Journal of Great Lakes Research 51 (2025) 102508

Contents lists available at ScienceDirect

Journal of Great Lakes Research

journal homepage: www.elsevier.com/locate/jglr

Age-dependent juvenile mortality explains delayed smolting in a declining steelhead population

Kyle Stratton [a,b,*], Jon George [f], Friedrich Fischer [b], Thomas R. Hrabik [d], Erin S. Dunlop [e,1], Brian J. Shuter [f,c], Michael D. Rennie [a,g,1]

[a] Department of Biology, Lakehead University, 955 Oliver Road, Thunder Bay, Ontario P7B 5E1, Canada
[b] Upper Great Lakes Management Unit, Ministry of Natural Resources, 435 S. James Street, Thunder Bay, Ontario P7E 6S8, Canada
[c] Ministry of Natural Resources, Emeritus, Canada
[d] Department of Biology, Swenson College of Science and Engineering, University of Minnesota Duluth, 207 Swenson Science Building, Duluth, MN 55812, USA
[e] Aquatic Research Section, Ministry of Natural Resources, 2140 East Bank Drive, Peterborough, Ontario K9J 7B8, Canada
[f] Department of Ecology and Evolutionary Biology, University of Toronto, 25 Willcocks St. Toronto, Ontario M5S 3B2, Canada
[g] IISD Experimental Lakes Area, 111 Lombard Ave, Suite 325, Winnipeg, Manitoba R3B 0T4, Canada

ARTICLE INFO

Communicated by Margaret Docker

Keywords:
Life history strategy
Early-stage mortality
Predation
Demographic response
Salmonidae
Sander vitreus

ABSTRACT

Fish populations in the Laurentian Great Lakes have undergone major changes over recent decades. Demographic changes in fish populations are often accompanied by changes in life history strategies that reflect variation in mortality applied to different life stages. We examined the steelhead (*Oncorhynchus mykiss*) population in Black Bay, Lake Superior, where a naturalized steelhead population experienced significant demographic changes over three decades. Initial increases in density in Portage Creek, Black Bay (1995–2007) were associated with reductions in angler mortality (applied to adult steelhead), but the population declined (2007–2018) despite no further changes in angler mortality. Simultaneously, the dominant life history among several Black Bay tributaries changed between 2013 and 2017, with returning spawners becoming primarily represented by individuals who smolted at age 2 (a more common pattern across other Lake Superior populations) from those who primarily smolted at age 1. To assess whether changes in juvenile mortality could explain observed life history shifts in surviving spawners and recent steelhead population declines, we constructed Leslie matrices with differential mortality applied to observed demographics from Portage Creek steelhead to evaluate scenarios representing increased parr (in-stream) mortality and increased smolt (in-lake) mortality. The observed demographic changes in Portage Creek (i.e., shift from 1 to 2 year smolts and associated population declines) were predicted by a model applying size-dependent smolt survivorship to female steelhead in a fashion consistent with increased in-lake mortality of age 1 smolts. This study provides an example of population-level responses to increased stage-specific mortality and offers an example of how in-lake conditions can influence potamodromous salmonids in the Laurentian Great Lakes.

1. Introduction

Mortality is a major driver in both the demographics and dominant life history outcomes in organisms. Changes in mortality alter population growth, and over generational timescales, have the potential to alter life history characteristics such as age at maturity, growth, reproductive rate, maximum size (Charnov, 1993; Roff, 1984), and migratory behaviours (Jorgensen et al., 2008; Roff, 1988; Theriault et al., 2008). These selective forces are often challenging to observe directly given the slow rate over which selection naturally occurs when applied to most species. However, this phenomenon has been documented across the animal kingdom (Stokes et al., 2000; Yadav et al., 2014). Mortality resulting from human activities can have substantial impacts on animal populations, especially fishes, and in some cases has proven to be catastrophic. For example, native salmonids like lake trout (*Salvelinus namaycush*) and many *Coregonus* species in the Laurentian Great Lakes

---

* Corresponding author.
E-mail address: kyle.stratton@ontario.ca (K. Stratton).

[1] Given their roles as Associate Editors, Erin Dunlop and Michael Rennie had no involvement in the peer-review of this article and have no access to information regarding its peer-review. Full responsibility for the editorial process for this article was delegated to Margaret Docker.

https://doi.org/10.1016/j.jglr.2025.102508
Received 7 July 2024; Accepted 31 December 2024

experienced severe declines from both the invasion of sea lamprey (*Petromyzon marinus*) and overfishing in the early part of the 20th century, extirpating naturally reproducing populations of several species from many regions (Cornelius et al., 1995; Dettmers et al., 2012; Schmidt et al., 2011).

While observed demographic changes have been significant in many populations for a variety of reasons, assigning cause is rarely straightforward. However, understanding at which life stage mortality is applied can help to provide insights based on how populations are expected to respond. For example, the application of high mortality on immature fish is likely to result in delayed maturity, increased immature growth rates, and larger maximum size (Dunlop et al., 2015). By contrast, increased mortality applied to mature fish is likely to result in earlier maturation and smaller maximum size (Beverton and Holt, 1993; Charnov et al., 2013). Thus, understanding the predominant outcomes of selection due to changes in mortality applied at different life stages can provide insight into the ultimate cause of demographic changes in a population. These demographic changes may eventually lead to evolutionary changes if the resulting phenotypic response is heritable (Kuparinen et al., 2007).

Rainbow trout (*Oncorhynchus mykiss,* hereafter “steelhead”; Pearse et al., 2009) are a species with highly variable life histories and exhibit rapid phenotypic changes in response to new or changing environments (Phillis et al., 2016). Further, their migratory forms have distinct transitional phases from juvenile to adult habitat, making them good candidates for understanding changes in stage-dependent mortality. Across their native and non-native range, steelhead are iteroparous, having been introduced across North America and the Great Lakes during the late 1800 s, with stocking efforts continued throughout the 20th and 21st centuries (Bronte et al., 2003). Despite being derived originally from stocking, populations in Lake Superior are now naturalized and display local genetic structuring (Addison, 2007; Krueger et al., 1994). In Lake Superior and the surrounding basin, steelhead have provided an important recreational fishery since the latter half of the 20th century (Bobrowicz, 2009; Schreiner, 2006).

Typically, in the Great Lakes, potamodromous adult steelhead migrate from open waters into their natal stream to spawn each spring. Once eggs hatch, juvenile steelhead (hereafter called ‘parr’) will typically live in the stream for 1–3 years at which point they will emigrate into the lake as smolts (Biette et al., 1981; Hrabik et al., 2023). Smolts will generally spend an additional 1–3 years in open water before reaching sexual maturation and migrating up their natal streams to spawn, returning to the lake once spent, only to spawn in a subsequent season. The timing of this life history transition from resident parr to moving out into the lake environment (i.e., smoltification) has important implications for the ability of these populations to cope with various environmental stressors. The observed variation in the duration of time spent in both stream and lake environments suggests significant adaptive capacity against ecosystem changes or size-selective pressures (Kruger et al., 1993). Further, steelhead returns have been associated with both in-stream and in-lake environmental conditions elsewhere in Lake Superior (Hrabik et al., 2023).

