Phenology and growth of rainbow smelt (*Osmerus mordax*) in Lake Melville, Labrador, under increasing pressure from climate change and anthropogenic activities

By

©Jordan Sutton

A thesis submitted to the School of Graduate Studies in partial fulfillment of the requirements for the degree of Master of Science in Fisheries Science and Technology

Fisheries and Marine Institute

Center for Fisheries Ecosystem Research

Memorial University of Newfoundland

April 2022

St. John's, Newfoundland and Labrador

General Abstract

The rainbow smelt (*Osmerus mordax*) is the most abundant and widespread forage fish residing within the Lake Melville estuary, Labrador, and plays a key role in the upcycling of energy from lower trophic levels to top predators. Rainbow smelt is an abundant prey for a myriad of animals, such as salmonids, gadids, flatfish, birds, and marine mammals, and is one of the preferred wild-caught fishes for subsistence and recreational fisheries in the region. The phenology, including spawning, of rainbow smelt is attuned to the hydrography of the Lake Melville estuary. For example, both spawning and hatching periods coincide with increased water temperature in the spring. With the completion of a new hydroelectric dam in Lake Melville's main tributary, the Churchill River, a modification to the natural flow regime of freshwater into the estuary is expected. Following the demand for electricity, the Churchill River will likely experience lower than normal runoffs in the spring and summer and higher than normal flows in the fall and winter, when demand for power is higher. Modifications in the inflow of freshwater in Lake Melville can result in temperature variations and change the timing of ice formation and break-up as well as the total duration of ice cover within the estuary. Such changes to the natural flow and hydrography can impact the life history of rainbow smelt, especially given that Lake Melville is at the northern limit of the distribution range of the species. Here, I examine the period of spawning and hatching, and variation in abundance of larvae in relation to temperature and salinity. Additionally, I document larval growth as well as the age structure, growth, and maturation of adult rainbow smelt in an effort to understand how the new hydroelectric facility and a changing climate may impact rainbow smelt phenology. Larval growth rate is up to 3.33 times faster than that of more southern regions, while the spawning season and hatching period occurred later, which is hypothesized as being a result of the shorter growth season prevailing at high latitudes. In contrast to early life stages, our findings confirm that adult rainbow smelt grow slower, mature later, and live longer in northern populations compared to southern populations, which is likely due to lower metabolic rate in colder waters prevailing at high latitudes. This thesis contributes to the relative scarcity of information on the life history processes of rainbow smelt in this region. These gaps in basic life history information hinder data-driven management decisions on population status and vulnerability. Additionally, this study provides important baseline information which can be referenced in future studies examining the impact of hydroelectric dam operation on the life history of rainbow smelt and, in turn, ecosystem health due to the species’ ecological importance.

Acknowledgements

Thanks to my supervisor Maxime Geoffroy for guidance and support during this thesis as well as for providing me with so many professional development opportunities outside the scope of this project. I am also thankful to my co-advisor, Pascal Sirois, for his support and advice while analysing the otoliths of rainbow smelt larvae. Special thanks to my colleagues at the Center for Fisheries and Ecosystems Research, especially Jenny Herbig and Julek Chawarski for their mentorship and assistance during this thesis. I am also grateful to Tiffany Small, whom I worked very closely with during my time as a graduate student. I would also like to thank our student research assistant Melinda Noad, who helped process samples, as well as Adam Templeton, who continues to provide technical support for the continuation of this project. Special thanks to Doug Blake for providing logistic support and knowledge of the ecosystem, to Hollis Yetman, Alex Reardon and Darryl Reardon for collecting rainbow smelt in winter, to Jim McCarthy and Mathew Gosse for conducting gill net sampling in the summer and fall, and to Stan Oliver for sampling advice. Lastly, I would like to thank my parents, Roxane and Jim Sutton, and my partner, Emily Underwood, for their unwavering support throughout my academic journey.

