DIVERISTY OF LIFE HISTORY CHARACTERISTICS OF LAKE SUPERIOR MIGRATORY RAINBOW TROUT

By

Kyle Stratton



FACULTY OF NATURAL RESOURCES MANAGEMENT LAKEHEAD UNIVERSITY THUNDER BAY, ONTARIO

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Kyle Stratton

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Major Advisor Dr. Mike Rennie

Second Reader Dr. Steve Hart

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ABSTRACT

Key Words: age at maturity, Cypress River, frequency, Lake Superior, localized adaptations, life history characteristics, McVicar creek, Portage creek, Rainbow Trout, relative abundance, smolt.

Rainbow Trout (Oncorhynchus mykiss) have been present in the Great Lakes since their introduction in the late 1800's (Clarkson et al. 1997). These fish have naturalized many streams and have established naturally reproducing populations in many of the Great Lakes tributaries. Localized adaptations have allowed for each population to thrive, given the natural conditions with which they are presented. When faced with ecological change, a population may alter life history strategies to better adapt to new conditions. We compared local adaptations in three of Lake Superior's North Shore streams, and evaluated how life history strategies have changed in a population that has experienced significant ecological changes to better understand why certain life histories strategies are selected for given a particular set of ecological conditions. Rainbow trout were angled during their annual spawning migration (April-June) on McVicar Creek (Thunder Bay), Portage Creek (Black Bay), and the Cypress River (Nipigon River) over multiple spawning seasons. Scales were taken and, length, and sex recorded from the captured Rainbow Trout. Growth annuli from the scales were analyzed to determine the number of years spent in the stream, number of years spent in the lake prior to first spawning, age at maturity, total age, and number of spawning events. Individual Rainbow Trout were then categorized based on similar life history traits (number of years spent in the stream and number of years spent in the lake prior to first spawning). Portage Creek life histories shifted with the closure of the fishery in 1994 from an older smolting life history with later maturity to a younger smolting age with faster maturity; they then reverted to the older smolting age with slower maturity since following a massive population decline in 2007 McVicar Creek and the Cypress River life histories have stayed fairly consistent while their populations have also remained stable. The Portage Creek population collapse, and subsequent shift in life histories, is likely a result of a change in the Black Bay fish community which has led to the predation of young Rainbow Trout smolts and a reduction in the food availability in the Lake Superior once the smolts migrate to the lake.

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INTRODUCTION

Rainbow Trout (*Oncorhynchus mykiss*) express a diversity of life history characteristics throughout their range and among individuals within a given population (Gharrett *et al.* 1993). This diversity is crucial as the life histories impact key ecological interactions such as predator prey relationships, growth, reproductive potential and mortality. Natural selection dictates that life histories that are more successful in particular environment will be selected for in order to best maximize an individual's chances of reproduction (De Roos *et al.* 2003). Variations in life histories may also provide adaptive capacity to withstand ecosystem changes (Kruger *et al.* 1993).

The current Rainbow Trout populations along the north shore of Lake Superior are stable, with the exception of the Black Bay tributaries (the Wolf River, Black Sturgeon River, Coldwater Creek, and Portage Creek). The number of years of each data set varies from stream to stream, yet there are a few streams that have been sampled repeatedly over the years which have the potential to show trends in life history within that particular stream. These streams are referred to as index streams as they likely give a representation of what is happening throughout the entire bay in which they are located.

Since 1994, Portage Creek has been posted as private property. The only access granted is for the purpose of collecting biological data for the purpose of the Portage Creek study. When the Portage Creek study started in 1991, the population was approximately 600 Rainbow Trout (a number that was deemed to be low as a result of over-exploitation from the previous years). After access was blocked to the general public there was effectively zero harvest from angling in the stream. As a result, the

population increased to over 2000 individuals by 2004. However, in 2007 the population began to decline, and as of 2015, the most recent population estimate for Portage Creek is 275 Rainbow Trout. The primary cause of the population decline remains unknown, but has been speculated to be associated with the recovery of a Walleye population in Black Bay (Berglund 2016). Although the other two index streams chosen for this study do not have data sets as long as Portage Creek, both their respective populations have remained fairly constant since 2012. McVicar Creek's population has been between 1181-1518, whereas the Cypress River's population has continually hovered around 2000. As we are only sampling mature Rainbow Trout during their yearly spawning migration, all population estimates are for adult fish only.

The objective of this study is to evaluate how changes in population size in Portage Creek may have affected life history strategies, and compare their life histories to two other relatively stable populations, McVicar Creek and the Cypress River. I hypothesize that there are differences in life history strategies between the streams as there are significant genetic differences between Thunder Bay streams, Black Bay streams, and Nipigon Bay streams indicating that since their establishment in Lake Superior, Rainbow Trout have been continually adapting (Addison 2007). I also hypothesize that there will be changes in the Portage Creek life histories since the population collapse of 2007 in response to changes in the Black Bay ecosystem (Berglund 2016). Lastly, I hypothesize that once the Portage Creek fishery was closed, the age at maturity should become delayed.

LITERATURE REVIEW

Life history of anadromous fish: relative importance of age at maturity, smolting age

Rainbow Trout exhibit a vast array of life histories, which increases their likelihood of persistence by spreading risk of extirpation among different pathways. For example, the Klamath River basin (California to Oregon) provides a particularly interesting environment for the study of life history diversity in Rainbow Trout because the river is scheduled for a historic and potentially influential dam removal and habitat recolonization project which is theorized to help increase the diversity of life history strategies used in the Klamath River. By increasing the diversity of life history strategies, the authors also theorized that the total population of the Klamath River Rainbow Trout should increase (Hodge *et al.* 2016). Hodge *et al.* used scale and otolith strontium isotope analyses to characterize life history diversity in wild Rainbow Trout from the lower Klamath River. They also determined maternal origin (anadromous or non-anadromous) and migratory history (anadromous or non-anadromous) of Rainbow Trout and compared the length and fecundity at age between anadromous (steelhead) and non-anadromous (Rainbow Trout) phenotypes. In total, they identified 38 life history categories at maturity, which differed in duration of freshwater and ocean rearing, age at maturation, and occurrence of repeat spawning. While this diversity in life history strategies among Klamath River Rainbow Trout should increase population resilience, a decline in the population of Klamath River Rainbow Trout suggest that life history diversity alone is not sufficient to stabilize a population. The decline of the Klamath River Rainbow Trout is attributed to the loss of historical spawning habitat as the result of four unpassable dams blocking their upstream migration. Their findings that both steelhead and Rainbow Trout give rise to progeny of the alternate form (anadromous or

non-anadromous from either migrating or non-migrating parents) suggests that dam removal might lead to a facultatively anadromous Rainbow Trout population in the upper basin. The reason why dam removal may lead to more anadromous behavior being displayed by Klamath River Rainbow Trout is because anadromy decreases as migrating difficulty increases. Therefore, the removal of the Klamath River dam would reduce the migration difficulty leading to more anadromous behaviour which is a phenotypic response. This is a phenotypic response because the anadromous fish are larger and have a much higher fecundity than the non-anadromous fish which presents a better evolutionary advantage; however, this can only happen if the fish are given the opportunity to be able to migrate. This raises the question of whether both forms of Rainbow Trout in the Klamath River should be managed under the same strategy (Hodge *et al.* 2016). This is relevant to the current study as we also examined scale samples to determine various life history characteristics of Rainbow Trout such as the number of years spent in the stream, number of years spent in the lake prior to the first spawn, and subsequent number of repeat spawning events. Their results are also relevant to this study as the Klamath River Rainbow Trout are exhibiting an overall decline in population even though they have a wide variety of life history traits. This may be similar to what we are seeing on Portage Creek, which could suggest that even though a population of Rainbow Trout adults show a wide array of life history diversity, it may not be sufficient enough to prevent the population from declining.

Juvenile Rainbow Trout will almost always spend between one and three years in their natal stream before smolting and heading out into Lake Superior (Boston 1998, Morrison 2004, Addison 2007). Often times, a particular stream will have a preferred age for smolting, although this may also be influenced by sex (Morrison 2004). Morrison (2004) performed a study examining the smolting age of Rainbow Trout in Portage Creek and compared it with other Black Bay tributaries (the Wolf River and Coldwater Creek), and a Nipigon Bay tributary (the Jackpine River). He noted that Portage Creek had a younger smolting age than the other tributaries (>80% of the population smolted at 1 year old: Morrison 2004). It was hypothesized that the lower age of smolting was a localized adaptive response leading to genetic differentiation within Black Bay and Nipigon Bay tributaries (Morrison 2004). However, only Coldwater Creek demonstrated significant genetic variation relative to the other populations. Although these results indicate that there is no genetic variability among Rainbow Trout of different streams, their results may not be indicative of what is actually being expressed amongst the fish as the sample sizes for their genetic tests results were small resulting in low statistical power.

Rainbow trout populations of the Great Lakes show a great variability in timing of spawning migrations and life histories forming discrete stocks (Boston 1998). This variability has been examined to determine if Rainbow Trout populations of the Great Lakes are comprised of discrete stocks. A stock is defined as a "fish spawning in a particular lake or stream (or portion of it) at a particular season, which fish to a substantial degree do not interbreed with any group at a different season" (Biette *et al.* 1981). Biette *et al.* (1981) found that differences in timing of migration, and spawning indicated that at least one spawning population may be distinctive and that others may be in progressive stages towards emergence of discrete stocks. The innate ability of Rainbow Trout to adapt to different environmental conditions, together with its ability to

return to its birth stream, provide Rainbow Trout in the Great Lakes with the ability to develop such discrete stocks.

On average, male Rainbow Trout spawn for the first time at a younger age than females, as the females generally spent an extra year in their natal streams or an extra year in the lake before reaching sexual maturity (George 1994, Morrison 2004). Hartman (1958) conducted a study on Rainbow Trout in Cayuga, Seneca, Skaneateles and Canandaigua Lakes, and their major spawning tributaries, which are maintained primarily by natural reproduction. In these lakes large numbers of fry hatched each year in each of the tributaries, serving as nursery areas holding many parr for up to 3 years. They found that the quality and abundance of food sources within their natal stream had an influence on the smolting age with females generally spending one more year in the stream than the males.