Steelhead are of importance to fishery managers in the Great Lakes because of their popularity in the recreational fishery. To effectively manage steelhead, a better understanding of steelhead ecology is needed to fill existing knowledge gaps, especially as the Great Lakes undergo environmental change. This study fills knowledge gaps for understanding how stage-dependent mortality alters life history strategies in the population of steelhead in Portage Creek, located on Black Bay, Lake Superior (Fig. 1). In 1991, a monitoring program was initiated during a period of high adult mortality imposed primarily through angling during spawning runs (George, 1994). In 1994, access to the lower reaches of

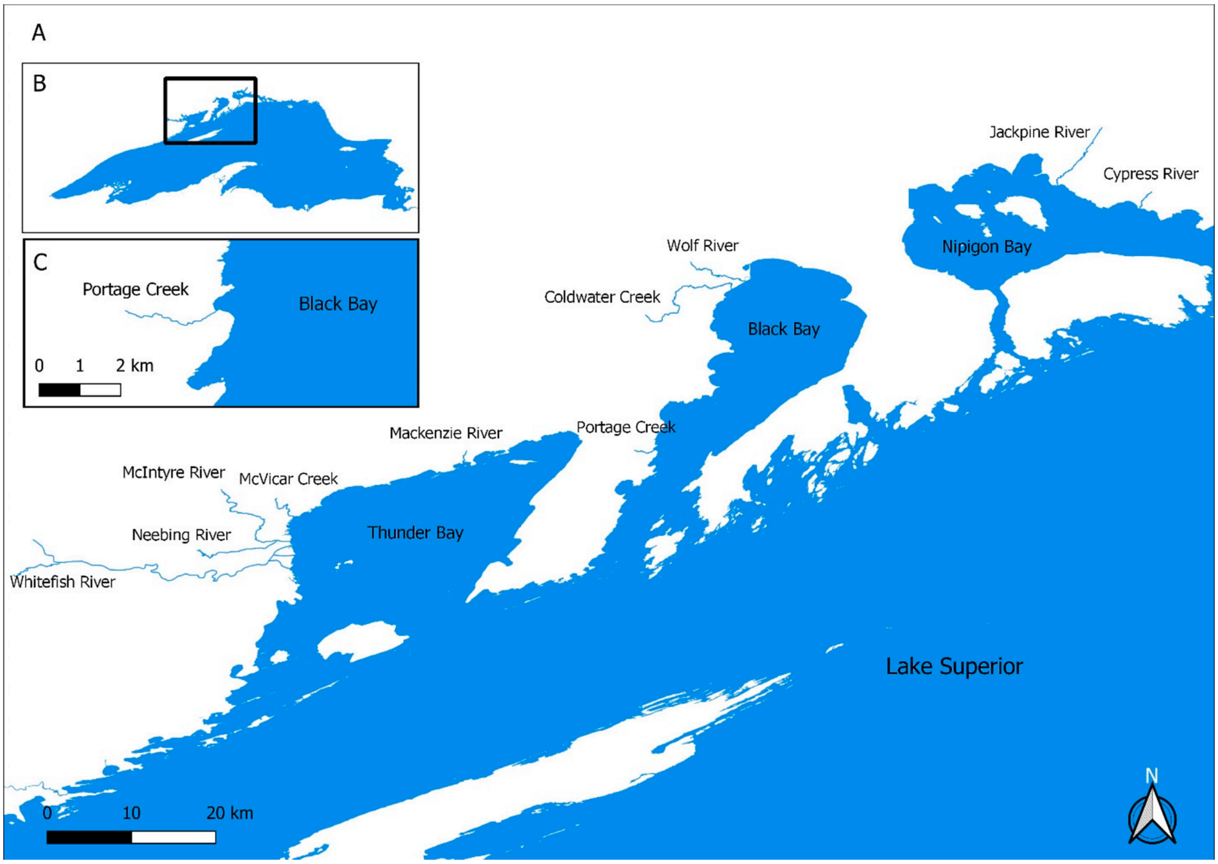

Fig. 1. Map A shows the streams that were angled for adult steelhead, and included in the contemporary comparison of life histories. Inset map B shows a zoomed out view of map A relative to the rest of Lake Superior. Inset map C shows a zoomed in view of Portage Creek.

Portage Creek became privatized, effectively eliminating the majority of angling-related mortality on adult steelhead. Following this change in the fishery, the density of the population increased substantially (Fig. 2), peaking between 2004 and 2007, after which drastic declines in adult abundance were observed.

Coincident with steelhead declines since 2007, walleye (*Sander vitreus*) populations in Black Bay increased (Berglund, 2016), which may have resulted in increased predation of juvenile steelhead smolts leaving the stream to grow in the lake. Size-selective predation of juvenile steelhead by walleye has been observed elsewhere (Baldwin et al., 2003; Yule et al., 2000). Though Black Bay once supported one of the largest walleye commercial fisheries in Lake Superior (Furlong et al., 2006), a combination of over-exploitation and/or loss of spawning habitat caused the Black Bay walleye population to collapse in 1968 (Furlong et al., 2006; Geiling et al., 1996). Various walleye rehabilitation efforts have been initiated since the collapse, including a moratorium on walleye harvest within a significant portion of Black Bay, and stocking of walleye from outside sources. Overall, there has been some evidence of success from these stocking efforts (Garner et al., 2013; Wilson et al., 2007), and an observed increase in walleye catch from fishery-independent surveys conducted between 2002 and 2008 (Berglund, 2016).

Over this same time period, brook trout (*Salvelinus fontinalis*) catches in Portage Creek have also increased since monitoring for this species began in 2014 (North Shore Steelhead Association, pers. comm). This increase in brook trout abundance could result in greater interspecific competition between steelhead parr and brook trout as they share similar diets (Rose, 1986) and have been shown to occupy similar in-stream habitats (Bear et al., 2007; Rose, 1986).

Based on these observations, we first sought to: 1) establish the most abundant life history strategies (age at smolting and age at maturity, i.e., age at maiden return to natal stream) present in Portage Creek steelhead and determine whether there were significant temporal changes in these traits during a period of change in the fish community of Black Bay and Portage Creek; 20) determine the degree to which temporal changes were shared by other tributaries within Black Bay, as well as to compare these temporal changes in Black Bay with a nearby tributary located outside of Black Bay (with sufficient long-term data) which did not experience similar population declines (Electronic Supplementary Material (ESM) Fig. S1); 3) evaluate the degree to which the dominant life history strategies observed in Black Bay (focusing on age at smolt and age at maturity) observed in three specific time periods compared to contemporaneous observations of populations located outside of Black Bay but along the Lake Superior shoreline; and finally, 4) a simple life history model was used to evaluate if differential changes in stage-dependent mortality could account for the observed recent demographic and life history changes in the Portage Creek steelhead population. Three different scenarios were implemented in this model: 1) simulated increased parr mortality, possibly caused by increased competition with brook trout in the stream environment; 2) increased smolt mortality, applied equally across age 1 and age 2 smolts, reflecting no gape limitation by in-lake predators (i.e., walleye); and 3) increased smolt mortality due to size-selective mortality by in-lake predators, caused by gape limitation of in-lake predators and resultant increased mortality among smaller age 1 smolts, relative to larger age 2 smolts. To test these scenarios, we constructed Leslie matrices for female steelhead, parameterized with observed estimates of fecundity, population estimates, and natural mortality for different age classes and life history strategies of steelhead in Portage Creek (as a data-rich representative of Black Bay streams, and of populations experiencing similar changes generally). In each scenario, stage-dependent mortality was adjusted in life tables given a common set of initial observed conditions to see which scenario most closely matched observed outcomes of frequency of steelhead life histories and population density.

