative to repeat spawning individuals from the same life history strategy. Since the maiden spawning individuals for those two life history strategies have spent one year in the lake their isotopic signatures were likely good representations of age-1 smolt isotopic signatures. By using the maiden spawning LH1.1 and LH2.1 isotopic signatures to represent the smolt signatures, the SEA across all years (Figure 2.2) showed that there was more overlap between smolts and Walleye compared to all other Steelhead life stage. The 2002 results also illustrated that mature Walleye were elevated in δ^{15}N by 0.9‰ when compared to Steelhead smolts. Because scales were used to determine the isotopic signatures of Walleye, it is possible that a sudden elevation in δ^{15}N associated with smolt consumption may not have been detected as scales are a more chemical reservoir when compared to other tissues types (Fincel *et al.* 2012).

Walleye niche widths have changed considerably in Black Bay between 2002 and 2010. During 2002 when Walleye abundances in Black Bay were low, Walleye isotopic signatures (based on bootstrapping) had a wider niche range compared to the other

groups examined in 2002, and compared to the bootstrapped 2010 results when Walleye abundances were high. This suggested that when Walleye abundances in Black Bay were low, mature Walleye were feeding on a wider variety of prey items/habitats relative to when abundance were higher.

Mature Walleye may have exhibited a broader array of niches when their abundance was lower in Black Bay because of adult Walleye stocking (Garner *et al.* 2013) which introduced Walleye from different in-land lakes and tributaries of Lake Superior that likely may have exhibited different niche preferences. To re-establish the Walleye population in Black Bay, the OMNRF stocked Black Bay with 1032 adult Walleye from the Current and Pigeon Rivers in 1972, and again with 768 adult Walleye from inland lakes between 1998-2000 (Garner *et al.* 2013). It appears as though these initial stocking events were relatively unsuccessful at re-establishing the Black Bay Walleye populations as the FWIN data showed that Walleye abundances were very low in Black Bay in 2002 (Garner *et al.* 2013, Berglund 2016). Even with the low abundance of Walleye in 2002, the adults displayed a much wider niche width when compared to later years of higher Walleye abundance. Perhaps some individuals from the stocking events prior to 2000 survived in Black Bay and were utilizing different foraging techniques and selecting different prey items as they likely would have done in their respective environments prior to being relocated to Black Bay (Fincel *et al.* 2012). This could explain why there was such a diverse range of mature Walleye niches in 2002. There were further stocking events in Black Bay; during 2003, 1 000 000 Walleye fry were released into Black Bay from Cloud Lake, and in 2004 and 2005, 260 000 Walleye fingerlings were released from the St. Mary's River (Garner *et al.* 2013). These stocking

events seemed to have a significant impact on the Walleye abundance in Black Bay as the average number of Walleye caught per net during the FWIN program increased from 0.16 in 2002 to 10.7 in 2008 (Garner *et al.* 2013, Berglund 2016). Genetic analysis conducted on Walleye collected during the 2008 FWIN program showed that most of the Walleye in Black Bay were comprised of fish originating from Black Bay and from the 2004 and 2005 stocking event from the St. Mary's River (Garner *et al.* 2013). With the majority of the 2008 Black Bay Walleye being comprised of two populations, the niche width area may have been smaller than it was during 2002 when the Black Bay Walleye population was comprised of stocked adult Walleye from various inland lakes. Additionally, because the stocking events of 2004 and 2005 from the St. Mary's River consisted of fingerlings instead of adults, the fingerlings may have been more inclined to adopt a specific feeding strategy in Black Bay compared to the adult transfers that had previously defined feeding habits. If the stocked fingerlings used a feeding strategy that best increased their overall fitness, this strategy would have likely also been used by the native Black Bay Walleye. Therefore, because of similar feeding patterns, it may be difficult to distinguish any isotopic differences between the two different Walleye stocks in 2010 which could cause the niche width to become smaller in size as the stocks became more refined in their feeding strategies.

Prey fish diversity and abundance decreased in Black Bay between 2002 and 2010 which could have influenced the reduction in Walleye niche width during those years. The 2002 FWIN results show high abundances of potential prey fishes species such as Spottail Shiner (*Notropis hudsonius*), Longnose Sucker (*Catostomus catostomus*), Lake Chub (*Couesius plumbeus*), as well as various *Coregonus* species (Table A11). With such

a wide array of potential prey items available, the expectation of a piscivorous predator such as a Walleye would be to exhibit a range of niches at the individual level which would allow the population to express a larger niche width area relative to if there were fewer potential prey items available. Relative to the 2002 results, the 2010 FWIN results showed substantial decreases in the abundances of major prey species in Black Bay. This decrease in potential prey abundance corresponded with the significant decrease in Walleye niche width area between 2002 and 2010. Therefore, Walleye may have been forced to become more dependent on a particular food item because of a general reduction in prey abundance and diversity in Black Bay.

The change in potential prey fish abundance in Black Bay from 2002-2010 (Table A11) did not seem to have a major impact on mature Steelhead niche width areas but may have influenced the smolt niche areas as shown by my analysis. The niche width of smolts in 2010 compared to 2002 is narrower, indicating that the smolts have adopted a more specific feeding habit in 2010. Steelhead will use a wide range of environments and will forage on a wide variety of items from small fishes, benthic invertebrates and terrestrial invertebrates (Brodeur 1990, Rand *et al.* 1993, Godby *et al.* 2007), therefore making Steelhead niches generally less susceptible to changes in response to prey fish species composition and abundance relative to Walleye who are primarily piscivores.