Application to fisheries management

Older individuals of fish species often produce the most offspring along with the offspring most likely to survive to be able to reproduce (Birkeland *et al.* 2005). This is often an issue forming regulations around commercial and recreation fishery as it the larger and older fish that are usually targeted, yet those are the fish that are necessary for the sustainability of that species. Public perception is often of the belief that by selectively harvesting the largest fish that they are causing less harm than if they were to take multiple smaller fish (Boston 1998). This impression is based upon the idea that by eliminating the dominance of the resources by larger, older fish they are allowing for the other smaller fish to get a chance to grow (Boston 1998, Birkeland *et al.* 2005). The management of the Rainbow Trout fishery along the North Shore of Lake Superior was

a topic of much debate back in the 1990's when over-exploitation had severely reduced the populations in many popular streams (George 1994, Boston 1998). In 1999, two Thunder Bay tributaries (the Neebing and MacIntyre Rivers) had a new harvest limit applied where only one 69cm total length rainbow trout could be harvested. This was a drastic change from the previous harvest limit of five fish of any size. Once those two populations had rebounded (indicating the success of the management strategy), the other streams in Fishery Management Zone (FMZ) 6 adopted the one Rainbow Trout harvest limit, however, without the 69cm minimum size. This is important as there is no minimum size restriction of either McVicar Creek, or the Cypress River (both populations included in this study) leaving the Rainbow Trout in those streams vulnerable to harvest.

METHODS AND MATERIALS

Data collection and site selection

Data collection, in part, has been occurring since 1991 when the North Shore Steelhead Association (NSSA) began working in partnership with the Ontario Ministry of Natural Resources and Forestry (OMNRF) to monitor the status and health of Rainbow Trout populations along the north shore of Lake Superior in a community-based project called the co-operative angler project (George 1994, Boston 1998). In this project, anglers are shown how to biologically sample Rainbow Trout (distinguish between sexes, how to remove scales, and proper measurement techniques). As the cooperative angler program depends on volunteer participation, the number of samples collected in during the sampling period (spawning run, April-June) regularly fluctuates. However, a few dedicated anglers have persisted with various streams for several years, allowing for population estimates which can show trends in population growth or decrease. For the purpose of this study, one index stream was selected from each bay. The index stream for Thunder Bay was McVicar Creek, for Black Bay it was Portage Creek, and for Nipigon Bay it was the Cypress River. Although the Portage Creek Rainbow Trout sampling began in 1991, data that was used for the purpose of this study began in 1992 as critical life history information was missing from the 1991 samples.

Rainbow Trout ages were determined by placing the scales on an acetate slide where they we examined with a microfiche reader. Growth annuli from the scales were utilized to determine life history traits such as: number of years spent in the stream, number of years spent in the lake prior to first spawning, lake years at first spawn, age at maturity (first spawn), and number of spawning events and total age. Since the inception of the co-operative angler project, all the aging across all the streams has been done by the same reader. Ages are validated through recaptures of tagged Rainbow Trout in subsequent years from the McIntyre River and Portage Creek.

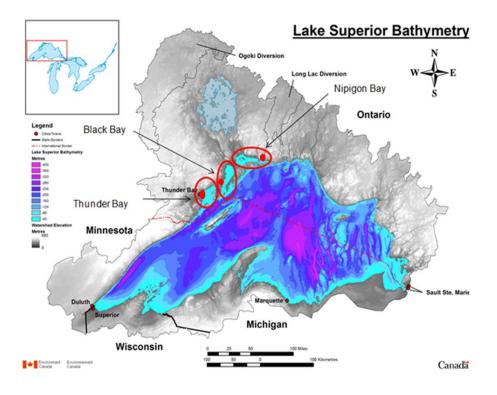


Figure 1. The location of the three study streams: McVicar Creek (Thunder Bay), Portage Creek (Black Bay), and the Cypress River (Nipigon Bay).

Data Analyses

Once all scales were analyzed, the information was recorded in a spreadsheet. This spreadsheet was provided by the North Shore Steelhead Association (NSSA) and contained the date that was extracted from analyzing the growth annuli of the scales: the fork length and sex of the fish at capture, number of previous spawning events, number of years spent in the lake at first spawn, number of years spent in the stream before smolting, total number of years spent in the lake, age at maturity, total age, clip applied and clip(s) on capture (if applicable). Males and females were sorted them into various life history categories. Categories were defined by the number of years spent in the stream before smolting, then by number of years spent in the lake prior to the first spawning event (Table 1). This process was repeated for each study site across all available years.

Multivariate Analyses

All analyses were conducted using R (R core team 2016). Distance measures were calculated for each sex in each year sampled across sites (Portage 1991-2016, McVicar and Cypress 2012-2016). Initially, I evaluated three distance measures: Bray-Curtis dissimilarity, chord distance, and chi-square distance. The Bray-Curtis dissimilarity measure is a common method of quantifying the differences between communities. However, it does not satisfy the triangle inequality axiom which means that it is not a true distance of measure between points (Goslee et al. 2007). The chord distance treats both abundant and rare variables (life histories) equally. Chi-square was the final distance measure we tested. Unlike the Bray-Curtis measure, chi-square produces a true distance metric. And unlike the chord distance, chi-square is influenced by the appearances of rare variables (Legendre et al. 2001, Goslee et al. 2007). To counteract the problem of rare life histories, we eliminated all life histories that appeared <1% of the time for all streams combined. Based upon our initial multivariate analysis of distance measure for life histories per stream, we decided to continue our analyses using the chord distance principle coordinate analysis (PCoA) values that we generated. Chord distance provides a meaningful interpretation of comparisons based on relative abundance and provided the best segregation of sites compared to the Bray-Curtis. Chord distance and chi-square were relatively similar in pattern.

RESULTS

Fifteen different life histories were identified and occurred at least one time for either male or female Rainbow Trout at McVicar Creek, Portage Creek, or the Cypress River (Table 1). Of the 15 total life histories, seven of them occurred >1% (Table 2) and were included in the multivariate ordinations.

The PCoA using chord distance explained 55% of the variation axis and 26% on the second axis. Males and females displayed different life histories and separated across all streams/years on axis 2, but within each stream along axis 1 (Figure 2). For males, McVicar Creek is more strongly correlated with life histories 7 and 11, while the Cypress River and Portage Creek are associated with life histories 1, 2, and 6 (separate along axis 2). For females, the three streams seem to separate into distinct groupings on axis 2. Portage Creek females are associated with LH2 and 3 on axis 1, while McVicar Creek and the Cypress River are associated with LH7 and 8.

I examined each life history individually to help understand significant variation observed in life history relative abundance in Portage Creek reflected in the multivariate analysis. The population in Portage Creek increased following the closure of the fishery after 1994, and declined after 2007 (Figure A1). Prior to 2007, Portage Creek females exhibited LH7 (2 stream years, 2 lake years) approximately 10% of the female population (Figure 3). However, four years after the 2007 population collapse, when the LH7 females return to Portage Creek to spawn for the first time, the females displaying LH7 showed an increase in relative abundance; by 2016 LH7 females made up over 30% of the female population (Figure 3). The relative abundance of Portage Creek LH7 females in their first spawning run (spring 2012) since the collapse is now more similar to the relative abundance of LH7 females in both McVicar Creek and Cypress River (Figure 3). A similar recent increase in female life history frequency can be seen in LH8 (2 stream years, 3 lake years) for females (Figure A10). We also see an increase in male LH7 (2 stream years, 2 lake years) relative abundance since the population collapse (Figure 4). Between 1992-2007, LH7 males made up between 2.2% - 9.5% of the overall male population. However, by 2015, LH7 males made up 20.8% of the total male population which is more similar to the relative abundances we see in McVicar Creek and the Cypress River for LH7 males. We see the opposite trend happening with LH2 females (1 stream year, 2 lake years) in Portage Creek (Figure 5). In 2007, LH2 females comprised 69.4% of the Portage Creek females. Three years later, after their first spawning event since the collapse LH2 females made up 55.4% of the Portage Creek females, and by 2015 they only made up 13.8% (Figure 5). Once again, the post population collapse relative abundance of LH2 females in Portage now more closely resembles the relative abundances of LH2 females for McVicar Creek and the Cypress River. The Portage Creek LH2 males show a similar trend to that of the LH2 females (Figure 6). In 2007, the Portage Creek LH2 males made up 66.5% of the male population. By 2010 their relative abundance had dropped to 58.4%. As of the last year sampled, their relative abundance was 42.9%. LH2 male relative abundance in Portage Creek since the population collapse is trending towards the LH2 male relative abundance for both McVicar Creek and the Cypress River (Figure 6).

The closure of the Portage Creek fishery (1994) also had an impact on life histories. The reduced adult mortality associated with the closure of the fishery lead to

a shift towards LH1 males and a shift away from LH7 females (Tables A7 and A8). These shifts indicate that once adult mortality was reduced younger maturity became more prevalent. The abundance of males with LH1 and females with LH7, as well as a few of the other life histories, are currently shifting towards the frequencies they were exhibiting when the population was being over exploited despite the fact that adult mortality is no longer the primary factor selecting for these traits.

Life histories that occurred >1% but did not demonstrate a shift through time are located in the Appendix. Many of the rare life histories seen in Portage Creek have not been occurring as much as they did prior to the population decline (Tables 1A and 2A). Although there does not appear to be a pattern shown by those rare life histories before 2007; many of them either occur even less frequently than before, or cease to occur all together (such as LH12 in males and LH9 in females). This reinforces the theory that a healthy population supports a more diverse abundance of life histories.

		l
Life	Number of years	Number of lake years
History	spent in the stream	at first spawn
1	1	1
2	1	2
3	1	3
4	1	4
5	1	5
6	2	1
7	2	2
8	2	3
9	2	4
10	3	0
11	3	1
12	3	2
13	3	3
14	4	1
15	4	2

Table 1. The 15 different life history categories expressed by both males and female Rainbow Trout in Portage Creek, McVicar Creek, and the Cypress River.

Table 2. Life histories that appeared >1% by both male and female Rainbow Trout in Portage Creek, McVicar Creek, and the Cypress River over all sample periods.