2. Methods

2.1. Steelhead collections

Since 1991, steelhead monitoring has been undertaken by the Ministry of Natural Resources (MNR) in partnership with the North Shore Steelhead Association (NSSA) in a program called the Co-operative Angler Program (George, 1994). Since the inception of this program, adult steelhead from various streams along the North Shore of Lake Superior have been biologically sampled by volunteer anglers and MNR staff. Information collected during biological sampling of steelhead include fork length measurements, determination of sex (based on external sexually dimorphic traits), and the removal of scales as a non-lethal aging structure. In 1994, a mark-recapture study was initiated in Portage Creek which required applying an external uniquely numbered sew-in tag in front of the dorsal fin, and a fin clip to all captured adult steelhead from this stream, in addition to biological sampling. All fish were collected and sampled with the permission of the MNR.

2.2. Assignment of steelhead life histories

Steelhead scales were pressed on acetate slides and examined with a

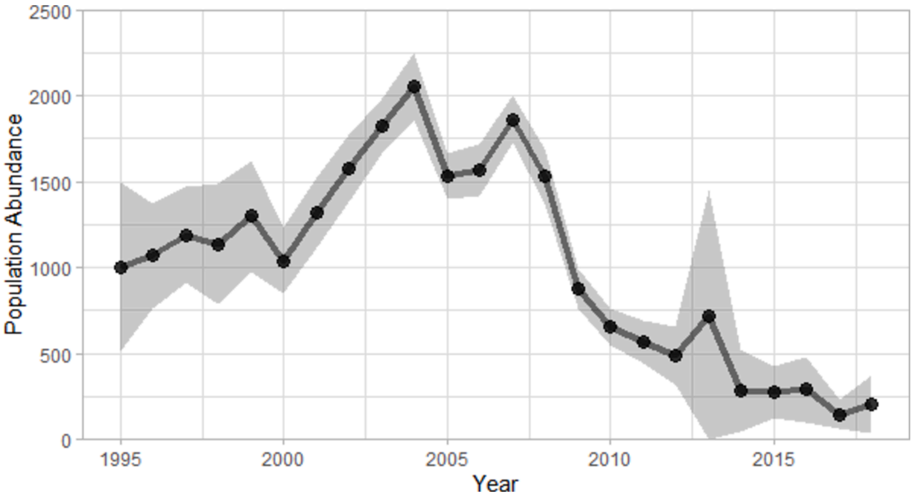

Fig. 2. Portage Creek adult steelhead population estimate (black points) with 95% confidence intervals (shaded regions) for the period 1995 to 2018, as calculated by a Lincoln-Petersen estimator from marked individuals captured within a season.

microfiche reader to identify life history traits from all captured steelhead. Based on accrual rates between annuli, scales of all captured fish were used to determine key life history traits such as the number of years spent in the stream as a parr, age at smolting, the number of years spent in Lake Superior as a smolt, age at maturity (i.e., age during a fish's maiden return to the stream), number of spawning events, and total age (ESM Fig. S2). Fifteen different life histories were identified as having been observed at least once in Portage Creek steelhead (ESM Table S1). These life histories corresponded to a unique combination of number of years spent in the stream as parr and number of years spent in the lake as smolt. However, only life history categories that were present in >1 % of the population for at least one of the sexes were selected for further analysis. Prominent life history categories differed firstly in the number of years spent in the stream as parr prior to smolting (1 or 2 years), and secondarily in the number of years spent in the lake prior to first spawn (1 to 3 years; Table 1). To provide a convenient shorthand to describe steelhead life histories, a Life History (LH) code was developed which indicates the number of years spent in the stream prior to smolting (digit to the left of the decimal) and the number of years at large in the lake as smolt prior to maiden spawning (digit to the right of the decimal; Table 1, ESM Table S1). Since the inception of the Co-operative Angler and Portage Creek steelhead monitoring programs, all aging has been performed by the same reader, standardizing the age determination process through time. Ages determined from scales of adult steelhead were validated through age determinations on scales collected from tagged steelhead of previously determined age, recaptured in subsequent years from Portage Creek. Length at maturity in this study was determined by the fork length (mm) of maiden spawning steelhead, which were identified by scale ages.

2.3. *Evaluating and contextualizing temporal changes in steelhead life histories*

We first determined temporal changes in the dominant life histories related primarily to the number of years before smolting in Portage Creek over time. To determine if potential life history strategy changes observed in Portage Creek occurred in other Black Bay tributaries, the proportion of captured, returning adult fish that smolted at age 1 and age 2 in their respective streams was estimated from all available data. Similar patterns of life history changes were also examined from two other Black Bay tributaries, the Wolf River and Coldwater Creek. Due to limited sample size over the period of sampling and considerable variation in sample sizes in each year, data from both the Wolf River and Coldwater Creek were pooled together to determine changes in the frequency (%) of smolting at age 1 or age 2 in returning adult fish over the period from 2002 to 2018 for adult steelhead captured in these streams. This pattern of change was then compared to the temporal trends observed in Portage Creek. As a reference population outside of Black Bay, temporal changes in the proportions of returning adult steelhead that smolted at age 1 and age 2 were also evaluated for fish captured in the McIntyre River (Thunder Bay, Lake Superior). The McIntyre River (ESM Fig. S1) was selected for comparison to Portage Creek; Like Portage Creek, the McIntyre River has undergone intensive sampling since 2009. Also, the McIntyre River has a highly restrictive harvest regulation in place (one fish over 69 cm limit) which likely limits exploitation (NSSA, pers. comm) and provides a nearby comparison river that is outside of Black Bay which also has limited exploitation.

To assess whether the relative abundance of the six predominant life histories in Portage Creek steelhead (Table 1) changed over time, as well as how they compared to contemporary steelhead life history abundances from populations occupying other Lake Superior streams outside of Black Bay (ESM Table S2), a Principal Coordinate Analysis (PCoA) using chord distance was applied to the relative frequencies of each of the dominant life history types from three time periods in Black Bay (1993, 2007, and 2018) and compared with seven other streams sampled in 2018 across the Lake Superior North Shore. This resulted in a 20 × 6 matrix (8 sites from 2018 plus two additional years of data for Portage Creek times two sexes) from which chord distances were derived. Chord distance was selected as a distance measure as it emphasizes proportional differences by treating common and uncommon groups equally, thus best describing changes in relative abundance among groups (Fernandez et al., 2009; Jiminez et al., 2011). We considered each sex from each population due to known sexual dimorphism in growth and maturity for this species (Kause et al., 2003). The three time periods for Portage Creek were included to assess broad temporal changes in this population relative to contemporary life history frequencies observed at sites across the north shore of Lake Superior, again including both male and female steelhead. The year 1993 represents a period of high adult fishing mortality and low adult abundance, 2007 represents a period of low adult fishing mortality and high adult abundance, and 2018 represents low adult fishing mortality and low adult abundance.