Temporal analysis of δ^{15}N and δ^{13}C for prominent life history strategies of adult Steelhead showed very few significant trends which indicated that adult Steelhead foraging in Lake Superior has been relatively stable over the past few decades. The only evidence of significant temporal change in adult Steelhead SIA was in LH2.1 which showed a decline in δ^{15}N over time. Likely because of their smaller size compared to

other Steelhead life histories, LH2.1 is being forced to feed on alternative prey items lower down on the food web in Lake Superior compared to the other Steelhead life histories. This temporal decrease in $\delta^{15}N$ for LH2.1 adult Steelhead may have been the result of a dietary shift that became more dependent on $\delta^{15}N$ depleted prey items such as benthic organisms and *Mysis diluviana* rather than $\delta^{15}N$ enriched potential prey items such as Lake Herring or Yellow Perch (Keough *et al.* 1996).

Temporal SIA of prominent life history strategies of Steelhead parr showed many significant trends in $\delta^{13}C$ which indicated that parr foraging in Portage Creek has changed over the past few decades. Four of six prominent life history categories examined displayed trends of becoming more enriched in $\delta^{13}C$ over time, strongly suggesting a shift in parr feeding in Portage Creek. Based on the 2018 baseline results, an enrichment in $\delta^{13}C$ for parr could be the result of a switch away from a diet of Trichoptera, chironomids and leeches and towards a diet consisting of more Odonata, amphipods and Isopods. This switch in parr diet may also be a result of competition with Brook Trout. Studies along the North Shore of Lake Superior have demonstrated that not only do Brook Trout and parr Steelhead occupy similar in-streams habitats, but they also have similar diets (Rose 1986). Similar studies have also shown that Trichoptera is a major food source in many streams for Brook Trout (Cunjak *et al.* 1987). Therefore, it appears as though the larger Brook Trout may be out-competing the Steelhead parr for resources and forcing the parr to find alternative prey.

In conclusion, stable isotope analyses have provided evidence regarding some potential competition and the possibility of predation between Walleye and Steelhead in Black Bay. Estimated parr Steelhead isotopic signatures vary considerably on an annual

basis, likely as a result of yearly changes in invertebrate availability, but also showed trends towards $\delta^{13}C$ enrichment over time likely as a result of competition with Brook Trout. Smolt isotopic signatures showed the greatest amount of overlap with Walleye and showed the possibility that predation of age-1 smolts may have occurred during the period of high Steelhead abundance as Walleye were more enriched in $\delta^{15}N$ relative to the smolts. Adult Steelhead also showed signs of potential competition with Walleye as they shared similar niche spaces. Both adult and parr Steelhead also showed signs of having a diverse diet with adult Steelhead isotopic signatures have been relatively stable since 1991 and indicated lots of individual variation in both habitat and forage. Temporal comparisons between low Walleye abundance in 2002 and high Walleye abundance in 2010 showed that mature Walleye niche area has decreased significantly since 2002 which was likely in response to fewer stocks being present in 2010 and less diverse prey species availability. While no isotopic evidence provided conclusive evidence of predation on parr or smolts, competitive overlap and potential insensitivity of scales to reflect pulses in resources (e.g., smolts leaving rivers in the spring) mean this possibility cannot be discounted, particularly in light of changes observed in life history shifts in this population (Chapter I).