Life	Number of years	Number of lake years
History	spent in the stream	at first spawn
1	1	1
2	1	2
3	1	3
6	2	1
7	2	2
8	2	3
11	3	1

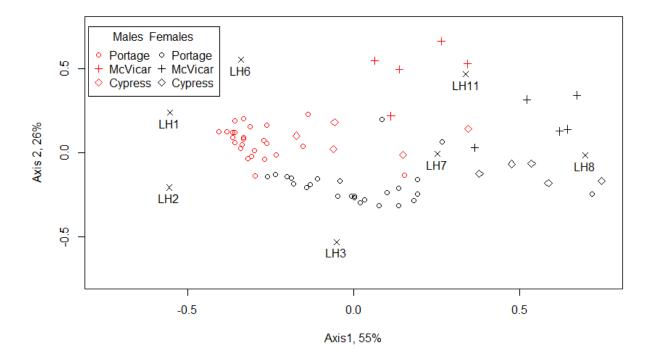


Figure 2. Site scores from Principal coordinates of chord comparing the relative similarities of life histories of male and female Rainbow Trout from Portage Creek, McVicar Creek, and the Cypress River; North Shore, Lake Superior. Each data point represents a single sampling event (year) for each sex at each location.

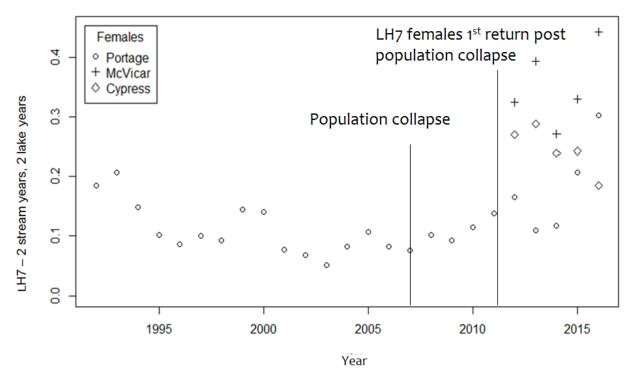


Figure 3. Relative abundances of LH7 females (2 stream years, 2 lake years at first spawn) over all sample periods over all study sites.

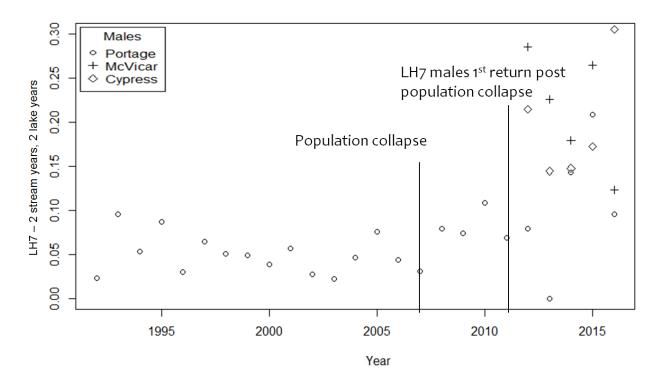


Figure 4. Relative abundances of LH7 males (2 stream years, 2 lake years at first spawn) over all sample periods over all study sites.

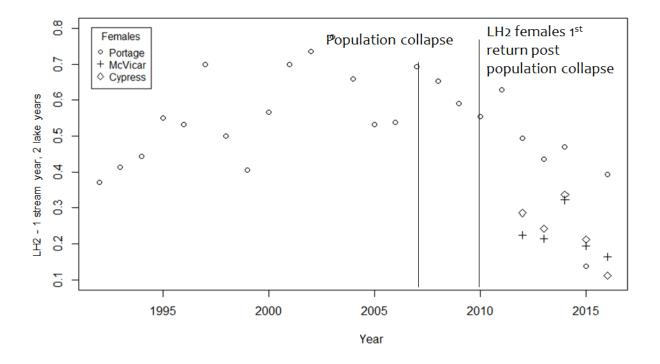


Figure 5. Relative abundances of LH2 females (1 stream year, 2 lake years at first spawn) over all sample periods over all study sites.

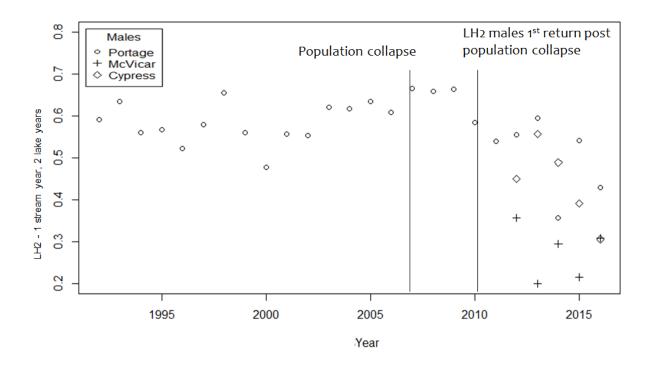


Figure 6. Relative abundances of LH2 males (1 stream year, 2 lake years at first spawn) over all sample periods over all study sites.

DISCUSSION

Since 1991, there have been significant changes in the relative abundances of various life histories for both males and females associated with changes in the ecosystem, which are associated with a population increase and decline in Portage Creek. My analysis indicated a shift away from younger smolting age and fewer years spent in the lake at first spawn towards an older smolting age (greater amount of time spent in the streams before migrating to Lake Superior) as well as an increase in the number of years spent in the lake at first spawn. Prior to 2007, the population in Portage Creek relied heavily upon LH2 (1 stream year, 2 lake years at first spawn) for both sexes with up to 77.6% of females (2003) and 66.5% of males (2007) being comprised of this single life history. After the spawn of 2007, LH2 reduced in frequency, associated with a dramatic decline in population estimates from approximately 1800

adults in 2007 to around 600 adults by 2010 (corresponding to the 1st spawn of LH2 fish that were born in 2007). In a span of only three years, Portage Creek saw a 66% reduction in the number of adults returning to spawn. Interestingly, in 2007, LH2 males made up 66.5% of the male population and LH2 females made up 69.4% of the female population. When the LH2 Rainbow Trout that were born in 2007 smolted one year later, a significant number of them did not return to spawn in 2010 which had an emphatic result on the overall population decline (Figure 1A). Yet, despite this shift, the relative frequency of this life history strategy that we are starting to see for Portage Creek LH2 Rainbow Trout is becoming more similar to the relative frequencies of LH2 for McVicar Creek and the Cypress River Rainbow Trout which are both currently stable self-sustaining populations.

Portage Creek is also shifting towards other certain life histories. For females, LH7 has become more prominent since the population collapse. LH7 is representative of 2 stream years and 2 lake years at first spawn. For males, LH7 has also become more prominent. These shifts in life history indicate that Rainbow Trout that smolt after 2 years and spend multiple years in the lake before returning to spawn for the first time are more likely to return to Portage to spawn than fish that spend 1 year in the stream before smolting and spend 2 years in the lake prior to first spawn.

Hydroelectric developments on the west coast have generated similar delays in smolting times as I have observed here in Portage Creek (McCormick 2009). On the West coast, many large rivers and tributaries are exhibiting trends like those on Portage Creek (population collapse accompanied with a shift towards later smolting ages; Raymond 1988, McCormick *et al.* 2009). In those systems, the reasoning is because of hydroelectric dams impeding migration. Dams interfere with the downstream and upstream migration of anadromous fish while also influencing the water velocity and temperature, and thus have an impact of the life histories of the fish that use those rivers and tributaries. Certain dams have fish ladders which permit fish to migrate both up and downstream. If a fish ladder is not present, fish must be manually carried above the dam and released. Sometimes fish are not permitted to go above the dam and must spawn downriver of it. When fish are able to spawn above a dam, the smolting age is often increased, and the population normally collapses (Raymond 1988, McCormick et al.2009, Marschall et al. 2011). The reasoning behind this is that the larger smolts have a better chance of being able to migrate over the dam versus the smaller (younger) smolts whereas the population collapse is a result of a loss of spawning habitat, and/or significant changes to water flow during critical periods (McCormick et al. 2009, Marschall et al. 2011). Despite the fact that dams provide a similar effect on salmonid stocks as we are seeing on Portage Creek, dams or any other type of migratory obstruction are not the cause of the Portage Creek population collapse and subsequent shifts in life history frequency as there are no definite migratory barriers on Portage Creek.

Climate change has been analyzed to predict the effects of global warming on anadromous salmonids. Although it remains unclear exactly what the implication of warmer weather will have on the fish, it is predicted to have an influence on age and size at maturity and to also decrease the success of reaching maturity (Mangel 1994). As anadromous and potandromous (Great Lakes) Rainbow Trout spend the vast majority of their lives in either the Pacific Ocean or the Great Lakes, the effects of global warming are predicted to have a more severe impact on the fish during their time spent in the streams, either as smolts or spawning adults (Bryant 2009). As climate change and global warming are large scale environmental issues, they are likely to affect systems within a large geographic region fairly similarly (Bryant 2009). This has already been shown to happen along Lake Superior's North Shore. A massive flood event in 1996 removed large quantities of in-stream habitat, widened the river channel and removed tree cover from the Jackpine and Cypress Rivers. This was associated with a significant increase in the proportion of adults with one stream year in subsequent years (Addison 2007). The changes to the rivers may have either allowed for faster growth permitting the fish to leave after only one year, or decreased the amount of habitat required by older smolts. Equal proportions of one to two year old smolts in surrounding streams indicate that the reported changes in life history in the Jackpine and Cypress Rivers are the result of local changes to their given environments (Addison 2007). However, there has not been any similar environmental changing occurrence on Portage Creek since 2007 that would cause a shift like the one seen on the Jackpine and Cypress Rivers. Therefore, it is unlikely that climate change or any outstanding climate events has been the primary ecological change that has been impacting Portage Creek.

An alternative and more likely reason to the changes being seen in Portage Creek could be because of predation. Predation of juvenile fish may lead to changes in population dynamics and alternative life histories becoming more common (He *et al.* 1990, Jepsen *et al.* 1998, Metcalfe *et al.* 1998). Northern Pike (*Esox Lucius*) has 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 a size-selective. Once the smolts reached a certain size, they were either too large for the Northern Pike to eat, or too fast for them to catch (Jepsen *et al.* 1998). It appears as though the cause of the shifts in significant life histories and subsequent population collapse of Portage Creek is due to an increase in predators (such as Northern Pike) present within the Black Bay fish community (Table 3) that are eating the Rainbow Trout once they've smolted and migrated to Lake Superior after one year in the stream. Since 2002, there has been an increase in the range of sizes, average age and abundance for both Northern Pike and Walleye (*Sander vitreus*) in Black Bay (Berglund 2016). Both Northern Pike and Walleye have piscivorous tendencies which have negatively impacted Rainbow Trout populations through predation (McMahon *et al.* 1996).