2.4. *Life history modelling*

Leslie matrices were constructed using age-specific mortality and fecundity estimates from the most prominent life history strategies identified for female Portage Creek steelhead (Table 1). Females were chosen as the focus of our modelling efforts because data were more readily available for parameterizing matrices. Fecundity of spawning females was estimated using the following equation (Dubois et al., 1989):

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

where y is the number of eggs and x is the total length of the fish in millimeters. Instantaneous mortality rates (Z) were calculated for female adult steelhead by creating catch curves and using the Robson-Chapman estimator of survival for each of the prominent life history strategies across all years (Ricker, 1975; Robson et al., 1961). These instantaneous mortality rates were then converted to annual mortality rates (A; Table 1) using:

$$A = 1 - \exp^{-z}$$

Average survival rates for steelhead from time of birth to age 1 and from age 1 to maiden spawning, for females, were based on estimates reported by Swanson (1985), reported as 0.79 % and 5 % respectively, and applied to all life histories. As most steelhead in Lake Superior emigrate at age 1 (Close et al., 1997; DuBois et al., 1994; Kwain, 1981; Peterson et al., 2023), the annual smolt survival rate of 5 % was used, describing the rate from age 1 to maiden spawning described by Swanson (1985). To test our hypotheses, annual survival rates during the parr and smolt life stages were adjusted for all life history strategies

Table 1
Summary of the six most prominent life histories present in Portage Creek steelhead. The digit to the left of the decimal in Life History Code indicates number of years spent in the stream prior to smolting, and the digit to the right of the decimal indicates number of years at large in the lake as a smolt prior to maiden spawning. Prevalence reported is across all years of study (1991–2018). Reported annual mortality rates are converted from instantaneous rates derived from Chapman-Robinson catch curves.

Life History Code	Number of Years as Parr	Number of Years as Smolt	Age at Maturation (Years)	Life History Prevalence (% Across Both Sexes)	Annual Mortality (*A*) Females
1.1	1	1	2	9.8 %	34.0 %
1.2	1	2	3	59.6 %	34.3 %
1.3	1	3	4	14.8 %	38.4 %
2.1	2	1	3	5.7 %	30.6 %
2.2	2	2	4	7.6 %	33.0 %
2.3	2	3	5	1.5 %	24.6 %

of female steelhead and adjusted/optimized until the population density from the Leslie matrix were similar to those observed from Portage Creek, as described below. In all cases, proportions of life histories (i.e., age 1 and 2 smolts) were bound between 0 and 1. To evaluate scenario 1 (i.e., increased in-stream mortality of parr), we reduced the initial annual survivorship of steelhead parr for all modelled life histories by 75 %, from 0.79 % to 0.2 %, regardless of how many years they spent in the stream as parr (1 vs. 2 years). To evaluate scenario 2 (i.e., equal vulnerability to mortality of age 1 and age 2 smolts entering the lake), we held parr morality at 0.79 % but reduced annual survivorship of both age 1 and age 2 smolts for all modelled life histories by 75 %, from 5 % to 1.25 %. These first two scenarios operated under the assumption that there were no unique age or size-selective pressures being applied to juvenile steelhead during a particular life stage. To evaluate scenario 3 (i.e., higher vulnerability to mortality of age 1 smolts vs. age 2 smolts entering the lake), parr mortality was again fixed for all life histories at 0.79 % but we reduced the annual survival of age 1 smolts by 20 % from 5 % to 4 % between 2002 and 2006, and then further reduced age 1 smolt survival by an additional 80 % from 4 % to 0.8 % between 2007 and 2018, representing an overall decrease in the survival of age 1 smolts of 84 % relative to the annual smolt mortality rate of 5 % as described by Swanson (1985). For age 2 smolts under this scenario, a 10 % reduction in survival was applied from 2002 until 2018 to 4.5 %. The increased rate of mortality applied primarily to age 1 smolts beginning in 2007 corresponds with a reported increase in putative predators (i.e., walleye) and competitors (i.e., yellow perch (*Perca flavescens*)) in Black Bay (Berglund, 2016). Results were summarized across these six main life history strategies to emphasize differences between age 1 and age 2 smolting strategies.

3. Results

3.1. Observed changes in Black Bay steelhead

Portage Creek exhibited major changes in the predominant smolting age for returning adults along with a reduction in adult steelhead population size over the period of investigation. From 1991 to 2016, the majority of adult steelhead returning to Portage Creek to spawn exhibited age 1 smolting characteristics. The population fell below historical abundance in 2009 and declined precipitously thereafter and, in 2017 and 2018, age 2 smolting characteristics became more common (Fig. 3A, B). Temporal analysis regarding the proportion of age 1 and age 2 smolts from other Black Bay tributaries showed trends similar to those observed in Portage Creek; combined data from both the Wolf River and Coldwater Creek showed that most returning adults historically displayed age 1 smolting characteristics, but more recent shifts towards adults that displayed age 2 smolting characteristics were observed between 2008 and 2013 (Fig. 3C, D), coincident with the period of population decline in the Black Bay tributary where population sizes were monitored, Portage Creek. Across these three major Black Bay tributaries, only 28–30 % of adult steelhead displayed age 1 smolting in 2018, while the remaining 70–72 % of adults displayed age 2 smolting characterictics. This is the inverse of historical levels, where 70–75 % of adult steelhead displayed age 1 smolting characteristics, while the remaining 25–30 % of adults displayed age 2 smolting characterictics (Fig. 3A–D). By comparison, temporal trends in the McIntyre River, Thunder Bay, showed no changes in smolting ages as observed in multiple Black Bay tributaries. The McIntyre River has continuously demonstrated that smolting at age 2 is the more common smolting strategy for both sexes over time (Fig. 3E, F). For adult males, age 2 smolts ranged between 52 and 83 % of the sampled population on an annual basis. For adult females, age 2 smolts comprised 57–89 % of the