The Marine Environment Observation, Prediction and Response Network (MEOPAR), the Department of Fisheries and Oceans — Oceans and Freshwater Contribution Program, the Natural Sciences and Engineering Research Council of Canada, and Memorial University's School of Graduate Studies provided funding to support this study. The NunatuKavut Community Council, Nunatsiavut Government, and Innu Nation were consulted and supported this research. This is a contribution to ArcticNet, a Network of Centres of Excellence Canada, and Ocean Frontier Institute through the Canada First Research Excellence fund.

Table of Contents

List of Figures

List of Tables

Co-authorship statement

I primarily conducted the work completed in this thesis with the support of my supervisor Dr. Maxime Geoffroy and my co-adviser Dr. Pascal Sirois. This thesis presents a two-year larval smelt study exploring abundance, hatch timing and growth in Lake Melville, Labrador. It also explores the spawning timing, maturity schedule and growth of adult rainbow smelt in the same region.

This thesis includes data that were collected a year before I began a Masters in Science, so my involvement in fieldwork and laboratory work began in 2019. Drs. Marie Clément and Maxime Geoffroy conducted larval smelt sampling in 2018 with support from the Nunatukavut Community Council, Nunatsiavut Government, and Innu Nation. I completed the fieldwork in 2019 with Dr. Maxime Geoffroy and Tiffany Small. I conducted the larval otolith extraction and analysis under the supervision of Dr. Pascal Sirois and Anne-Lise Fortin at the Université du Québec à Chicoutimi. All adult smelt samples were collected by Mathew Gosse, Doug Blake, Hollis Yetman, Alex Reardon, and Darryl Reardon. Adult otolith extraction and fish measurements were done by Melinda Noad, Tiffany Small and myself, while adult otolith readings were conducted by Steve Campana at the University of Iceland. Gonad measurement and maturity classification were conducted primarily by myself with support from Tiffany Small. I conducted all the statistical analyses and manuscript preparation for the thesis with editorial support from my committee.

The first chapter of thesis includes a literature review, which is structured as a general introduction, and provides background information on topics relevant to the studies presented herein. The core chapter (chapter 2) is the manuscript for this study, which examines the impacts of temperature and salinity on the period of spawning, hatching, and larval smelt abundance. Chapter 2 also provides baseline information on the age structure and maturity of adult smelt as well as growth of both larvae and adult smelt. This core chapter is to be submitted as a peer-reviewed article to Canadian Journal of Fisheries and Aquatic Science. Chapter 3 consists of a general conclusion, which puts the key findings of the research contained in this thesis in a larger context. This chapter also addresses areas of improvement as well as suggestions for future research in the area.

Chapter 1: General Introduction

1.1 Estuaries

Estuaries are semi-enclosed, coastal bodies of water which stand at the interface between fresh and salt water (Couillard et al., 2017; Lu et al., 2013; Sun, 2020). An "estuarine circulation" is characterized by less dense fresh water flowing into the estuary from upstream rivers, while an open connection to the ocean transports deep saline water inland (Lu et al., 2013). This cycling of water within the estuary continuously replenishes nutrients such as carbon, nitrogen and phosphorus (Nielsen et al., 2004), and supports a myriad of marine species such as invertebrates, fish, birds and marine mammals (McCarthy, 2018). Consequently, estuaries are highly diverse, containing many species of bacteria, zooplankton, phytoplankton, animals and plants from both marine and freshwater systems, and also act as crucial migratory and nursery grounds for a variety of species (Bradbury et al., 2006; Sun, 2020; Vanalderweireldt et al., 2020).