After spending one year in the stream, juvenile Rainbow Trout from a Lake Superior stream generally range between 50-60mm (Biette *et al.* 1981, Addison 2007), with two year old smolts being much larger than the one year old smolts at first entry to Lake Superior (Kwain 1981). After spending two years in Lake Superior, there is no significant size gaps between Rainbow Trout that spent one or two years in the stream (Kwain 1981), this indicates that the only period when small size is a disadvantage is during the first lake year after smolting. During their first year in Lake Superior, juvenile Rainbow Trout are the most susceptible to predation. It has been demonstrated that the number of 1 year old smolts that leave a stream does not positively influence the number of returning adults with one stream year (Kwain 1981, Addison 2007). Stokley Creek (Lake Superior) had 76% of the rainbow trout leaving the stream after only one year, 23% leaving after two years and 1% leaving after three years. However, only 41% of the returning adults had spent one year in the stream whereas 53% had spent two years and 3% had spent three years (Kwain 1981). Therefore, even though most juveniles smolted after one year, the number of returning adults was dominated by fish that spent two years in the stream. The difference in proportion of returning adult Rainbow Trout is attributed to a higher survival rate of two and three year old smolts in Lake Superior, likely because of their increase in size over the one year old smolts (Kwain 1981).

Table 3. Catch summary of potential Rainbow Trout predators from Fall Walleye Index Netting, Black Bay, 2002-2014 (Berglund 2016).

Species	2002	2008	2010	2012	2013	2014
Yellow Perch	40	1293	810	1562	1272	967
Walleye	13	212	106	193	143	111
Northern Pike	2	17	17	35	44	49
Smallmouth bass	1	24	3	18	6	5

It has been shown that smolting age can be influenced by predators. Older smolts will be larger than younger smolts which may improve escapement from sizeselective predators (Holtby *et al.* 1990, McCormick *et al.* 1998, Jonsson *et al.* 2005). Age at smolting has also been shown to be a heritable trait (Thorpe 1986, Glebe *et al.* 1986), although it may be influenced by environmental factors (Peven *et al.* 1994, Hodge *et al.* 2016). Therefore, when the older smolts are able to evade predation, they are more likely to be able to reproduce, subsequently passing on the older smolting age trait to the next generation (McCormick *et al.* 1998).

When the offspring of the 2007 year class migrated into Lake Superior after only one year in Portage Creek, they were likely subjected to many more predators than would have been present before 2007. Because there were fewer predators in the Black Bay before 2007, the younger smolts could survive out in the bay and return to spawn at a relatively young age. As they could spawn at a young age, the population was able to increase rapidly once access was prohibited in 1994 and over harvesting was no longer a factor. Since the increase in predators densities of Northern Pike and Walleye (Berglund 2016), the young smolting age and ability to spawn at a young age is no longer a viable option as the one year old smolts are likely being eaten once they reach the lake. There has been a severe reduction in the relative abundance of 1 year old smolts for both males and females in Portage Creek, whereas the abundance of 2 year old smolts has been increasing since 2007 (Figure 6, Figure 7). The increase in relative abundance of 2 year old smolts since 2007 is likely due to the fact that they have become more successful than the 1 year old smolts since the population collapse. Therefore, I believe that as the relative abundance of successful 2 year old smolts continues to increase, the population of Portage Creek should follow suit as this life history trait is now being selected as it was prior to the closure of the fishery.

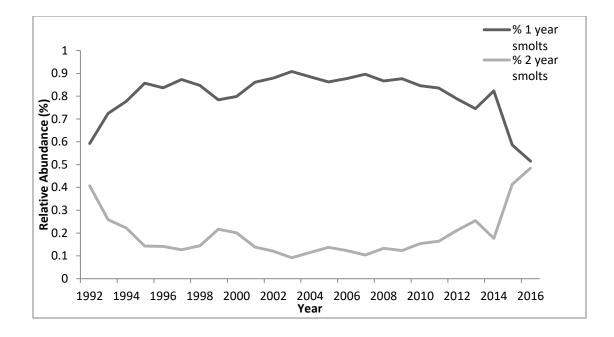


Figure 7. The relative abundances of 1 year old and 2 year old female smolts in Portage Creek from 1992-2016.

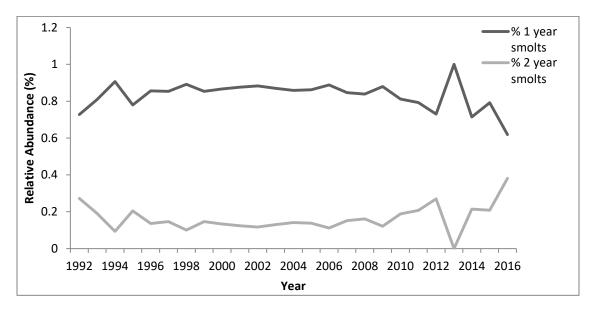


Figure 8. The relative abundances of 1 year old and 2 year old male smolts in Portage Creek from 1992-2016.

Adult mortality trades off with age at maturity (Abrams 1995). One hypothesis is that as post-maturation mortality increases in comparison to juvenile mortality, reproductive effort is increased while age at maturity is decreased (Gadgil *et al.* 1997, Addison

2007). However, this is not consistent with what the results have indicated for Portage Creek. Prior to 1994 when adult mortality was high, we see delayed maturity. Once the fishery was closed, more rapid maturity became common, until the decline of the population in 2007 when maturity once again becomes delayed (Tables A7 and A8). Principle component analysis performed by Addison (2007) shows that lake age at maturity is strongly associated with age and size at maturity more than stream age. This suggests that growth during the lake phase prior to maturity is more important that growth during the stream phase in determining age and size at maturity. Since age at maturity is related to juvenile growth (especially in females), and the most growth occurs in Lake Superior (Kwain 1981), the faster growing Rainbow Trout should spawn at earlier ages (Swank 2005). Male Rainbow Trout tend to have two distinct life histories that relate to age at maturity. The first is to mature quickly and at relatively small size which is commonly referred to as the "jack" strategy, in which males try and use a sneaking behavior to fertilize eggs during spawning events. The other, more common, maturation strategy is to mature later at a larger size which permits them to compete with other males for desired females (Swank 2005). It has been shown that the "jack" strategy can be influenced by anthropogenic changes (such as fishing mortality) and environmental changes (Swank 2005). When there was fishing mortality occurring on Portage Creek, the proportion of "jack" males (LH1) was very low. Once fishing mortality was removed, the frequency of the early maturing males increased significantly. In order for males to mature quickly, they must migrate to Lake Superior after one year in the stream which makes them vulnerable to predation (Kwain 1981, Swank 2005), which could explain why the frequency of early maturing males has

decreased since 2007 even though there is no fishing mortality. The age at maturity for female Rainbow Trout is more strongly associated with growth than it is for males (Swank 2005). This is important as the time period after the closure of the fishery (1994) and before the population decline (2007) is when we see the highest proportions of rapid maturity for both sexes. Based upon those results we can assume that the conditions in Black Bay between 1994-2007 allowed for optimum growth of juvenile Rainbow Trout as indicated by the proportion of fish that reached maturity at a young age.

Given the weight of evidence, predation of juvenile Rainbow Trout in Black Bay appears to be the simplest explanation for shift of an older smolting age in Portage Creek. Previous to the population collapse, the majority of both males and females became mature at age 3 (LH2 – 1 stream year, 2 lakes years) (Figures 5 and 6). Since the collapse, males are shifting towards maturing at age 4 (LH 7 – 2 stream years, 2 lake years: Figure 4), while females are making a similar shift towards maturing at age 4 (LH7 – 2 stream years, 2 lake years: Figure 3). Unlike smolting age, age at maturity is not typically an inheritable trait; rather it is a reflection of the quality and abundance of resources available. A faster juvenile growth rate will tend to decrease the age at maturity (Thorpe 1986, Jonsson *et al.* 2005). As the Rainbow Trout have to migrate up the rivers to spawn, they must attain high energy thresholds just to be able to reach maturity (Metcalfe 1998, Jonsson *et al.* 2005). As the age at maturity for Portage Creek Rainbow Trout has increased, this would suggest that there has been a delay in the ability to reach the energy threshold necessary to attain maturity. Poor feeding

opportunities are typically associated with slow growth which could cause the delay in age at maturity (Metcalfe 1998, Jonsson *et al.* 2005).

CONCLUSION

Since the population collapse of 2007, Portage Creek has seen a shift in life histories away from a young smolting age, and quick maturity to an older smolting age and slower maturity. Predation of 1 year old smolts has likely resulted in the shift towards a higher frequency of 2 year old smolts in the population since 2007 whereas competition is the probable reason for the delayed age at maturity. These changes are most likely the result of a significant change in the Black Bay fish community. Although the Portage Creek population is currently the lowest it has ever been since the inception of the study in 1991 when the population was subjected to over-harvest, we believe that the population will bounce back in the future. As the number of individuals within the newly successful life history categories increases, so too should the overall population. Therefore, it is paramount that the Portage Creek study continues in order to document these theorized changes.

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APPENDIX

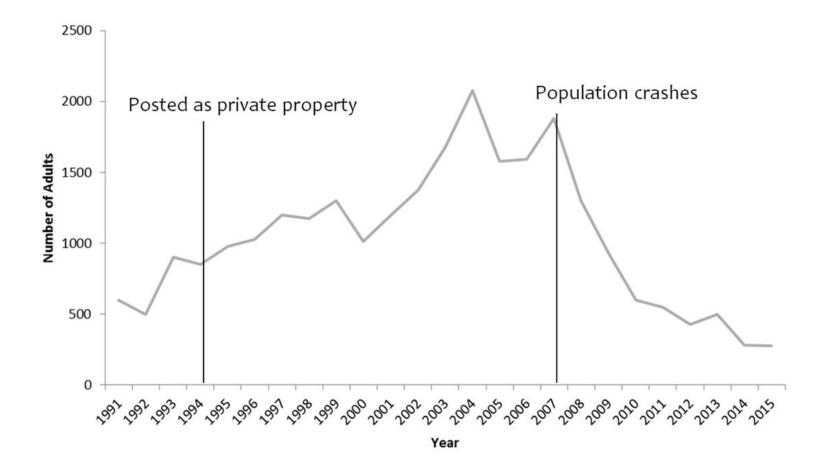


Figure A1. Portage Creek population estimates derived from Lincoln-Peterson estimates, 1991-2015.