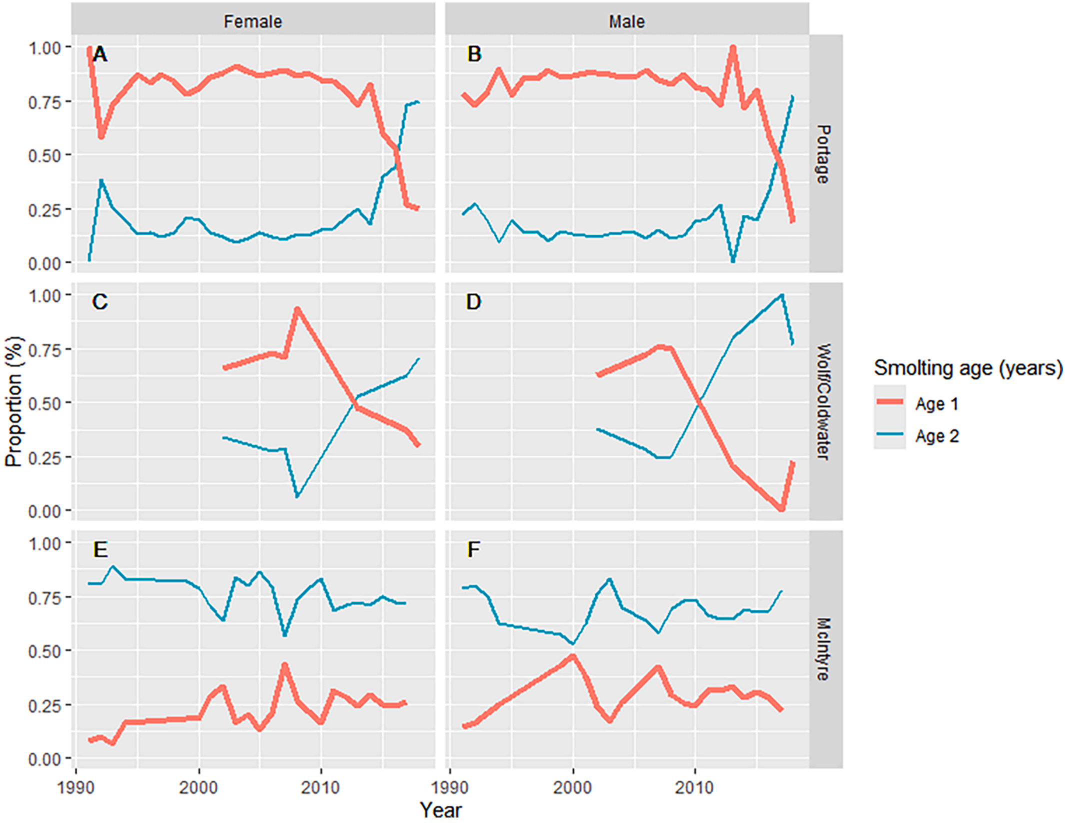

Fig. 3. Temporal variation in the relative abundance of adult male and female steelhead that returned to spawn after smolting at age 1 and age 2 from Portage Creek (Black Bay; A and B), the Wolf River/Coldwater Creek (Black Bay; C and D), and the McIntyre River (Thunder Bay; E and F).

sampled population annually (Fig. 3E, F).

Principal Coordinate Analysis (PCoA) explained 47.8 % of the variation in predominant life history strategies among steelhead collected from North Shore tributaries in Lake Superior on the first axis, and an additional 34.3 % of the variation on the second axis (Fig. 4). The first principal coordinate axis appeared to separate life histories based on number of years in the stream prior to smolting (1 or 2 years), whereas the second axis tended to separate life histories by numbers of years in the lake after smolting (1–3 years). Using our life-history shorthand (see Methods), Portage Creek males most frequently displayed LH1.2 from 1993 until 2007 whereas females altered their predominant life history from LH1.3 to LH1.2, reducing the number of years in the lake after smolting from 3 to 2 following the reduction of exploitation in 1994 (Fig. 4). Between 2007 and 2018, when the adult population decreased by an order of magnitude, the dominant life history of both sexes shifted towards one that delayed smolting (and, in turn, maturation) by 1 year by spending an additional year in the stream as parr (Fig. 4). Further, females appeared to shift from LH1.2 in 2007 to LH2.3 in 2018, spending an additional year both in the stream and in the lake. Comparing temporal changes in Portage Creek steelhead life histories to the variation among other steelhead populations, historical Portage Creek life histories appear to be relatively unique; female Portage Creek steelhead historically showed an age 1 smolting pattern, whereas this life history is typically only observed among males from other locations. By contrast, contemporary (2018) Portage Creek steelhead life histories for both males and females were similar to returning steelhead life histories from various other streams along the North Shore, which were dominated by age 2 smolting strategies (especially among females; Fig. 4).

3.2. Modelled changes in Black Bay steelhead

We captured the demographic induced phenotypic responses in life history strategies by modelling juvenile steelhead survivorship across three scenarios. Under scenario 1, where parr survivorship was reduced by 75 % across all life history strategies, adult steelhead population density decreased over time; however, the proportion of age 1 smolts continued to be more abundant relative to age 2 old smolts (Fig. 5A). The results from this scenario contradict what was observed within the population, as age 2 smolts became more abundant relative to age 1 smolts in 2017 and 2018. The second scenario, where smolt survivorship (i.e., fish leaving the stream and entering the lake) was reduced by 75 % for both age 1 and age 2 smolts, yielded identical results to the first scenario (Fig. 5B), indicating that indiscriminate change in survivorship across life histories was also not responsible for the observed changes in both life history strategies and the adult population. The final scenario, where age 1 smolt survivorship was reduced relative to age 2 smolt survivorship, provided the only set of model results considered here (based on *a priori* hypotheses) that matched the observed shift to age 2 smolts that began around 2015 (Fig. 5C).

4. Discussion

Life histories strategies of returning adult steelhead in Portage Creek have changed since observed population declines in the late 2000 s, shifting from a predominant strategy of returning adults smolting at age 1 to smolting at age 2, the latter being a strategy reflected by most other populations along the North Shore of Lake Superior. Of the Leslie matricies we constructed by altering juvenile mortality in response to hypothesized effects of increased competition or predation, the only scenario that was capable of producing a shift towards a predominance of age 2 smolts involved increasing mortality on age 1 smolts, suggesting

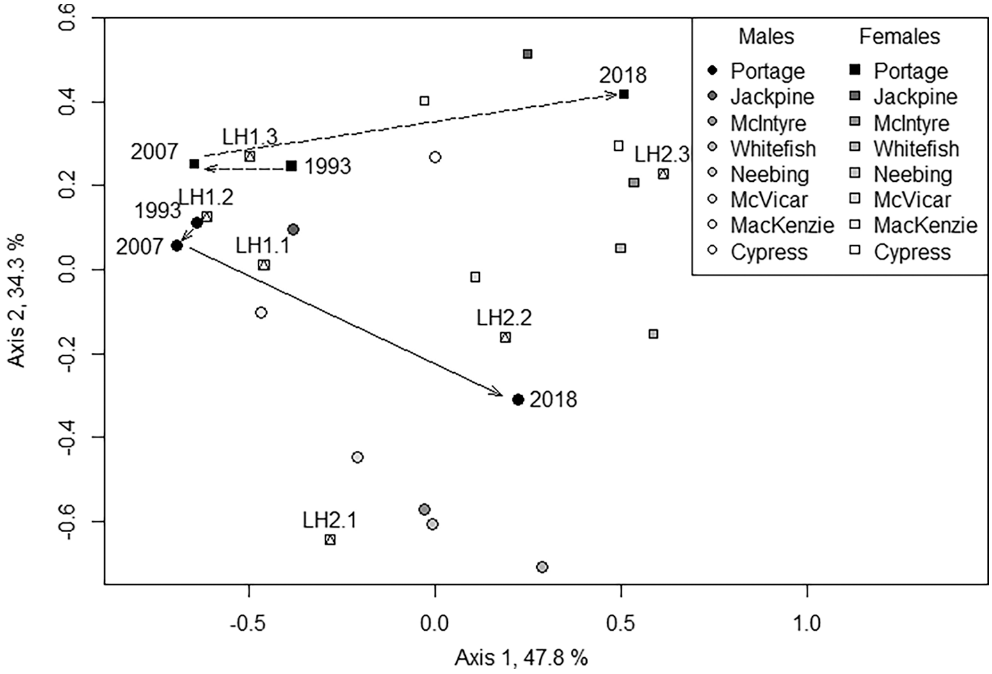

Fig. 4. Biplot from Principal Coordinates Analysis (PCoA) of chord distance representing the dominant life histories in multivariate space for North Shore Lake Superior populations of male (shown as circles) and female (shown as squares) steelhead from Portage Creek, the Jackpine River, McIntyre River, Whitefish River, Neebing River, McVicar Creek, MacKenzie River, and the Cypress River. Also included are two historical time points from Portage Creek (1993 and 2007) which represent different selective pressures that were present on the stream during historically low (high adult fishing mortality) and high (low adult fishing mortality) adult population sizes, respectively. Arrows represent direction of shifts in dominant life histories in Portage Creek over time. Positions of dominant life histories are represented by a triangle embedded in a square and labelled with codes matching descriptions presented in Table 1, corresponding to "years as parr" and "years as smolt" separated by a period. Outside of Portage Creek, each tributary data point represents a single sampling event (2018) for each sex (males in black; females in red) at each location.