There are 4 main classifications of estuaries based on type of circulation: salt-wedge, slightly stratified, vertically mixed, and fjords. Each type of circulation relies on a varying levels of mixing between saline ocean water and fresh river water (Dyer, 2001). For instance, salt-wedge estuaries are among the most stratified and are driven by rapidly flowing river discharge and weak tidal currents, causing freshwater to flow on the surface and salt water to remain almost stagnant near the seabed (Krvavica et al., 2021). Slightly stratified or "partially mixed" estuaries occur when salt and freshwater mix at all depths due to strong tides and turbulent eddies (Geyer et al., 2000) and vertically mixed estuaries occur when river discharge is low and tidal influence is high, thus creating homogeneity throughout the water column (Dyer, 2001). Fjord estuaries (Fig. 1) are mainly found at higher latitudes and result from glacial erosion (Lu et al., 2013). They usually have one or more freshwater tributaries and are defined by the occurrence of a shallow glacial sill at their mouth, which limits circulation of deeper and denser waters. Similar to fjords, “fjards” differ only in their topographical relief, being characterized as shallow glacial depressions, in contrast to the high relief cliffs of fjords (Kamula, 2020). In both cases, deeper more saline waters are trapped near the bottom and freshwater flows freely along the surface. This results in a high degree of stratification within the estuary (Lu et al., 2013). Consequently, the halocline acts as a barrier or “density surface”, where large aggregations of zooplankton and phytoplankton form vertically thin, horizontally dispersed biological hotspots (Schartup et al., 2015). These hotspots provide forage for a variety of fish species in the more saline waters below, as well as the larval fish residing in the low salinity layer above (Schartup et al., 2015). Furthermore, fresher surface waters confer protection from their predators which have different salinity and temperature requirements and occupy the deeper more saline waters (Simonin et al., 2016).

Because they are exposed to pressures from both the river and ocean as well as from anthropogenic activities such as urbanization, shipping and fishing, estuaries are particularly prone to natural and anthropogenic environmental stressors as well as natural annual fluctuations in abiotic factors driven by natural changes in hydrology (Possamai et al., 2021; Sun, 2020). The historical degradation of estuaries, which are key forage and nursery sites for fishes, has led to global conservation efforts aimed at restoring and protecting habitat integrity in estuaries (McLusky & Elliott, 2004; Ramos et al., 2015).

1.2 Study area: Lake Melville

Lake Melville (Fig. 2) is a subarctic estuarine “fjard” located within the boreal forest ecoregion of central Labrador (Kamula, 2020; M. Li et al., 2016; Lu et al., 2013; Ramos et al., 2015; Schartup et al., 2015). It is formally classified as a fjards due to its irregular bathymetry and shallow topographical relief (Kamula, 2020). Lake Melville is long (180 km), and deep (maximum depth of 256 m) with a total surface area of 3,000 km^2 (Schartup et al., 2015). In the west, Lake Melville connects to a smaller basin, Goose Bay, by way of a shallow (8 m), narrow (2.5 km) sill, the Goose Bay Narrows (Durkalec, 2016; Kamula, 2020; McCarthy, 2018). Similarly, in the east Lake Melville connects to the Labrador Sea through another sill (30 m deep, 2.8 km wide), the Rigolet Narrows, which limits the exchange of seawater between Lake Melville and the Labrador Sea (Kamula, 2020; Lu et al., 2013; McCarthy, 2018). Freshwater input into the estuary primarily comes from four major rivers, the Churchill, Goose, Northwest, and Kenamu (Durkalec et al., 2016; Kamula, 2020; Lu et al., 2013). Of these rivers, the Churchill is the largest with a mean discharge of 1700 m^{3}s^{-1} (Durkalec et al., 2016; Kamula, 2020). Within Lake Melville, smaller rivers provide freshwater discharge to both the north and south shorelines (Kamula, 2020).

The Lake Melville System, which consists of both Goose Bay and Lake Melville, exhibits a low rate of exchange and high input of freshwater, making a steep halocline its dominant characteristic, which persists year round at a depth of 10-25 m (Bobbit & Akenhead, 1982; Kamula, 2020; McCarthy, 2018; Schartup et al., 2015). The Lake Melville System is regulated by estuarine circulation, whereby low-salinity surface waters flow seaward on top of saline waters flowing inward from the Labrador Sea (Kamula, 2020; McCarthy, 2018). The fresh surface layer, however, decreases in depth as it flows eastward to the Rigolet Narrows (Kamula, 2020). The residence time (i.e. how long water remains within the estuary) in Lake Melville increases with depth due to the sill, with surface waters exchanging more regularly and quicker than deeper waters. The rate of exchange for deeper water within Lake Melville is reliant on the density of water outside the sill. If the deep water is more dense than water outside the sill it will remain stagnant, while in contrast, if the deep water is less dense, flushing will occur (Bobbit & Akenhead, 1982). The flushing time of the estuary (i.e. the turn over time) is 192 d after entry (Durkalec, 2016; Kamula, 2020;

McCarthy, 2009). From December to May the Lake Melville System is ice covered, with ice reaching an average thickness of 1 m (Kamula, 2020).