Site	Sex	Year	LH1	LH2	LH3	LH4	LH5	LH6	LH7	LH8	LH9	LH10	LH11	LH12	LH13	LH14	LH15	Total
Portage	М	1992	5	26	1	0	0	10	1	1	0	0	0	0	0	0	0	44
Portage	М	1993	4	40	7	0	0	6	6	0	0	0	0	1	0	0	0	64
Portage	М	1994	22	42	4	0	0	3	4	0	0	0	0	0	0	1	0	76
Portage	М	1995	18	72	9	2	0	12	11	3	0	0	2	0	1	0	0	130
Portage	М	1996	32	69	12	0	0	13	4	1	0	0	1	0	0	0	0	132
Portage	М	1997	36	99	11	1	0	14	11	0	0	0	0	0	0	0	0	172
Portage	М	1998	20	91	13	1	0	6	7	1	0	0	1	0	0	0	0	140
Portage	М	1999	40	92	8	1	1	15	8	1	0	0	0	0	0	0	0	166
Portage	М	2000	61	86	9	2	0	16	7	1	0	0	0	0	0	0	0	182
Portage	М	2001	54	108	8	0	0	12	11	1	0	0	0	0	0	0	0	194
Portage	М	2002	93	185	17	0	0	30	9	0	0	0	0	1	0	0	0	335
Portage	М	2003	103	277	8	0	0	48	10	0	0	0	0	0	0	0	0	446
Portage	Μ	2004	73	267	32	1	0	41	20	0	0	0	0	1	0	0	0	435
Portage	Μ	2005	33	184	33	0	0	17	22	1	0	1	0	1	0	0	0	292
Portage	Μ	2006	64	196	26	0	0	20	14	2	0	0	0	0	0	0	0	322
Portage	Μ	2007	64	320	23	0	0	56	15	2	0	0	1	0	0	0	0	481
Portage	Μ	2008	35	209	22	0	0	24	25	2	0	0	0	0	0	0	0	317
Portage	Μ	2009	20	99	12	0	0	6	11	1	1	0	0	0	0	0	0	150
Portage	Μ	2010	15	59	8	0	0	8	11	0	0	0	0	0	0	0	0	101
Portage	Μ	2011	17	47	5	2	0	12	6	0	0	0	0	0	0	0	0	89
Portage	Μ	2012	7	35	4	0	0	12	5	0	0	0	0	0	0	0	0	63
Portage	Μ	2013	8	22	7	0	0	0	0	0	0	0	0	0	0	0	0	37
Portage	Μ	2014	1	5	4	0	0	1	2	0	0	0	1	0	0	0	0	14
Portage	Μ	2015	4	13	2	1	0	0	5	0	0	0	0	0	0	0	0	25
Portage	Μ	2016	3	9	1	1	0	3	2	3	0	0	0	0	1	0	1	24
		Total	832	2652	286	12	1	385	227	20	1	1	6	4	2	1	1	4431

Table A1. Frequency of occurrence of life history characteristics in male Portage Creek Rainbow Trout from 1992-2016.

Site	Sex	Year	LH1	LH2	LH3	LH4	LH5	LH6	LH7	LH8	LH9	LH10	LH11	LH12	LH13	LH14	LH15	Total
Portage	F	1992	2	10	4	2	0	5	5	1	1	0	0	1	0	0	0	31
Portage	F	1993	1	24	17	0	1	3	12	0	0	0	1	0	0	0	0	59
Portage	F	1994	0	12	9	3	0	0	4	2	0	0	0	0	0	0	0	30
Portage	F	1995	0	27	15	4	1	1	5	1	0	0	0	0	0	0	0	54
Portage	F	1996	1	49	27	2	0	2	8	3	0	0	2	1	0	0	0	95
Portage	F	1997	1	105	25	4	0	3	15	1	0	0	0	1	0	0	0	155
Portage	F	1998	0	59	41	3	0	1	11	5	0	0	1	1	1	0	0	123
Portage	F	1999	3	45	39	1	0	5	16	3	0	0	0	0	1	0	0	113
Portage	F	2000	2	93	36	4	0	4	23	6	0	0	0	0	0	0	0	168
Portage	F	2001	1	126	28	1	0	5	14	6	0	0	0	0	0	0	0	181
Portage	F	2002	1	195	37	1	0	10	18	4	0	0	0	0	0	0	0	266
Portage	F	2003	0	229	39	2	0	7	15	5	0	0	0	0	0	0	0	297
Portage	F	2004	1	258	87	2	0	7	32	6	0	0	0	0	0	0	0	393
Portage	F	2005	1	190	117	2	0	6	38	5	0	0	0	0	0	0	0	359
Portage	F	2006	0	162	102	2	0	6	25	6	0	0	0	1	0	0	0	304
Portage	F	2007	2	309	88	4	0	8	34	4	2	0	0	0	0	0	0	451
Portage	F	2008	0	251	82	2	0	8	39	4	0	0	0	0	0	0	0	386
Portage	F	2009	0	134	65	1	0	3	21	4	0	0	0	0	0	0	0	228
Portage	F	2010	0	97	51	0	0	2	20	5	0	0	0	2	0	0	0	177
Portage	F	2011	1	73	23	3	0	3	16	0	0	0	0	0	0	0	0	119
Portage	F	2012	0	42	25	1	0	1	14	3	0	0	0	0	0	0	0	86
Portage	F	2013	0	24	17	0	0	4	6	4	0	0	0	1	0	0	0	56
Portage	F	2014	0	8	6	0	0	0	2	1	0	0	0	0	0	0	0	17
Portage	F	2015	0	4	13	1	0	0	6	6	0	0	0	0	0	0	0	30
Portage	F	2016	0	13	4	2	0	1	10	5	0	0	0	0	1	0	0	36
		Total	17	2539	997	47	2	95	409	90	3	0	4	8	3	0	0	4214

Table A2. Frequency of occurrence of life history characteristics in female Portage Creek Rainbow Trout from 1992-2016.

Site	Sex	Year	LH1	LH2	LH3	LH4	LH5	LH6	LH7	LH8	LH9	LH10	LH11	LH12	LH13	LH14	LH15	Total
McVicar	Μ	2012	6	15	4	1	0	3	12	1	0	0	1	0	0	0	0	43
McVicar	Μ	2013	9	23	7	1	0	43	26	5	0	0	2	0	0	0	0	116
McVicar	Μ	2014	3	23	6	0	0	26	14	3	1	0	3	0	0	0	0	79
McVicar	Μ	2015	5	22	11	1	0	31	27	3	2	0	3	0	1	0	0	106
McVicar	М	2016	2	25	4	0	0	33	10	4	2	0	3	0	0	0	0	83
		Total	25	108	32	3	0	136	89	16	5	0	12	0	1	0	0	427

Table A3. Frequency of occurrence of life history characteristics in male McVicar Creek Rainbow Trout from 2012-2016.

Table A4. Frequency of occurrence of life history characteristics in female McVicar Creek Rainbow Trout from 2012-2016.

Site	Sex	Year	LH1	LH2	LH3	LH4	LH5	LH6	LH7	LH8	LH9	LH10	LH11	LH12	LH13	LH14	LH15	Total
McVicar	F	2012	0	9	5	0	0	6	13	6	0	1	1	0	0	0	0	41
McVicar	F	2013	0	18	15	0	0	2	33	13	0	0	3	0	0	0	0	84
McVicar	F	2014	1	19	11	0	0	3	16	8	0	2	1	0	0	0	0	61
McVicar	F	2015	0	20	21	2	0	8	34	19	3	1	1	0	0	0	0	109
McVicar	F	2016	0	10	6	2	0	5	27	13	2	0	0	0	0	0	0	65
		Total	1	76	58	4	0	24	123	59	5	4	6	0	0	0	0	360

Site	Sex	Year	LH1	LH2	LH3	LH4	LH5	LH6	LH7	LH8	LH9	LH10	LH11	LH12	LH13	LH14	LH15	Total
Cypress	М	2012	22	86	15	0	0	21	41	3	0	0	3	0	0	0	0	191
Cypress	М	2013	7	54	7	0	0	12	14	3	0	0	0	1	0	0	0	98
Cypress	М	2014	6	43	13	0	0	9	13	4	0	0	0	1	0	0	0	89
Cypress	М	2015	3	34	20	0	0	11	15	4	2	0	0	0	0	0	0	89
Cypress	М	2016	2	11	5	0	0	2	11	4	0	0	1	0	1	0	0	37
		Total	40	228	60	0	0	55	94	18	2	0	4	2	1	0	0	504

Table A5. Frequency of occurrence of life history characteristics in the male Cypress River Rainbow Trout from 2012-2016.

Table A6. Frequency of occurrence of life history characteristics in the female Cypress River Rainbow Trout from 2012-2016.