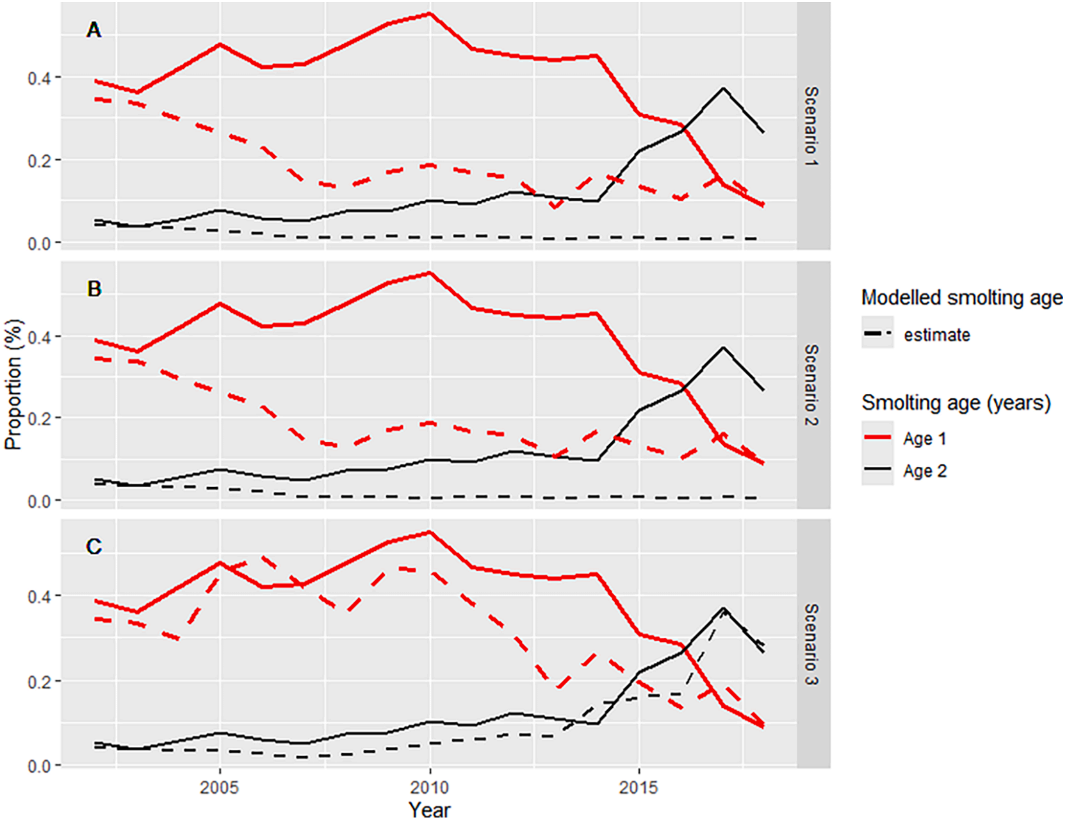

Fig. 5. Proportion of age 1 and age 2 smolts observed in female Portage Creek steelhead and estimated under three different scenarios from 1999 to 2018. Scenario 1 (A) is reduced parr survivorship, scenario 2 (B) is reduced smolt survivorship (equal reductions for both age 1 and 2 smolts), and scenario 3 (C) is higher mortality applied to age 1 smolts relative to age 2 smolts. Solid lines show observed changes in the proportion of smolts returning to spawn, and dashed lines show estimated proportions of returning smolts based on those modelled using Leslie matrices required to maintain the observed adult population size (see Methods).

that a similar process may be occurring in Black Bay steelhead. Size is strongly correlated with age of juvenile salmonids (Sethi et al., 2017), and size is an important factor in determining the fate of outmigrating juvenile steelhead (Hrabik et al., 2023; Surrock et al., 2015). Although the exact cause of increased juvenile mortality in Black Bay may be due to several reasons, it coincides with increases of walleye and yellow perch abundance in Black Bay (Berglund, 2016). The larger body size of age 2 smolts (152 mm on average; Stauffer, 1972) may result in reduced mortality relative to age 1 smolts (76 mm on average; Stauffer, 1972) due to decreased susceptibility to predation and/or more effective foraging (Hrabik et al., 2023). Walleye have been known to consume small rainbow trout (Baldwin et al., 2003). Further, walleye prefer smaller prey regardless of body size, and even at large sizes infrequently consume prey over 100 mm total length (Gaeta et al., 2018; Liao et al., 2002). Thus, as walleye abundance increased in Black Bay, predation susceptibility of age 1 smolts would have increased, whereas age 2 smolts would have been large enough to escape the majority of walleye predation pressure. Moreover, it has been shown that stocked walleye of St. Marys River origin introduced to Black Bay in 2004–2005 (and captured as adults between 2007 and 2010 through index netting) represented approximately 25 % of all fish captured through genetic assignment within Black Bay compared to endemic walleye of Black Sturgeon River origin (Garner et al., 2013). Thus, it is possible that the apparent differential preference for the bay habitat of these stocked fish may have contributed additional predation pressure of rainbow trout smolts in Black Bay at the time coincident with significant steelhead declines observed in Portage Creek.

While age 1 smolts previously were the most common life history strategy observed in returning spawners in Black Bay tributaries, the success of this strategy was unusual compared to that observed in other Lake Superior tributaries. Age 1 smolting was a successful strategy for returning adults in Portage Creek and other Black Bay tributaries for many years, but occurred during a period of suppressed predator abundance in Black Bay due mainly to overfishing and/or loss of suitable spawning habitat (Wilson et al., 2007). In other Lake Superior tributaries, age 1 smolting in steelhead is common and often observed to be more common relative to age 2 smolting (Close et al., 1997; DuBois et al., 1994; Hrabik et al., 2023; Kwain, 1981; Peterson et al., 2023). However, returning adults elsewhere in the lake are rarely those that smolted at age 1, and the majority of returning adults elsewhere in the lake are those that were smolted at age 2 (Close et al., 1997; DuBois et al., 1994; Hrabik et al., 2023; Kwain, 1981; Peterson et al., 2023), suggesting that age 1 smolts have poor survival relative to age 2 smolts in Lake Superior generally (Ward, 2011). Assuming that smolting patterns in Portage Creek steelhead reflect those observed in many other Lake Superior tributaries, then the dominant life history strategy of returning adults in Portage Creek would have been an anomaly until 2017. A trade-off associated with entering the lake at age 1 instead of age 2 is that individuals that smolt at age 1 have reduced adult mortality relative to those that smolt at age 2 (Table 1); however, this also comes at the expense of reduced lifetime fecundity (Stratton, 2019).