FIGURES
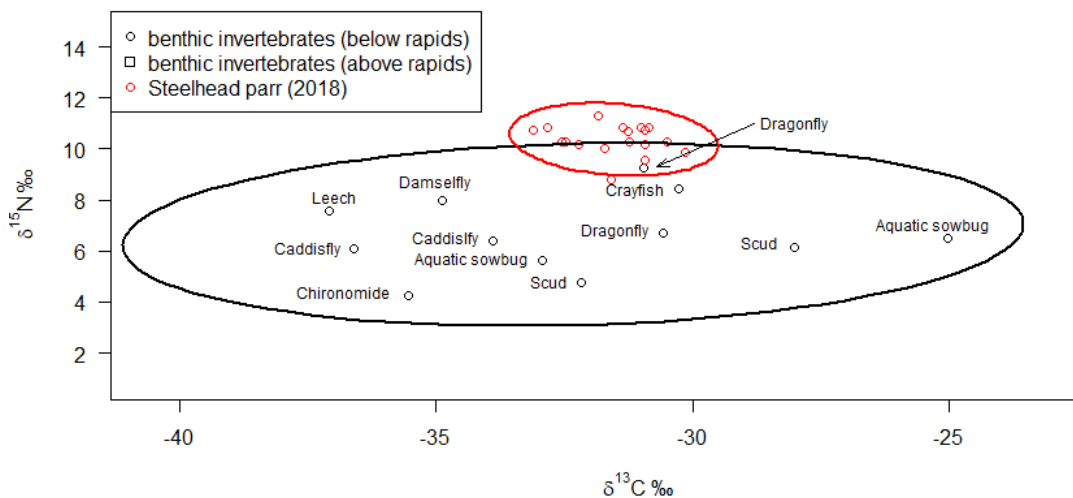
Figure 2.1. Standard ellipse areas (SEA) to illustrate isotope niche width for benthic invertebrates collected above (hollow squares) and below (hollow circles) the rapids and Steelhead parr collected in 2018 from Portage Creek. All Steelhead parr were collected below the rapids.
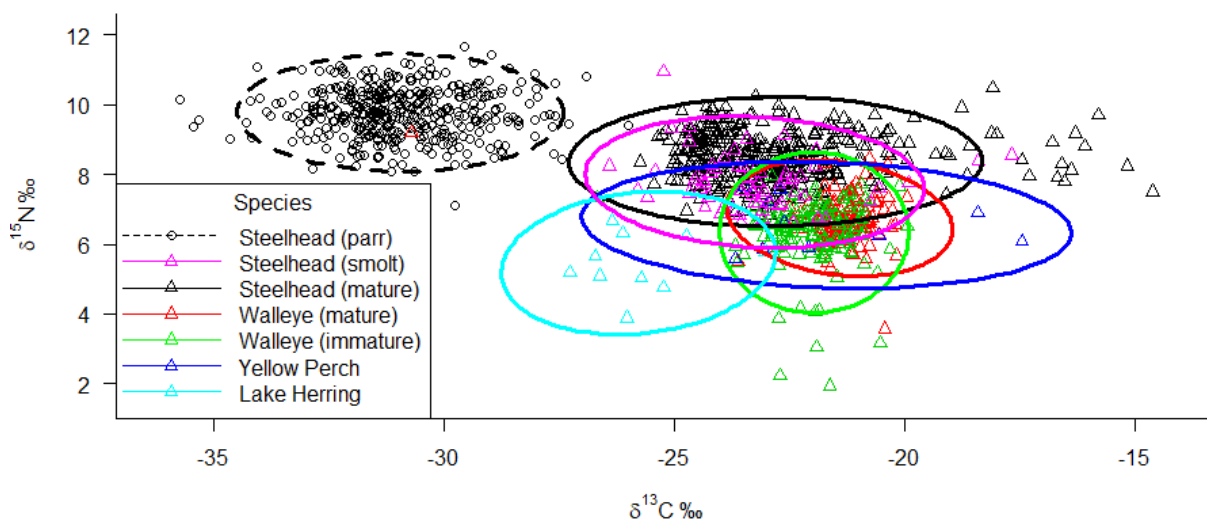
Figure 2.2. Standard ellipse areas (SEAs, solid lines) to estimate isotope niche width across all years for Walleye (mature and immature), mature Steelhead, Steelhead smolt, Yellow Perch and Lake Herring from Black Bay, and Steelhead parr from Portage Creek. The $\delta^{13}C$ for all groups were Suess corrected to 1985 levels of CO_2.
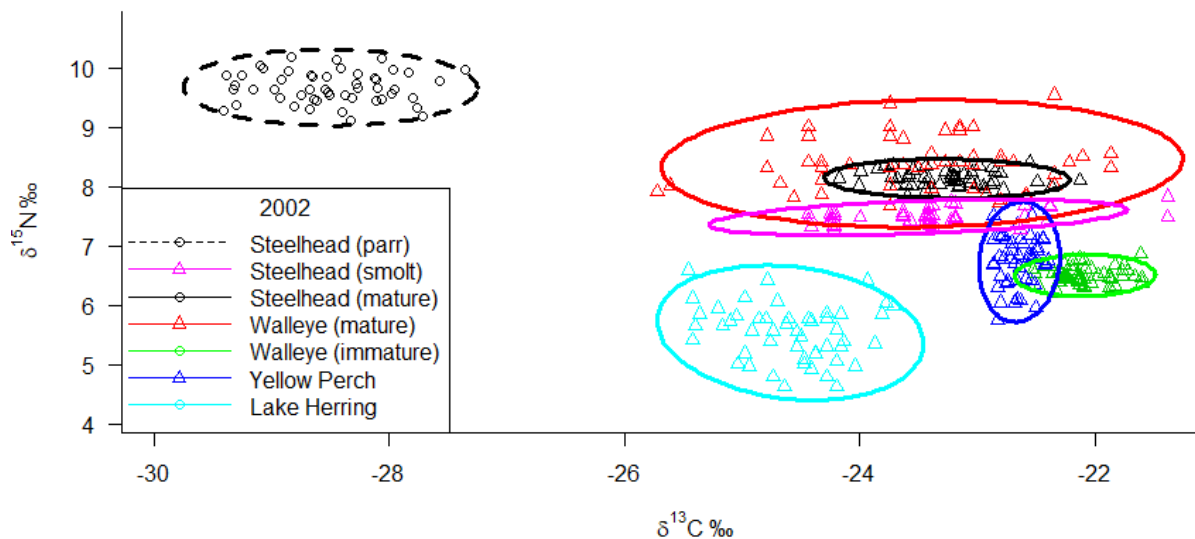
Figure 2.3. Standard ellipse areas (SEA, solid lines) based on bootstrapped isotopic signatures (n=50 per group) to estimate isotope niche width in 2002 for Walleye (mature and immature), mature Steelhead, Steelhead smolt, Yellow Perch and Lake Herring from Black Bay, and Steelhead parr from Portage Creek.
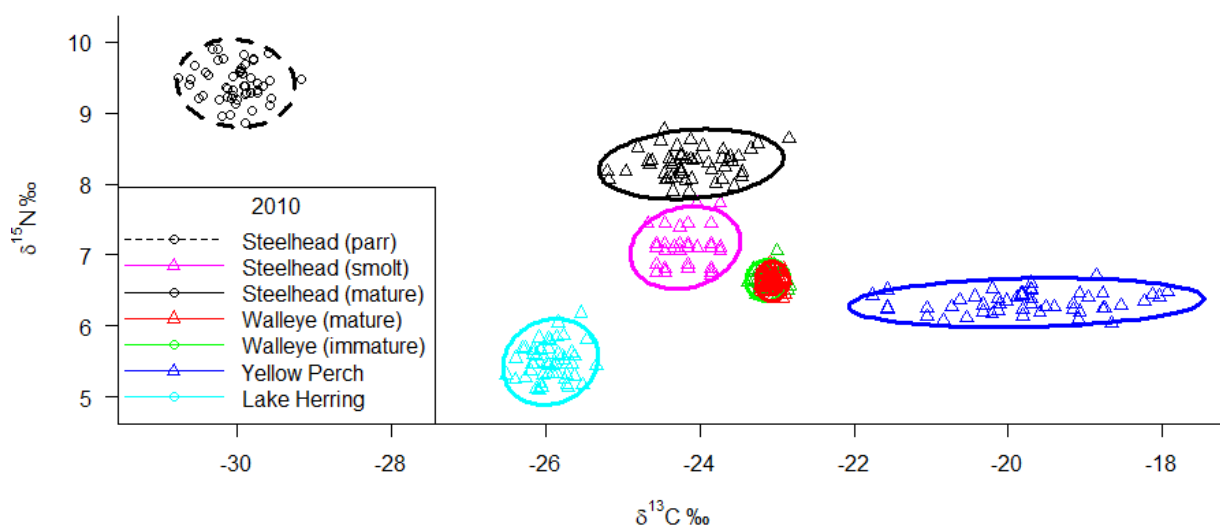