Site	Sex	Year	LH1	LH2	LH3	LH4	LH5	LH6	LH7	LH8	LH9	LH10	LH11	LH12	LH13	LH14	LH15	Total
Cypress	F	2012	0	36	32	0	0	4	34	18	0	0	2	1	0	0	0	127
Cypress	F	2013	2	16	20	1	0	3	19	6	0	0	0	0	0	0	0	67
Cypress	F	2014	0	31	24	0	0	2	22	13	0	0	0	1	0	0	0	93
Cypress	F	2015	1	14	25	2	0	2	16	6	0	0	2	0	0	0	0	68
Cypress	F	2016	0	3	11	0	0	1	5	7	0	0	0	0	0	0	0	27
			3	100	112	3	0	12	96	50	0	0	4	2	0	0	0	382

Portage M 1992 0.114 0.591 0.023 0.227 0.023 0.023 0.000 Portage M 1993 0.063 0.635 0.111 0.095 0.000 0.000 Portage M 1994 0.293 0.560 0.053 0.040 0.053 0.000 0.000 Portage M 1995 0.142 0.567 0.071 0.094 0.087 0.024 0.016 Portage M 1996 0.242 0.523 0.091 0.098 0.000 0.000 Portage M 1997 0.211 0.579 0.064 0.082 0.064 0.000 0.000 Portage M 1999 0.244 0.561 0.049 0.049 0.006 0.000 Portage M 2000 0.339 0.478 0.055 0.041 0.062 0.057 0.000 0.000 Portage M 2002 0.278 0.554	Site	Sex	Year	LH1	LH2	LH3	LH6	LH7	LH8	LH11
Portage M 1994 0.293 0.560 0.053 0.040 0.053 0.000 0.000 Portage M 1995 0.142 0.567 0.071 0.094 0.087 0.024 0.016 Portage M 1996 0.242 0.523 0.091 0.098 0.030 0.008 0.000 Portage M 1997 0.211 0.579 0.064 0.082 0.064 0.000 0.000 Portage M 1998 0.144 0.655 0.094 0.043 0.050 0.007 0.007 Portage M 1999 0.244 0.561 0.049 0.091 0.049 0.006 0.000 Portage M 2000 0.339 0.478 0.050 0.089 0.039 0.006 0.000 Portage M 2001 0.278 0.557 0.041 0.062 0.057 0.000 0.000 Portage M 2003	Portage	Μ	1992	0.114	0.591	0.023	0.227	0.023	0.023	0.000
PortageM19950.1420.5670.0710.0940.0870.0240.016PortageM19960.2420.5230.0910.0980.0300.0080.008PortageM19970.2110.5790.0640.0820.0640.0000.000PortageM19980.1440.6550.0940.0430.0500.0070.007PortageM19990.2440.5610.0490.0910.0490.0060.000PortageM20000.3390.4780.5500.0890.0390.0060.000PortageM20010.2780.5570.0410.0620.0570.0050.000PortageM20020.2780.5540.0510.0900.0270.0000.000PortageM20030.2310.6210.0180.1080.0220.0000.000PortageM20030.2310.6210.0180.1080.0220.0000.000PortageM20030.1140.6340.1140.0590.0460.0000.000PortageM20050.1140.6340.1140.0590.0760.0330.000PortageM20070.1330.6650.0480.1160.310.0040.002PortageM20090.1340.6640.0810.0400.0740.0070.000	Portage	Μ	1993	0.063	0.635	0.111	0.095	0.095	0.000	0.000
PortageM19960.2420.5230.0910.0980.0300.0080.008PortageM19970.2110.5790.0640.0820.0640.0000.000PortageM19980.1440.6550.0940.0430.0500.0070.007PortageM19990.2440.5610.0490.0910.0490.0060.000PortageM20000.3390.4780.0500.0890.0390.0060.000PortageM20010.2780.5570.0410.0620.0570.0050.000PortageM20020.2780.5540.0510.0900.0270.0000.000PortageM20030.2310.6210.1180.1080.0220.0000.000PortageM20030.2310.6210.0180.1080.0220.0000.000PortageM20030.2310.6210.0180.1080.0220.0000.000PortageM20050.1140.6340.1140.0590.0460.0000.000PortageM20060.1990.6090.810.0620.0430.0060.000PortageM20070.1330.6650.0480.1160.0310.0040.002PortageM20080.1100.6590.0690.0760.0790.0060.000	Portage	М	1994	0.293	0.560	0.053	0.040	0.053	0.000	0.000
PortageM19970.2110.5790.0640.0820.0640.0000.000PortageM19980.1440.6550.0940.0430.0500.0070.007PortageM19990.2440.5610.0490.0910.0490.0060.000PortageM20000.3390.4780.0500.0890.0390.0060.000PortageM20010.2780.5570.0410.0620.0570.0050.000PortageM20020.2780.5540.0510.0900.0270.0000.000PortageM20030.2310.6210.0180.1080.0220.0000.000PortageM20030.2310.6210.0180.1080.0220.0000.000PortageM20030.1140.6340.1140.0590.0460.0000.000PortageM20050.1140.6340.1140.0590.0460.0030.000PortageM20060.1990.6090.0810.0620.0430.0060.000PortageM20070.1330.6650.0480.1160.0310.0040.002PortageM20080.1100.6590.0690.0760.0790.0060.000PortageM20100.1490.5840.0790.0790.0000.0000.000 <td>Portage</td> <td>Μ</td> <td>1995</td> <td>0.142</td> <td>0.567</td> <td>0.071</td> <td>0.094</td> <td>0.087</td> <td>0.024</td> <td>0.016</td>	Portage	Μ	1995	0.142	0.567	0.071	0.094	0.087	0.024	0.016
PortageM19980.1440.6550.0940.0430.0500.0070.007PortageM19990.2440.5610.0490.0910.0490.0060.000PortageM20000.3390.4780.0500.0890.0390.0060.000PortageM20010.2780.5570.0410.0620.0570.0050.000PortageM20020.2780.5540.0510.0900.0270.0000.000PortageM20030.2310.6210.0180.1080.0220.0000.000PortageM20040.1690.6170.0740.0950.0460.0000.000PortageM20050.1140.6340.1140.0590.0760.0030.000PortageM20060.1990.6090.0810.0620.0430.0060.000PortageM20070.1330.6650.0480.1160.0310.0040.002PortageM20090.1340.6640.0810.0400.0740.0070.000PortageM20100.1490.5840.0790.1380.0690.0000.000PortageM20110.1950.5400.570.1380.0690.0000.000PortageM20120.1110.5560.630.1900.0000.0000.000<	Portage	Μ	1996	0.242	0.523	0.091	0.098	0.030	0.008	0.008
PortageM19990.2440.5610.0490.0910.0490.0060.000PortageM20000.3390.4780.0500.0890.0390.0060.000PortageM20010.2780.5570.0410.0620.0570.0050.000PortageM20020.2780.5540.0510.0900.0270.0000.000PortageM20030.2310.6210.0180.1080.0220.0000.000PortageM20030.2310.6210.0180.1080.0220.0000.000PortageM20030.2310.6210.0180.1080.0220.0000.000PortageM20040.1690.6170.0740.0950.0460.0000.000PortageM20050.1140.6340.1140.0590.0760.0030.000PortageM20060.1990.6090.0810.6620.0430.0060.000PortageM20070.1330.6650.0480.1160.0310.0040.002PortageM20080.1100.6590.0690.0760.0790.0060.000PortageM20100.1490.5840.0790.0790.1090.0000.000PortageM20120.1110.5560.1890.0000.0000.0000.000 <td>Portage</td> <td>Μ</td> <td>1997</td> <td>0.211</td> <td>0.579</td> <td>0.064</td> <td>0.082</td> <td>0.064</td> <td>0.000</td> <td>0.000</td>	Portage	Μ	1997	0.211	0.579	0.064	0.082	0.064	0.000	0.000
PortageM20000.3390.4780.0500.0890.0390.0060.000PortageM20010.2780.5570.0410.0620.0570.0050.000PortageM20020.2780.5540.0510.0900.0270.0000.000PortageM20030.2310.6210.180.1080.0220.0000.000PortageM20030.2310.6210.0180.1080.0220.0000.000PortageM20040.1690.6170.0740.0950.0460.0000.000PortageM20050.1140.6340.1140.0590.0760.0030.000PortageM20060.1990.6090.0810.0620.0430.0060.000PortageM20070.1330.6650.0480.1160.0310.0040.002PortageM20080.1100.6590.0690.0760.0790.0060.000PortageM20100.1490.5840.0790.0790.1090.0000.000PortageM20110.1950.5400.0570.1380.0690.0000.000PortageM20130.2160.5950.1890.0000.0000.000PortageM20130.2160.5950.1890.0000.0000.000Portage <th< td=""><td>Portage</td><td>Μ</td><td>1998</td><td>0.144</td><td>0.655</td><td>0.094</td><td>0.043</td><td>0.050</td><td>0.007</td><td>0.007</td></th<>	Portage	Μ	1998	0.144	0.655	0.094	0.043	0.050	0.007	0.007
PortageM20010.2780.5570.0410.0620.0570.0050.000PortageM20020.2780.5540.0510.0900.0270.0000.000PortageM20030.2310.6210.0180.1080.0220.0000.000PortageM20040.1690.6170.0740.0950.0460.0000.000PortageM20050.1140.6340.1140.0590.0760.0030.000PortageM20060.1990.6090.0810.0620.0430.0060.000PortageM20070.1330.6650.0480.1160.0310.0040.002PortageM20080.1100.6590.0690.0760.0790.0060.000PortageM20090.1340.6640.0810.0400.0740.0070.000PortageM20100.1490.5840.0790.0790.1090.0000.000PortageM20110.1950.5400.0570.1380.6690.0000.000PortageM20120.1110.5560.0630.1900.0000.0000.000PortageM20130.2160.5950.1890.0000.0000.0000.000PortageM20140.0710.3570.2860.0710.1430.0000.001 <td>Portage</td> <td>М</td> <td>1999</td> <td>0.244</td> <td>0.561</td> <td>0.049</td> <td>0.091</td> <td>0.049</td> <td>0.006</td> <td>0.000</td>	Portage	М	1999	0.244	0.561	0.049	0.091	0.049	0.006	0.000
PortageM20020.2780.5540.0510.0900.0270.0000.000PortageM20030.2310.6210.0180.1080.0220.0000.000PortageM20040.1690.6170.0740.0950.0460.0000.000PortageM20050.1140.6340.1140.0590.0760.0030.000PortageM20060.1990.6090.0810.0620.0430.0060.000PortageM20060.1100.6590.0690.0760.0790.0060.000PortageM20080.1100.6590.0690.0760.0790.0060.000PortageM20090.1340.6640.0810.0400.0740.0070.000PortageM20100.1490.5840.0790.1380.0690.0000.000PortageM20120.1110.5560.0630.1900.0790.0000.000PortageM20130.2160.5950.1890.0000.0000.0000.000PortageM20140.0710.3570.2860.0710.1430.0000.071PortageM20150.1670.5420.0830.0000.2080.0000.000	Portage	М	2000	0.339	0.478	0.050	0.089	0.039	0.006	0.000
PortageM20030.2310.6210.0180.1080.0220.0000.000PortageM20040.1690.6170.0740.0950.0460.0000.000PortageM20050.1140.6340.1140.0590.0760.0030.000PortageM20060.1990.6090.0810.0620.0430.0060.000PortageM20070.1330.6650.0480.1160.0310.0040.002PortageM20080.1100.6590.0690.0760.0790.0060.000PortageM20090.1340.6640.0810.0400.0740.0070.000PortageM20100.1490.5840.0790.0790.1090.0000.000PortageM20110.1950.5400.0570.1380.0690.0000.000PortageM20130.2160.5950.1890.0000.0000.000PortageM20140.0710.3570.2860.0710.1430.0000.071PortageM20150.1670.5420.0830.0000.2080.0000.000	Portage	М	2001	0.278	0.557	0.041	0.062	0.057	0.005	0.000
PortageM20040.1690.6170.0740.0950.0460.0000.000PortageM20050.1140.6340.1140.0590.0760.0030.000PortageM20060.1990.6090.0810.0620.0430.0060.000PortageM20070.1330.6650.0480.1160.0310.0040.002PortageM20080.1100.6590.0690.0760.0790.0060.000PortageM20090.1340.6640.0810.0400.0740.0070.000PortageM20100.1490.5840.0790.0790.1090.0000.000PortageM20120.1110.5560.0630.1900.0790.0000.000PortageM20130.2160.5950.1890.0000.0000.0000.001PortageM20130.2160.5950.1890.0000.0000.001PortageM20140.0710.3570.2860.0710.1430.0000.071PortageM20150.1670.5420.0830.0000.2080.0000.000	Portage	М	2002	0.278	0.554	0.051	0.090	0.027	0.000	0.000
PortageM20050.1140.6340.1140.0590.0760.0030.000PortageM20060.1990.6090.0810.0620.0430.0060.000PortageM20070.1330.6650.0480.1160.0310.0040.002PortageM20080.1100.6590.0690.0760.0790.0060.000PortageM20090.1340.6640.0810.0400.0740.0070.000PortageM20100.1490.5840.0790.0790.1090.0000.000PortageM20110.1950.5400.0570.1380.0690.0000.000PortageM20120.1110.5560.0630.1900.0790.0000.000PortageM20130.2160.5950.1890.0000.0000.0000.001PortageM20140.0710.3570.2860.0710.1430.0000.071PortageM20150.1670.5420.0830.0000.2080.0000.001	Portage	Μ	2003	0.231	0.621	0.018	0.108	0.022	0.000	0.000
PortageM20060.1990.6090.0810.0620.0430.0060.000PortageM20070.1330.6650.0480.1160.0310.0040.002PortageM20080.1100.6590.0690.0760.0790.0060.000PortageM20090.1340.6640.0810.0400.0740.0070.000PortageM20100.1490.5840.0790.0790.1090.0000.000PortageM20110.1950.5400.0570.1380.0690.0000.000PortageM20120.1110.5560.0630.1900.0790.0000.000PortageM20130.2160.5950.1890.0000.0000.0000.000PortageM20140.0710.3570.2860.0710.1430.0000.071PortageM20150.1670.5420.0830.0000.2080.0000.001	Portage	М	2004	0.169	0.617	0.074	0.095	0.046	0.000	0.000
PortageM20070.1330.6650.0480.1160.0310.0040.002PortageM20080.1100.6590.0690.0760.0790.0060.000PortageM20090.1340.6640.0810.0400.0740.0070.000PortageM20100.1490.5840.0790.0790.1090.0000.000PortageM20110.1950.5400.0570.1380.0690.0000.000PortageM20120.1110.5560.0630.1900.0790.0000.000PortageM20130.2160.5950.1890.0000.0000.0000.001PortageM20140.0710.3570.2860.0710.1430.0000.071PortageM20150.1670.5420.0830.0000.2080.0000.000	Portage	М	2005	0.114	0.634	0.114	0.059	0.076	0.003	0.000
PortageM20080.1100.6590.0690.0760.0790.0060.000PortageM20090.1340.6640.0810.0400.0740.0070.000PortageM20100.1490.5840.0790.0790.1090.0000.000PortageM20110.1950.5400.0570.1380.0690.0000.000PortageM20120.1110.5560.0630.1900.0790.0000.000PortageM20130.2160.5950.1890.0000.0000.0000.000PortageM20140.0710.3570.2860.0710.1430.0000.071PortageM20150.1670.5420.0830.0000.2080.0000.000	Portage	М	2006	0.199	0.609	0.081	0.062	0.043	0.006	0.000
PortageM20090.1340.6640.0810.0400.0740.0070.000PortageM20100.1490.5840.0790.0790.1090.0000.000PortageM20110.1950.5400.0570.1380.0690.0000.000PortageM20120.1110.5560.0630.1900.0790.0000.000PortageM20130.2160.5950.1890.0000.0000.0000.000PortageM20140.0710.3570.2860.0710.1430.0000.071PortageM20150.1670.5420.0830.0000.2080.0000.000	Portage	М	2007	0.133	0.665	0.048	0.116	0.031	0.004	0.002
PortageM20100.1490.5840.0790.0790.1090.0000.000PortageM20110.1950.5400.0570.1380.0690.0000.000PortageM20120.1110.5560.0630.1900.0790.0000.000PortageM20130.2160.5950.1890.0000.0000.0000.000PortageM20140.0710.3570.2860.0710.1430.0000.071PortageM20150.1670.5420.0830.0000.2080.0000.000	Portage	М	2008	0.110	0.659	0.069	0.076	0.079	0.006	0.000
PortageM20110.1950.5400.0570.1380.0690.0000.000PortageM20120.1110.5560.0630.1900.0790.0000.000PortageM20130.2160.5950.1890.0000.0000.0000.000PortageM20140.0710.3570.2860.0710.1430.0000.071PortageM20150.1670.5420.0830.0000.2080.0000.000	Portage	М	2009	0.134	0.664	0.081	0.040	0.074	0.007	0.000
PortageM20120.1110.5560.0630.1900.0790.0000.000PortageM20130.2160.5950.1890.0000.0000.0000.0000.000PortageM20140.0710.3570.2860.0710.1430.0000.001PortageM20150.1670.5420.0830.0000.2080.0000.000	Portage	М	2010	0.149	0.584	0.079	0.079	0.109	0.000	0.000
PortageM20130.2160.5950.1890.0000.0000.0000.000PortageM20140.0710.3570.2860.0710.1430.0000.071PortageM20150.1670.5420.0830.0000.2080.0000.000	Portage	М	2011	0.195	0.540	0.057	0.138	0.069	0.000	0.000
PortageM20140.0710.3570.2860.0710.1430.0000.071PortageM20150.1670.5420.0830.0000.2080.0000.000	Portage	Μ	2012	0.111	0.556	0.063	0.190	0.079	0.000	0.000
Portage M 2015 0.167 0.542 0.083 0.000 0.208 0.000 0.000	Portage	М	2013	0.216	0.595	0.189	0.000	0.000	0.000	0.000
5	Portage	М	2014	0.071	0.357	0.286	0.071	0.143	0.000	0.071
Portage M 2016 0.143 0.429 0.048 0.143 0.095 0.143 0.000	Portage	М	2015	0.167	0.542	0.083	0.000	0.208	0.000	0.000
	Portage	М	2016	0.143	0.429	0.048	0.143	0.095	0.143	0.000