It has been hypothesized that the broadly observed high proportion of juvenile steelhead entering Lake Superior at age 1 are not truly undergoing smoltification, but rather are forced to leave the stream environment due to a lack of suitable habitat and/or competition with larger conspecifics (Close et al., 1997). As such, smaller tributaries (like Portage Creek) may ultimately be limited by total habitat availability in their capacity to support steelhead in stream for a period of 2 years. While most other tributaries included in this analysis where age 2 smolting was the more common life history strategy in returning adults are larger than Portage Creek (Fig. 1), the Wolf River and Coldwater Creek are also larger than Portage Creek and responded in similar fashion over time with regards to shifts in life histories, suggesting that the changes observed in Black Bay tributaries generally are not likely linked to in-stream variation only. If habitat availability is a function of tributary size, then anticipated changes due to climate (including climate extremes such as reduced winter and spring precipitation causing low flows, or excessively high flows during spring flooding) may act to further limit steelhead production, particularly in smaller tributaries with more limited habitat compared to larger tributaries (Hrabik et al., 2023). Though our analysis demonstrated that changes in in-stream mortality (due to competition with other stream residents, e.g., brook trout) could not generate the shift in abundance and life history patterns reported here, increased in-stream competition with brook trout could potentially reduce steelhead parr growth rates, potentially reducing both size at smolting and delayed smoltification (Beakes et al., 2010); however, slower in-stream growth alone (without an increase in in-lake mortality post-smoltification, which is the main finding in our simulations) would not produce the patterns in abundance and life history shifts reported here. Smaller fish would indeed be more vulnerable to predation, but we argue that the magnitude of the increase in mortality indicated in our simulations (more than 80 %) is more indicative of a change in the standing stock of in-lake predators rather than increased vulnerability due to changes in body size of smolts alone (without an increase in predator standing stock). Regardless of the ultimate driver of smoltification (environmental vs. physiological) or the degree to which in-stream competition may also be contributing to slower growth rates of parr, differential in-lake mortality between age 1 and age 2 smolts ultimately produced the variation required for natural selection to emphasize the success of one phenotype over the other.

While our analysis indicates that increased mortality of age 1 smolts is a likely driver of changes in the frequency of life history strategies in returning adults to Black Bay tributaries, we cannot definitively conclude that in-lake predators, such as walleye, are the ultimate cause of this increased mortality and decline in adult steelhead abundance in these tributaries. While this scenario is likely, additional information regarding walleye diet, collected near the mouths of streams that flow into Black Bay during late spring when the smolt steelhead enter the lake environment, could help provide additional information to test this hypothesis. Alternatively, the implantation of acoustic transmitters with predation sensors into age 1 and age 2 smolts prior to emigration from Portage Creek (similar to Daniels et al., 2019) could also be used. Once these acoustically tagged individuals leave the stream, they could be detected on existing acoustic arrays in the region (e.g., McKee et al., 2023), providing predation information independent of the identity of the predators involved. Additionally, future analysis could utilize archived steelhead aging structures of returning adults to back-calculate size at smolting to evaluate changes in growth rate (size-at-age of smolts), and more explicitly evaluate the degree to which size (rather than age) of smolting is responsible for the patterns proposed here.

Steelhead are known to demonstrate phenotypic plasticity when faced with adverse environmental conditions (Phillis et al., 2016). Additionally, analyses of phenotypic variation between steelhead populations often reveals large differences, which are likely a function of localized adaptations to a particular set of environmental conditions (Hendry et al., 2002). Our results are consistent with this notion as we have observed a significant shift in steelhead life history strategies following the decrease in adult steelhead abundance, which our model indicates was caused by an increase in mortality of age 1 smolts. Given the adaptive capacity of steelhead to alter their life history strategies when challenged, it is possible that the Portage Creek steelhead population could experience an increase in adult abundance in the future relative to the contemporary abundance levels as they shift their dominant life history strategies of returning individuals to one more commonly observed in other Lake Superior tributaries. Indeed, directional, phenotypic changes in salmonids elsewhere in response to major environmental changes have been observed, and potentially an evolutionary response depending on the degree of heritability involved with stream residency of parr (Williams et al., 2008). However, habitat limitation associated with small ecosystem size may ultimately limit the capacity for Portage Creek to support a sufficient density of individuals to age 2 prior to smolting for the adult density to return to levels previously reached in the mid 2000 s, particularly in the face of climate extremes associated with global warming. We suggest that the Portage Creek and Co-operative Angler steelhead monitoring programs continue as a way to monitor any possible future changes in steelhead population dynamics, not only in Portage Creek and Black Bay, but along the entire North Shore of Lake Superior.

CRediT authorship contribution statement

Kyle Stratton: Writing – original draft, Formal analysis, Conceptualization. **Jon George:** Resources, Project administration, Methodology, Conceptualization. **Friedrich Fischer:** Resources, Conceptualization. **Thomas R. Hrabik:** Writing – review & editing, Conceptualization. **Erin S. Dunlop:** Writing – review & editing. **Brian J. Shuter:** Writing – review & editing. **Michael D. Rennie:** Supervision, Writing – review & editing, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank Norm Stieh and all the other volunteer anglers who participated in the Co-operative Angler and Portage Creek steelhead monitoring projects, along with landowners Ray Dee and Hector Dougall, who allowed angler access on their property. We also thank two anonymous reviewers and the associate editor for their helpful comments which improved the manuscript. This work was supported by the Ontario Ministry of Natural Resources and Forestry, the North Shore Steelhead Association, Lakehead University, and the Canada Research Chair program and Discovery Grant funding through the Natural Sciences and Engineering Research Council of Canada.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jglr.2025.102508.

References

Addison, A.P., 2007. Adaptive naturalization of steelhead (*Oncorhynchus mykiss*) populations from northern Lake Superior tributaries. University of Toronto, Toronto, Canada. MSc thesis.

Baldwin, C.M., McLellan, J.G., Polacek, M.C., Underwood, K., 2003. Walleye predation on hatchery releases of kokanees and rainbow trout in Lake Roosevelt Washington. n. Am. J. Fish. Manag. 23 (3), 660–676.

Beakes, M.P., Satterthwaite, W.H., Collins, E.M., Swank, D.R., Merz, J.E., Titus, R.G., Sogard, S.M., Mangel, M., 2010. Smolt transformation in two California steelhead populations: effects of temporal variability in growth. Trans. Am. Fish. Soc. 139 (5), 1263–1275.

Berglund, E., 2016. Assessment and monitoring of Black Bay, Lake Superior walleye using Fall Walleye Index Netting (FWIN) 2002–2014. Upper Great Lakes Management Unit, Ontario Ministry of Natural Resources, Thunder Bay, Ontario.

Beverton, R.J., Holt, S.J., 1993. On the dynamics of exploited fish populations. Springer, Dordrecht.

Biette, R.M., Dodge, D.P., Hassinger, R.L., Stauffer, T.M., 1981. Life history and timing of migrations and spawning behavior of rainbow trout (*Salmo gairdneri*) populations of the Great Lakes. Can. J. Fish. Aquat. Sci. 38, 1759–1771.

Bobrowicz, S.M., 2009. Rainbow Trout Management Plan for the Canadian waters of Lake Superior. Upper Great Lakes Management Unit, Ontario Ministry of Natural Resources, Thunder Bay, Ontario.

Charnov, E.L., Gislason, H., Pope, J.G., 2013. Evolutionary assembly rules for fish life histories. Fish Fish. 14 (2), 213–224.

Close, T.L., Anderson, C.S., 1997. Factors limiting juvenile steelhead survival in streams tributary to Minnesota waters of Lake Superior. Minnesota Department of Natural Resources, Section of Fisheries, Duluth, Minnesota.

Cornelius, F.C., Muth, K.M., Kenyon, R., 1995. Lake trout rehabilitation in Lake Erie: a case history. J. Great Lakes Res. 21, 65–82.