Figure 2.4. Standard ellipse areas (SEA, solid lines) based on bootstrapped isotopic signatures (n=50 per group) to estimate isotope niche width in 2010 for Walleye (mature and immature), mature Steelhead, Steelhead smolt, Yellow Perch and Lake Herring from Black Bay, and Steelhead parr from Portage Creek. The $\delta^{13}C$ for all groups were Suess corrected to 2002 levels of CO_2.
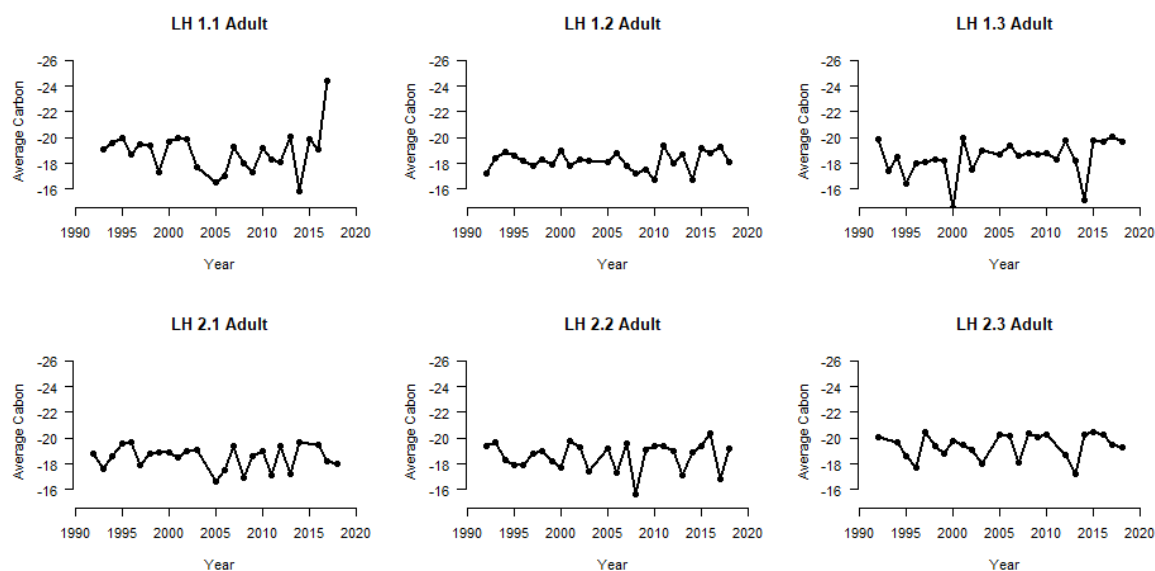
Figure 2.5. Average δ^{13}C‰ for prominent adult Steelhead life history strategies found in Lake Superior between 1991-2018. Average δ^{13}C values were Suess corrected to 1991 levels of CO_2.
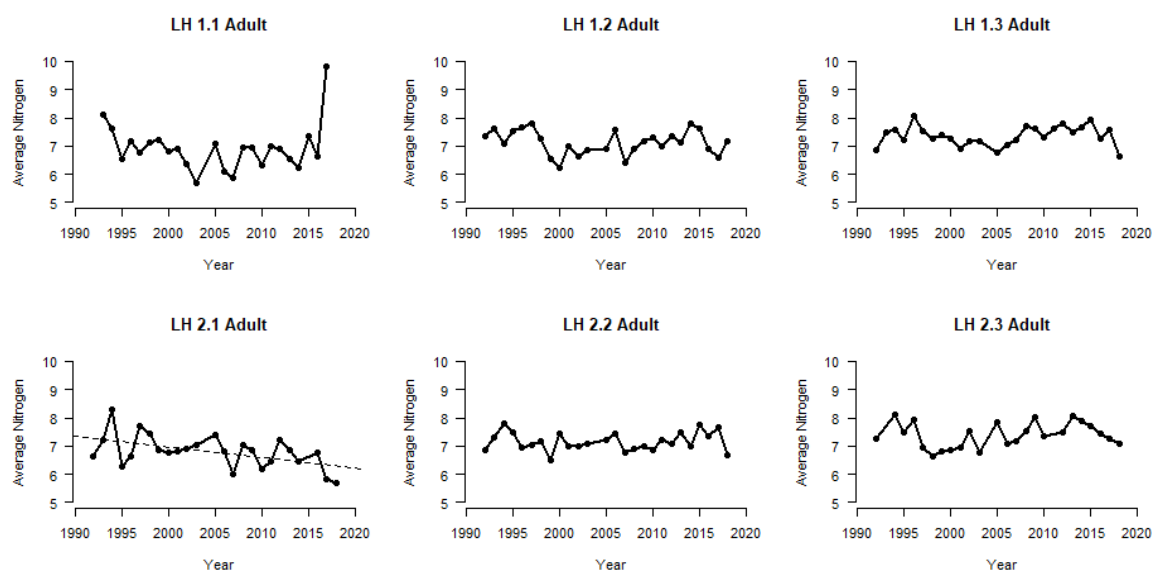
Figure 2.6. Average δ^{15}N‰ for prominent adult Steelhead life history strategies found in Lake Superior between 1991-2018.
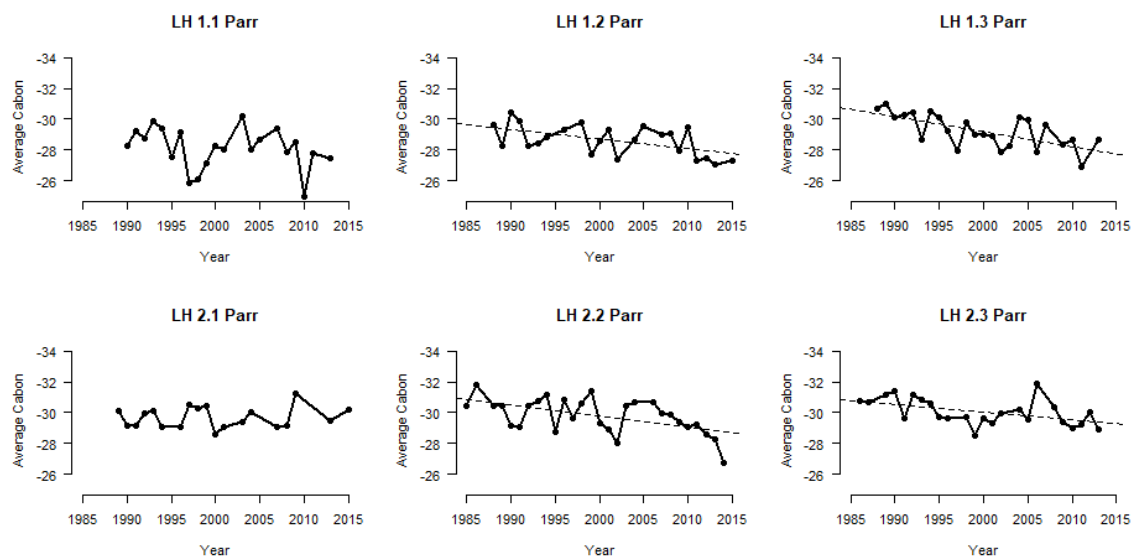
Figure 2.7. Average δ¹³C‰ for prominent Steelhead parr life history strategies found in parr from Portage Creek between 1985-2015. Average δ¹³C values were Suess corrected to 1985 levels of CO_2.
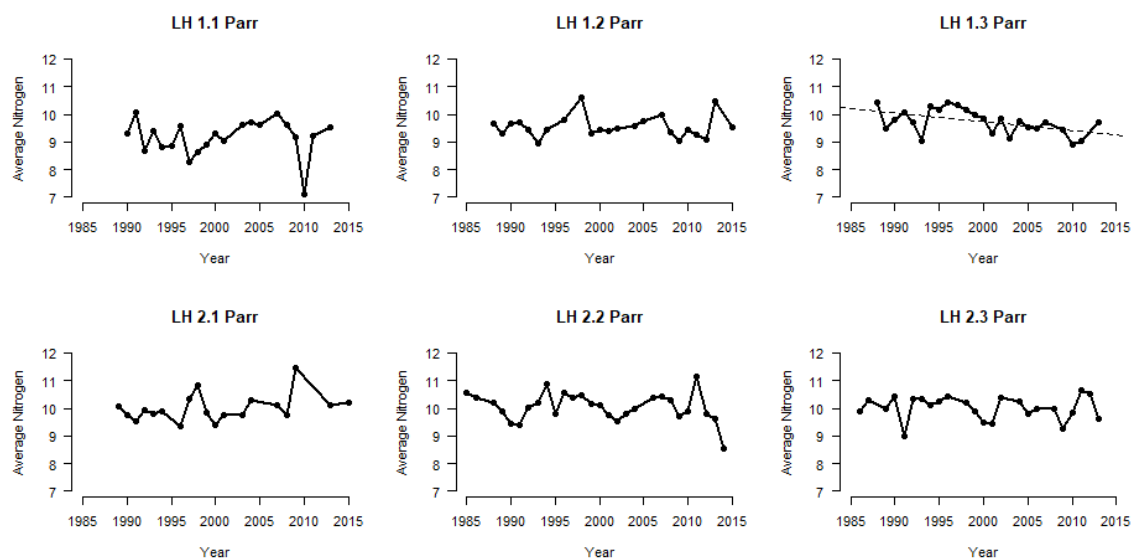
Figure 2.8. Average δ¹⁵N‰ for prominent Steelhead parr life history strategies found in parr from Portage Creek between 1985-2015.