Table A7. Relative abundances of the significant life histories (occurred >1% of the time in all years) in male Portage Creek Rainbow Trout from 1992-2016

Site	Sex	Year	LH1	LH2	LH3	LH6	LH7	LH8	LH11
Portage	F	1992	0.074	0.370	0.148	0.185	0.185	0.037	0.000
Portage	F	1993	0.017	0.414	0.293	0.052	0.207	0.000	0.017
Portage	F	1994	0.000	0.444	0.333	0.000	0.148	0.074	0.000
Portage	F	1995	0.000	0.551	0.306	0.020	0.102	0.020	0.000
Portage	F	1996	0.011	0.533	0.293	0.022	0.087	0.033	0.022
Portage	F	1997	0.007	0.700	0.167	0.020	0.100	0.007	0.000
Portage	F	1998	0.000	0.500	0.347	0.008	0.093	0.042	0.008
Portage	F	1999	0.027	0.405	0.351	0.045	0.144	0.027	0.000
Portage	F	2000	0.012	0.567	0.220	0.024	0.140	0.037	0.000
Portage	F	2001	0.006	0.700	0.156	0.028	0.078	0.033	0.000
Portage	F	2002	0.004	0.736	0.140	0.038	0.068	0.015	0.000
Portage	F	2003	0.000	0.776	0.132	0.024	0.051	0.017	0.000
Portage	F	2004	0.003	0.660	0.223	0.018	0.082	0.015	0.000
Portage	F	2005	0.003	0.532	0.328	0.017	0.106	0.014	0.000
Portage	F	2006	0.000	0.538	0.339	0.020	0.083	0.020	0.000
Portage	F	2007	0.004	0.694	0.198	0.018	0.076	0.009	0.000
Portage	F	2008	0.000	0.654	0.214	0.021	0.102	0.010	0.000
Portage	F	2009	0.000	0.590	0.286	0.013	0.093	0.018	0.000
Portage	F	2010	0.000	0.554	0.291	0.011	0.114	0.029	0.000
Portage	F	2011	0.009	0.629	0.198	0.026	0.138	0.000	0.000
Portage	F	2012	0.000	0.494	0.294	0.012	0.165	0.035	0.000
Portage	F	2013	0.000	0.436	0.309	0.073	0.109	0.073	0.000
Portage	F	2014	0.000	0.471	0.353	0.000	0.118	0.059	0.000
Portage	F	2015	0.000	0.138	0.448	0.000	0.207	0.207	0.000
Portage	F	2016	0.000	0.394	0.121	0.030	0.303	0.152	0.000

Table A8. Relative abundances of the significant life histories (occurred >1% of the time in all years) in female Portage Creek Rainbow Trout from 1992-2016

Site	Sex	Year	LH1	LH2	LH3	LH6	LH7	LH8	LH11
McVicar	Μ	2012	0.143	0.357	0.095	0.071	0.286	0.024	0.024
McVicar	Μ	2013	0.078	0.2	0.061	0.374	0.226	0.043	0.017
McVicar	Μ	2014	0.038	0.295	0.077	0.333	0.179	0.038	0.038
McVicar	Μ	2015	0.049	0.216	0.108	0.304	0.265	0.029	0.029
McVicar	Μ	2016	0.025	0.309	0.049	0.407	0.123	0.049	0.037

Table A9. Relative abundances of the significant life histories (occurred >1% of the time in all years) in male McVicar Creek Rainbow Trout from 2012-2016

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Table A10. Relative abundances of the significant life histories (occurred >1% of the time in all years) in female McVicar Creek Rainbow Trout from 2012-2016