Daniels, J., Sutton, S., Webber, D., Carr, J., 2019. Extent of predation bias present in migration survival and timing of Atlantic salmon smolt (*Salmo salar*) as suggested by a novel acoustic tag. Anim. Biotelemetry 7, 16.

Dettmers, J.M., Goddard, C.I., Smith, K.D., 2012. Management of alewife using Pacific salmon in the Great Lakes: whether to manage for economics or the ecosystem? Fisheries 37 (11), 495–501.

Dubois, R.B., Plaster, S.D., Rasmussen, P.W., 1989. Fecundity of spring-and fall-run steelhead from two western Lake Superior tributaries. Trans. Am. Fish. Soc. 118 (3), 311–316.

DuBois, R.B., Pratt, D.M., 1994. History of the fishes of the Bois Brule River system, Wisconsin, with emphasis on the salmonids and their management. Trans. Wis. Acad. Sci. Arts Lett. 82, 33–71.

Dunlop, E.S., Eikeset, A.M., Stenseth, N.C., 2015. From genes to populations: how fisheries-induced evolution alters stock productivity. Ecol. Appl. 25 (7), 1860–1868.

Fernandez, R.J., Rennie, M.D., Sprules, W.G., 2009. Changes in nearshore zooplankton associated with species invasions and potential effects on larval lake whitefish (*Coregonus clupeaformis*). Int. Rev. Hydrobiol. 94 (2), 226–243.

Gaeta, J.W., Ahrenstorff, T.D., Diana, J.S., Fetzer, W.W., Jones, T.S., Lawson, Z.J., McInerny, M.C., Santucci Jr, V.J., Vander Zanden, M.J., 2018. Go big or… don't? A field-based diet evaluation of freshwater piscivore and prey fish size relationships. PLoS One 13 (3), e0194092.

Garner, S.R., Bobrowicz, S.M., Wilson, C.C., 2013. Genetic and ecological assessment of population rehabilitation: walleye in Lake Superior. Ecol. Appl. 23, 594–605.

George, J., 1994. The status of rainbow trout (*Oncorhynchus mykiss*) in the Canadian waters of Lake Superior based on frequency of repeat spawners 1991–1993. Ontario Ministry of Natural Resources and Forestry. Thunder Bay, Ontario.

Hendry, M.A., Wenburg, J.K., Myers, K.W., Hendry, A.P., 2002. Genetic and phenotypic variation through the migratory season provides evidence for multiple populations of wild steelhead in the Dean River. British Columbia. Trans. Am. Fish. Soc. 131 (3), 418–434.

Hrabik, T.R., Olson, K.W., Kaspar, T.J., Sierszen, M.E., Matthias, B.G., 2023. The influence of conditions in Lake Superior and the Bois Brule River, Wisconsin on returns of migratory rainbow trout. J. Great Lakes Res. 49 (2), 506–514.

Jorgensen, C., Dunlop, E.S., Opdal, A.F., Fiksen, O., 2008. The evolution of spawning migrations: state dependence and fishing-induced changes. Ecology 89 (12), 3436–3448.

Kause, A., Ritola, O., Paananen, T., Mäntysaari, E., Eskelinen, U., 2003. Selection against early maturity in large rainbow trout *Oncorhynchus mykiss*: the quantitative genetics of sexual dimorphism and genotype-by-environment interactions. Aquaculture 228 (1–4), 53–68.

Krueger, C.C., Perkins, D.L., Everett, R.J., Schreiner, D.R., May, B., 1994. Genetic variation in naturalized rainbow trout (*Oncorhynchus mykiss*) from Minnesota tributaries to Lake Superior. J. Great Lakes Res. 20 (1), 299–316.

Kuparinen, A., Merilä, J., 2007. Detecting and managing fisheries-induced evolution. Trends Ecol. Evol. 22 (12), 652–659.

Kwain, W.H., 1981. Population dynamics and exploitation of rainbow trout in Stokely Creek, eastern Lake Superior. Trans. Am. Fish. Soc. 110 (2), 210–215.

Liao, H., Pierce, C.L., Larscheid, J.G., 2002. Diet dynamics of the adult piscivorous fish community in Spirit Lake, Iowa, USA 1995–1997. Ecol. Freshw. Fish 11 (3), 178–189.

Pearse, D.E., Hayes, S.A., Bond, M.H., Hanson, C.V., Anderson, E.C., Macfarlane, R.B., Garza, J.C., 2009. Over the falls? Rapid evolution of ecotypic differentiation in steelhead/rainbow trout (*Oncorhynchus mykiss*). J. Hered. 100 (5), 515–525.

Peterson, N., Goldsworthy, C., 2023. Knife River Fish Trap Report 2023. Minnesota Department of Natural Resources, Duluth, Minnesota.

Phillis, C.C., Moore, J.W., Buoro, M., Hayes, S.A., Garza, J.C., Pearse, D.E., 2016. Shifting thresholds: rapid evolution of migratory life histories in steelhead/rainbow trout. *Oncorhynchus Mykiss*. J. Hered. 107 (1), 51–60.

Ricker, W.E., 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Bd Can. 191, 382.

Robson, D.S., Chapman, D.G., 1961. Catch curves and mortality rates. Trans. Am. Fish. Soc. 90, 181–189.

Schmidt, S.N., Harvey, C.J.V., Zanden, M.J., 2011. Historical and contemporary trophic niche partitioning among Laurentian Great Lakes coregonines. Ecol. Appl. 21, 888–896.

Sethi, S.A., Gerken, J., Ashline, J., 2017. Accurate aging of juvenile salmonids using fork lengths. Fish. Res. 185, 161–168.

Stauffer, T.M., 1972. Age, growth, and downstream migration of juvenile rainbow trout in a Lake Michigan tributary. Trans. Am. Fish. Soc. 101 (1), 18–28.

Stokes, K., Law, R., 2000. Fishing as an evolutionary force. Marine Ecol. Prog. Ser. 208, 307–309.

Stratton, K., 2019. Causes and consequences of population changes in Black Bay Steelhead, Lake Superior. Lakehead University, Thunder Bay, Canada. MSc thesis.

Swanson, B. L., 1985. Pikes Creek/Lake Superior steelhead population: population dynamics, fishery and management alternatives. Bureau of Fish Management, Wisconsin Department of Natural Resources, Madison, Wisconsin.

Theriault, V., Dunlop, E.S., Dieckmann, U., Bernatchez, L., Dodson, J.J., 2008. The impact of fishing-induced mortality on the evolution of alternative life-history tactics in brook charr. Evol. Appl. 1 (2), 409–423.

Ward, M.C., 2011. Results of operating the juvenile and adult fish trap on the Knife River, 2011. Minnesota Department of Natural Resources, Section of Fisheries, Project F-29-R-30, Completion Report, St. Paul.

Williams, J.G., Zabel, R.W., Waples, R.S., Hutchings, J.A., Connor, W.P., 2008. Potential for anthropogenic disturbances to influence evolutionary change in the life history of a threatened salmonid. Evol. Appl. 1 (2), 271–285.

Wilson, C.C., Lavender, M., Black, J., 2007. Genetic assessment of walleye (*Sander vitreus*) restoration efforts and options in Nipigon Bay and Black Bay. Lake Superior. J. Great Lakes Res. 33, 133–144.

Yadav, P., Sharma, V.K., 2014. Correlated changes in life history traits in response to selection for faster pre-adult development in the fruit fly *Drosophila melanogaster*. J. Exp. Biol. 217 (4), 580–589.