TABLES

Table 2.1. Summary of the δ^{13}C (‰) and δ^{15}N (‰) corrections factors applied to scales to obtain muscle tissue results.

Species	δ^{13}C (‰)	δ^{15}N (‰)	References
Lake Herring	+4.0	-0.6	Langen (in prep)
Perch	+3.1	-1.2	Rennie (unpubl)
Walleye	+2.4	-0.2	Fincel *et al.* 2012
Steelhead (lake)	+4.2	-1.3	This study
Steelhead (parr)	+2.1	-0.3	This study

Table 2.2. Summary of the stream, littoral and pelagic isotopic baseline results. The stream baseline values are comprised of benthic invertebrates, while Yellow Perch comprise the littoral zone and Lake Herring comprise the pelagic zone. All values are expressed as part per thousand (‰).

Area (baseline)	δ^{15}N (‰)	δ^{13}C (‰)
Stream (benthic invertebrates)	6.6	-32.3
Littoral (Yellow Perch)	6.6	-21.0
Pelagic (Lake Herring)	5.5	-25.1

Table 2.3. Summarized t-test results comparing δ^{13}C (‰) and δ^{15}N (‰) for Yellow Perch and Lake Herring from Black Bay, Lake Superior, between 2002 and 2010. All isotopic values are expressed as part per thousand (‰).

Species (lake area)	Year	Isotope δ^{15}N	*P* Value
Yellow Perch (littoral)	2002	6.8	0.46
	2010	6.3	
Lake Herring (pelagic)	2002	5.5	0.96
	2010	5.5	
		δ^{13}C	
Yellow Perch (littoral)	2002	-22.6	0.03
	2010	-19.4	
Lake Herring (pelagic)	2002	-24.5	0.26
	2010	-25.6	

Table 2.4. Calculated niche overlap across all years between Walleye (mature and immature) and Steelhead (lake and parr) corresponding with the 95% confidence intervals generated by the ellipses in Figure 2.3.