Site	Sex	Year	LH1	LH2	LH3	LH6	LH7	LH8	LH11
McVicar	F	2012	0.000	0.225	0.125	0.150	0.325	0.150	0.025
McVicar	F	2013	0.000	0.214	0.179	0.024	0.393	0.155	0.036
McVicar	F	2014	0.017	0.322	0.186	0.051	0.271	0.136	0.017
McVicar	F	2015	0.000	0.194	0.204	0.078	0.330	0.184	0.010
McVicar	F	2016	0.000	0.164	0.098	0.082	0.443	0.213	0.000

Table A11. Relative abundances of the significant life histories (occurred >1% of the time in all years) in the male Cypress River Rainbow Trout from 2012-2016

Site	Year	Sex	LH1	LH2	LH3	LH6	LH7	LH8	LH11
Cypress	2012	М	0.115	0.450	0.079	0.110	0.215	0.016	0.016
Cypress	2013	Μ	0.072	0.557	0.072	0.124	0.144	0.031	0.000
Cypress	2014	Μ	0.068	0.489	0.148	0.102	0.148	0.045	0.000
Cypress	2015	Μ	0.034	0.391	0.230	0.126	0.172	0.046	0.000
Cypress	2016	Μ	0.056	0.306	0.139	0.056	0.306	0.111	0.028

Table A12. Relative abundances of the significant life histories (occurred >1% of the time in all years) in the female Cypress River Rainbow Trout from 2012-2016

Site	Sex	Year	LH1	LH2	LH3	LH6	LH7	LH8	LH11
Cypress	F	2012	0.000	0.286	0.254	0.032	0.270	0.143	0.016
Cypress	F	2013	0.030	0.242	0.303	0.045	0.288	0.091	0.000
Cypress	F	2014	0.000	0.337	0.261	0.022	0.239	0.141	0.000
Cypress	F	2015	0.015	0.212	0.379	0.030	0.242	0.091	0.030
Cypress	F	2016	0.000	0.111	0.407	0.037	0.185	0.259	0.000

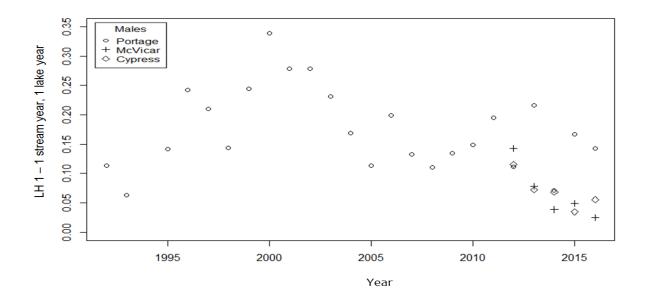


Figure A2. Relative abundances of LH1 males (1 stream year, 1 lake year at first spawn) over all sample periods over all study sites.

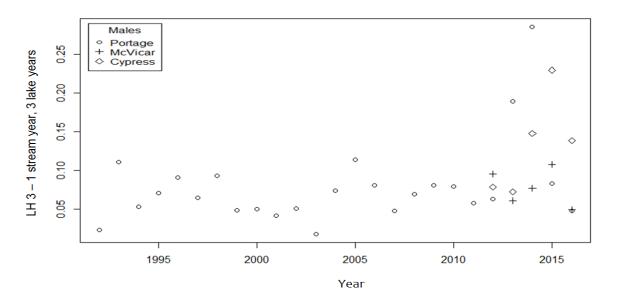


Figure A3. Relative abundances of LH3 males (1 stream year, 3 lake year at first spawn) over all sample periods over all study sites.

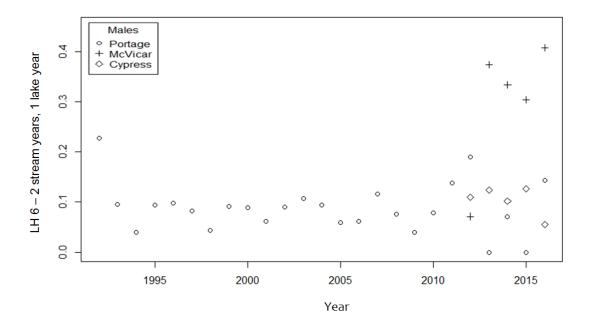


Figure A4. Relative abundances of LH6 males (2 stream years, 1 lake year at first spawn) over all sample periods over all study sites.

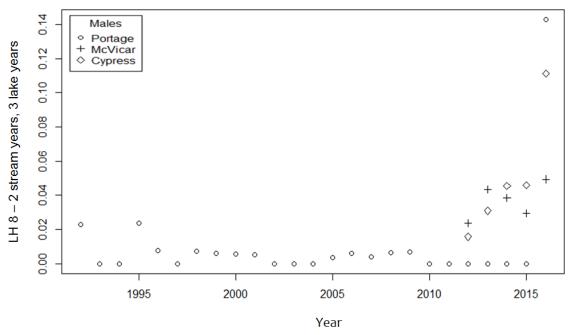


Figure A5. Relative abundances of LH8 males (2 stream years, 3 lake years at first spawn) over all sample periods over all study sites.

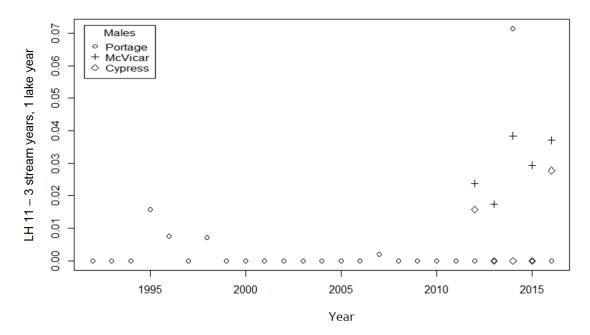


Figure A6. Relative abundances of LH11 males (3 stream years, 1 lake year at first spawn) over all sample periods over all study sites.

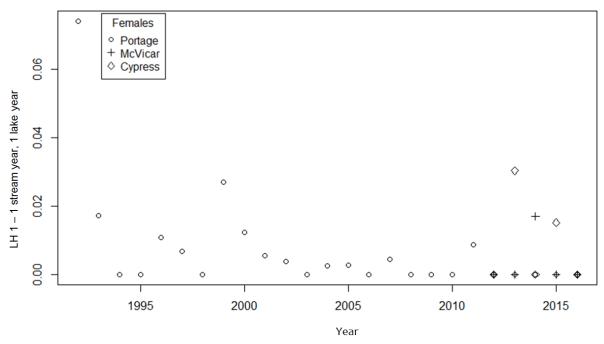


Figure A7. Relative abundances of LH1 females (1 stream year, 1 lake year at first spawn) over all sample periods over all study sites.

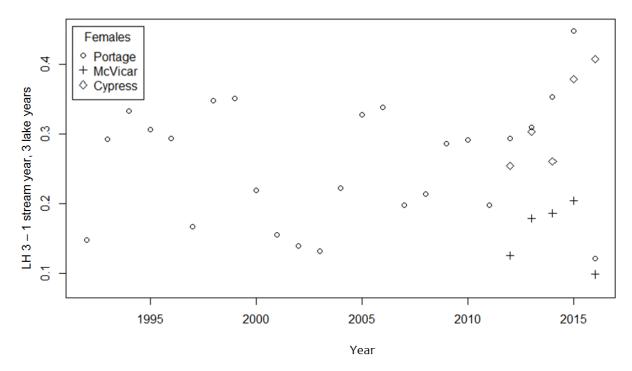


Figure A8. Relative abundances of LH3 females (1 stream year, 3 lake years at first spawn) over all sample periods over all study sites.

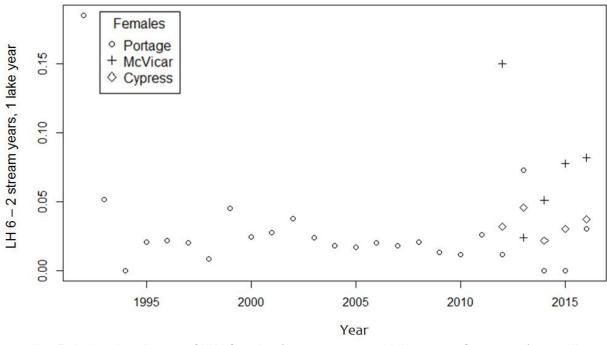


Figure A9. Relative abundances of LH6 females (2 stream years, 1 lake year at first spawn) over all sample periods over all study sites.

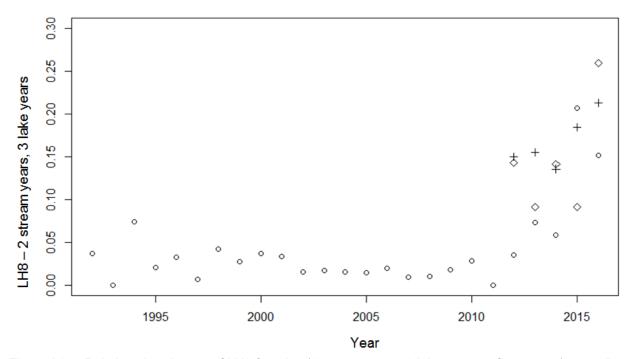


Figure A10. Relative abundances of LH8 females (2 stream years, 8 lake years at first spawn) over all sample periods over all study sites.

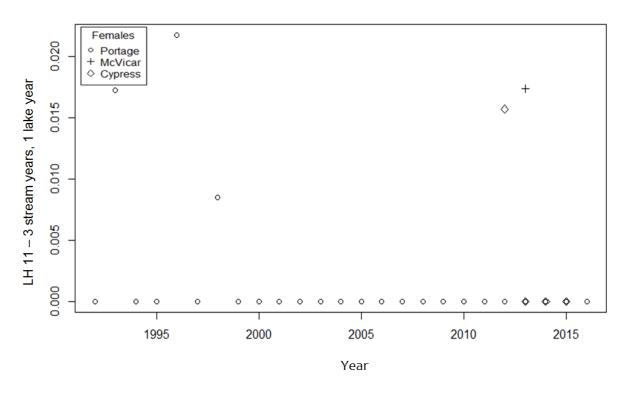


Figure A11. Relative abundances of LH11 females (3 stream years, 1 lake years at first spawn) over all sample periods over all study sites.