Interaction	Overlap (%)
Walleye (mature) - Steelhead (parr)	0.00
Walleye (immature) – Steelhead (parr)	0.00
Walleye (mature) – Steelhead (smolt)	31.96
Walleye (immature) – Steelhead (smolt)	30.23
Walleye (mature) - Steelhead (adult)	19.97
Walleye (immature) - Steelhead (adult)	18.10

Table 2.5. Summary of the Dunn's test results comparing the isotopic signatures of $\delta^{13}C$ and $\delta^{15}N$ for adult Steelhead that exhibit prominent life history strategies from Portage Creek. Significantly different $\delta^{13}C$ and $\delta^{15}N$ values between prominent life history strategies for adult Steelhead are bolded.

Life history strategy Comparison	p-values for $\delta^{13}C$	p-values for $\delta^{15}N$
LH1.1 - LH1.2	**< 0.05**	> 0.05
LH1.1 - LH1.3	> 0.05	**< 0.05**
LH1.2 - LH1.3	**< 0.05**	**< 0.05**
LH1.1 - LH2.1	> 0.05	> 0.05
LH1.2 - LH2.1	**< 0.05**	**> 0.05**
LH1.3 - LH2.1	> 0.05	**< 0.05**
LH1.1 - LH2.2	> 0.05	**< 0.05**
LH1.2 - LH2.2	**< 0.05**	> 0.05
LH1.3 - LH2.2	> 0.05	**< 0.05**
LH2.1 - LH2.2	> 0.05	**< 0.05**
LH1.1 - LH2.3	**< 0.05**	**< 0.05**
LH1.2 - LH2.3	**< 0.05**	**< 0.05**
LH1.3 - LH2.3	**< 0.05**	> 0.05
LH2.1 - LH2.3	**< 0.05**	**< 0.05**
LH2.2 - LH2.3	**< 0.05**	> 0.05

Table 2.6. Summary of the Dunn's test comparing the isotopic signatures of $\delta^{13}C$ and $\delta^{15}N$ for Steelhead parr that exhibit prominent life history strategies from Portage Creek. Significantly different $\delta^{13}C$ and $\delta^{15}N$ values between prominent life history strategies for Steelhead parr are bolded.

Life history strategy comparison	p-values for	p-values for
LH1.1 - LH1.2	> 0.05	**< 0.05**
LH1.1 - LH1.3	**< 0.05**	**< 0.05**
LH1.2 - LH1.3	**< 0.05**	> 0.05
LH1.1 - LH2.1	**< 0.05**	**< 0.05**
LH1.2 - LH2.1	**< 0.05**	**< 0.05**
LH1.3 - LH2.1	> 0.05	**< 0.05**
LH1.1 - LH2.2	**< 0.05**	**< 0.05**
LH1.2 - LH2.2	**< 0.05**	**< 0.05**
LH1.3 - LH2.2	**< 0.05**	**< 0.05**
LH2.1 - LH2.2	> 0.05	> 0.05
LH1.1 - LH2.3	**< 0.05**	**< 0.05**
LH1.2 - LH2.3	**< 0.05**	**< 0.05**
LH1.3 - LH2.3	**< 0.05**	**< 0.05**
LH2.1 - LH2.3	> 0.05	> 0.05
LH2.2 - LH2.3	> 0.05	> 0.05

Table 2.7. The average $\delta^{13}C$ and $\delta^{15}N$ (‰) for adult Steelhead that exhibit prominent life history strategies from Portage Creek.

Life History	$\delta^{13}C$	Number of years as parr	$\delta^{15}N$	Age at maturation (years)
LH1.1	-22.8	1	8.1	2
LH1.2	-22.1	1	8.3	3
LH1.3	-22.6	1	8.7	4
LH2.1	-22.8	2	8.0	3
LH2.2	-23.0	2	8.4	4
LH2.3	-23.6	2	8.6	5

Table 2.8. The average $\delta^{13}C$ and $\delta^{15}N$ (‰) for Steelhead parr that exhibit prominent life history strategies from Portage Creek.

Life history	Number of years in stream	$\delta^{13}C$	$\delta^{15}N$
LH1.1	1	-28.7	9.2
LH1.2	1	-29.2	9.5
LH1.3	1	-29.9	9.7
LH2.1	2	-30.2	10.0
LH2.2	2	-30.3	10.0
LH2.3	2	-30.5	10.0

GENERAL CONCLUSION

The main objective of this study was to use life history theory and trophic ecology to determine the causes and consequences of population changes in Black Bay Steelhead. This was performed by assessing the interactions, such as competition and predation, that Steelhead have with other fish species throughout their different life stages. Initial results provided by life history theory indicated that the likely reason for the adult Steelhead population decline and subsequent shift in life history strategies was associated with reduced juvenile survival of age-1 smolts in Black Bay. The sum of evidence presented here is consistent with the hypothesis that reduced survival of age-1 smolts resulted from size-selective mortality caused by predation or possibly in-stream competition.

Temporal analysis of parr isotopic signatures from Portage Creek supported the notion that competition was occurring during the parr life stage; as indicated by the enrichment in parr $\delta^{13}C$ over time which is associated with a change in resource use. Brook Trout capture rates have also increased substantially in Portage Creek in recent years and have likely been a contributing factor in supressing the adult Steelhead population since it declined by limiting the number of age-2 smolts that the stream can support. These results were suggestive of potential competition between Steelhead parr and Brook Trout as most of the prominent life history strategies for parr displayed increasing $\delta^{13}C$ over time, which was likely a result of changes in parr diets because of competition with Brook Trout.

Further evidence of competition along with potential predation was found for Steelhead migrating into Black Bay. Niche width analysis of Steelhead smolts showed that there was evidence of niche overlap between smolts and Walleye as well as some

potential predation of age-1 smolts by mature Walleye, during the period of high smolt abundance. Results also indicated that there was some niche overlap between adult Steelhead and both immature and mature Walleye in Black Bay, which is suggestive of competition.

Life history theory suggested that increased mortality in age-1 smolts, possibly caused by either predation in Black Bay, or competition in-stream could be contributing factors in the observed Black Bay and Portage Creek Steelhead population declines. However, my stable isotope results were unable to provide concrete evidence showing that predation of juvenile Steelhead by Walleye has occurred in Black Bay. Some results did indicate that mature Walleye were operating at a slightly elevated δ^{15}N relative to age-1 smolts along with similar δ^{13}C; however, the mean difference in δ^{15}N between groups was only 0.9‰. Although the isotope analysis does hint at the possibility of Walleye eating smolts, there are a few reasons why the results might not have been able to fully detect direct predation of smolts. To determine that Walleye were eating smolts, those Walleye that consumed the smolts would have to have eaten them during a short timeframe in the summer months due to tissue turnover rates, and those Walleye would have to have been captured during the FWIN program that fall. Walleye that consumed smolts during the necessary timeframe also would have needed to be included in the OMNRF's stable isotope analysis. Even during periods of relatively greater Steelhead abundance, Walleye may not have been focusing on smolts as one of their primary resources. Therefore, the chances of capturing enough Walleye to clearly show that they operate at a higher trophic level compared to smolts because of smolt consumption was likely very small. Another possible explanation for why I was unable to explicitly show

that smolts were being eaten is because I only examined one potential predator. Northern Pike, Smallmouth Bass and double-crested cormorant (*Phalacrocorax auritus*) numbers have all increased over the past few decades (Weseloh *et al.* 1994, Berglund 2016) and all pose a risk as possible predators of juvenile Steelhead. Even though I was unable to provide enough evidence to show that Walleye are predating upon smolts in this study, it is very likely that smolts were being predated upon by some composition of predators in Black Bay.

Based on this research, Steelhead found in Black Bay tributaries all historically demonstrated similar life history strategies of smolting at age-1; this life history strategy of age-1 smolting is an outlier when compared to most Steelhead populations found around the Lake Superior basin. Although Black Bay Steelhead are currently demonstrating life history strategies that are commonly found among Lake Superior Steelhead (predominantly age-2 smolting characteristics), their population sizes remain relatively small compared to when they were demonstrating less common life history strategies of age-1 smolting.

Although age-2 smolting seems to be the most successful smolting strategy in Black Bay in recent years, it is unlikely that the adult populations will ever completely recover as a result of smolting at age-2. Given the limited resources found in the sterile Lake Superior stream environment along with the added resource use by the twice as large age-2 parr (relative to age-1 parr), the juvenile Steelhead carrying capacity of the stream has likely been reduced. Moreover, the increase in Brook Trout abundance and resulting interspecific competition with the age-2 parr Steelhead will likely further reduce the maximum potential number of parr Steelhead that can be supported by Portage Creek.

As such, the adult Steelhead population is unlikely to see any major increases in size given these current sets of ecological conditions that are likely supressing the population size by limiting the number of parr that can be supported in the stream environment.

A potential management strategy that would help to protect the dwindling Black Bay Steelhead populations is to make Steelhead a catch-and-release fishery in Black Bay, and all its tributaries. By removing any potential harvest that may be taking place either in the bay or in the tributaries (not just Portage Creek as it is already a closed fishery), managers would be able to ensure that the maximum number of adult Steelhead have the potential to spawn, thereby maximizing the potential for Steelhead recruitment. A second management strategy would be to open the Walleye fishery in Black Bay. Opening the Walleye fishery would result in reduced numbers of Walleye which could alleviate some of the possible competition and potential predation that is occurring with Steelhead in the bay. An experimental strategy to determine which set of interactions had the greatest impact on the Black Bay Steelhead population decline and subsequent shift in life history strategies could be to reduce Brook Trout abundance in Portage Creek without deliberately reducing Walleye abundance. Reducing Brook Trout numbers in Portage Creek could reduce potential interspecific competition with Steelhead parr. If adult Steelhead populations in Portage Creek do not increase after the potential competitive interaction between parr Steelhead and Brook Trout is removed, then the evidence would suggest that the interactions in the lake environment (predation of smolts by Walleye and competition between smolts and adult Steelhead with Walleye) were having a greater impact on the low Steelhead abundances than the interactions (competition with Brook Trout) in the stream. However, if adult Steelhead do increase in population size following

the removal of Brook Trout from Portage Creek, then the competitive interactions between the Steelhead parr and Brook Trout in the stream environment were likely the main causes of the observed Steelhead population decline in Black Bay.

In conclusion, the results of this research have provided evidence that competition in the lake and stream environments and possibly predation in the lake environment have had a negative impact on the Steelhead populations in Black Bay, Lake Superior over the past decade. This study adds to a growing body of information (Kitchell *et al.* 2000, Bronte *et al.* 2003, Schmidt *et al.* 2009) that describes how changes in a fish community can have profound impacts on species interactions. A continued focus on the monitoring of Lake Superior's fish communities will provide information that will be essential for the conservation and management of aquatic species as the Lake Superior environment continues to change.

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APPENDIX

Figure A1. Map of all stream sites examined along the North Shore of Lake Superior. Black circles represent streams that flow into Thunder Bay, black squares represent streams that flow in to Black Bay, and black triangles represent streams that flow into Nipigon Bay.

Table A1. Count of the six most prominent life history categories for 2018 Whitefish River Steelhead.

Site	Year	Sex	LH1.1	LH1.2	LH1.3	LH2.1	LH2.2	LH2.3
Whitefish	2018	M	0	0	0	23	13	1
		F	0	1	0	12	30	13
		Total	0	1	0	35	43	14

Table A2. Count of the six most prominent life history categories for 2018 Neebing River Steelhead.

Site	Year	Sex	LH1.1	LH1.2	LH1.3	LH2.1	LH2.2	LH2.3
Neebing	2018	M	1	12	1	32	12	4
		F	0	4	4	2	41	8
		Total	1	16	5	34	53	12

Table A3. Count of the six most prominent life history categories for 2018 McIntyre River Steelhead.

Site	Year	Sex	LH1.1	LH1.2	LH1.3	LH2.1	LH2.2	LH2.3
McIntyre	2018	M	2	26	6	65	23	9
		F	0	6	4	3	25	27
		Total	2	32	10	68	48	36

Table A4. Count of the six most prominent life history categories for 2018 McVicar Creek Steelhead.

Site	Year	Sex	LH1.1	LH1.2	LH1.3	LH2.1	LH2.2	LH2.3
McVicar	2018	M	4	26	2	34	14	5
		F	3	19	6	9	33	25
		Total	7	45	8	43	47	30

Table A5. Count of the six most prominent life history categories for 2018 MacKenzie River Steelhead.

Site	Year	Sex	LH1.1	LH1.2	LH1.3	LH2.1	LH2.2	LH2.3
MacKenzie	2018	M	5	20	3	9	7	1
		F	0	10	6	1	7	8
		Total	5	30	9	10	14	9

Table A6. Count of the six most prominent life history categories for 2018 Portage Creek Steelhead.

Site	Year	Sex	LH1.1	LH1.2	LH1.3	LH2.1	LH2.2	LH2.3
Portage	2018	M	0	4	0	6	9	2
		F	0	1	2	0	4	5
		Total	0	5	2	6	13	7

Table A7. Count of the six most prominent life history categories for 2018 Jackpine River Steelhead.

Site	Year	Sex	LH1.1	LH1.2	LH1.3	LH2.1	LH2.2	LH2.3
Jackpine	2018	M	3	12	6	5	4	3
		F	0	6	10	0	8	12
		Total	3	18	16	5	12	15

Table A8. Count of the six most prominent life history categories for 2018 Cypress River Steelhead.

Site	Year	Sex	LH1.1	LH1.2	LH1.3	LH2.1	LH2.2	LH2.3
Cypress	2018	M	0	5	4	2	4	4
		F	0	1	5	3	5	11
		Total	0	6	9	5	9	15

Table A9. Count of the six most prominent life history categories for 1993 Portage Creek Steelhead.

Site	Year	Sex	LH1.1	LH1.2	LH1.3	LH2.1	LH2.2	LH2.3
Portage	1993	M	4	40	7	6	6	0
		F	1	24	17	3	12	0
		Total	5	44	23	9	18	0

Table A10. Count of the six most prominent life history categories for 2007 Portage Creek Steelhead.

Site	Year	Sex	LH1.1	LH1.2	LH1.3	LH2.1	LH2.2	LH2.3
Portage	2007	M	64	320	23	56	15	2
		F	2	309	88	8	34	4
		Total	66	629	111	64	49	6

Table A11. Catch summary for potential prey fishes species from Fall Walleye Index Netting, Black Bay, Lake Superior, 2002 and 2010.

Species	2002	2008
Spottail Shiner	1282	648
Longnose sucker	771	134
Lake Chub	512	34
Round Whitefish	188	81
Yellow Perch	240	810
Lake Herring	25	61

Table A12. Proportion (%) of each life history category for both male and female Steelhead from Portage Creek (1991-2018).

	Portage Creek	
LH	Male (%)	Female (%)
1.1	9.9	0.2
1.2	31.2	28.5
1.3	3.4	11.8
2.1	4.7	1.1
2.2	2.8	4.9
2.3	0.3	1.2

Table A13. δ^{13}C (‰) and δ^{15}N (‰) for benthic invertebrates collected from Portage Creek in 2018. Benthic invertebrates were classified to order.

Order	δ^{13}C (‰)	δ^{15}N (‰)
Odonata	-31.0	9.2
Odonata	-34.9	8.0
Odonata	-30.6	6.7
Amphipoda	-28.0	6.2
Amphipoda	-32.2	4.8
Trichoptera	-33.9	6.4
Trichoptera	-36.6	6.1
Isopoda	-25.0	6.5
Isopoda	-32.9	5.6
Diptera	-35.5	4.3
Decapoda	-30.3	8.4
Subclass		
Hirudinea	-37.1	7.6

Table A14. Frequency (%) of each prominent life history category for both sexes across all study sites.

Site	Sex	Prominent life history category					
		LH1.1	LH1.2	LH1.3	LH2.1	LH2.2	LH2.3
Portage 1993	M	0.06	0.63	0.11	0.10	0.10	0.00
	F	0.02	0.42	0.30	0.05	0.21	0.00
Portage 2007	M	0.13	0.67	0.05	0.12	0.03	0.00
	F	0.00	0.69	0.20	0.02	0.08	0.01
Portage 2018	M	0.00	0.19	0.00	0.29	0.43	0.10
	F	0.00	0.08	0.17	0.00	0.33	0.42
Whitefish	M	0.00	0.00	0.00	0.62	0.35	0.03
	F	0.00	0.02	0.00	0.21	0.54	0.23
Neebing	M	0.02	0.19	0.02	0.52	0.19	0.06
	F	0.00	0.07	0.07	0.03	0.69	0.14
McIntyre	M	0.02	0.20	0.05	0.50	0.18	0.07
	F	0.00	0.09	0.06	0.05	0.38	0.42
McVicar	M	0.05	0.31	0.02	0.40	0.16	0.06
	F	0.03	0.20	0.06	0.09	0.35	0.26
MacKenzie	M	0.11	0.44	0.07	0.20	0.16	0.02
	F	0.00	0.31	0.19	0.03	0.22	0.25
Jackpine	M	0.09	0.36	0.18	0.15	0.12	0.09
	F	0.00	0.17	0.28	0.00	0.22	0.33
Cypress	M	0.00	0.26	0.21	0.11	0.21	0.21
	F	0.00	0.04	0.20	0.12	0.20	0.44