The construction of the Upper Churchill Hydroelectric Project and flooding of the Smallwood Reservoir in the 1970's significantly modified the natural seasonal runoff patterns of the Churchill River (Fig. 3) (Durkalec et al., 2016). Although annual flow volume remained relatively unchanged after the construction and operation of the Churchill Falls Dam, the discharge significantly increased during the winter season, tripling in volume as a result of an increased demand for power (load following) (Clarke et al., 2008; Durkalec, 2016; McCarthy, 2018). In contrast, the natural flow regime is characterized by lower freshwater flows in the winter due to precipitation accumulating as snow, followed by high run-off in spring and early summer when the snow melts (Clarke et al., 2008). Regulated rivers tend to store this high spring run-off for future power generation, dampening freshwater input in the spring and summer (Casado et al., 2013). This alteration of the natural flow regime to that of a regulated river may have impacts on the ecology of fish species living downstream, potentially delaying migratory cues and disrupting the dynamic habitat structures used for refuge, reproduction, feeding and growth (Clarke et al., 2008; Petts, 1984; Small et al., in preparation).

In addition to the Churchill Falls project, the construction of a second dam, Muskrat Falls, in the lower Churchill River is nearing completion and an increased "flattening" of the seasonal inflow into Lake Melville could occur. Additionally, a third dam, Gull Island, has been proposed for future construction and could flatten seasonal inflow even further. Although the impacts of these future projects are unclear, McCarthy (2009) suggests that due to the construction of the Muskrat Falls Project, there may be a shortening in length of winter ice conditions by up to one week, while the variation in water temperature below the dam post-project is expected to be two times less than that of pre-project temperatures (McCarthy, 2009). Additionally, Durkalec (2016) predicted a decrease in salinity of Lake Melville during the winter, and an increase in salinity in the spring and summer when flows are less. Furthermore, at the Kielder Dam, UK, Archer (2008) observed a thermal influence as far as 60 km downstream from the main reservoir, with lower than normal temperatures in the spring and higher than normal temperatures in the fall. The predicted changes to seasonal temperature and salinity variation may impact the depth of the pycnocline within Lake Melville. If waters are colder and saltier during the summer the pycnocline may decrease in depth and, similarly, if waters are warmer and less salty in the winter, the pycnocline may increase in depth. In Lake Melville, these potential impacts on downstream water temperature are compounded by an increase in warm winter anomalies since the late 1990's (Finnis & Bell, 2015). Yet, the impacts of hydroelectric dam operation and climate warming on the ecology of the Lake Melville System remain poorly understood (Durkalec et al., 2016).

1.3 Trophic intermediates and anadromous fishes

In highly productive coastal marine environments, such as many estuaries, one or few small planktivorous, pelagic fish species dominate the intermediate trophic level (Cury et al., 2000). These species, termed “forage fish”, regulate the abundance of both the lower and higher trophic levels, bottle-necking energy transfer from prey items to higher order predators (Bakun, 2006; Hunt & McKinnell, 2006). In the instance where the intermediate trophic level is dominated by one or few species, a “wasp-waist” system is established (Bakun, 2006; Cury et al., 2000). In such systems, forage fish play a dynamic role within the food web, controlling the abundance of prey through top-down interactions and the abundance of predators through bottom-up interactions (Bakun, 2006; Hunt & McKinnell, 2006). Thus, any environmental or anthropogenic stressors that influence the abundance of trophic intermediates in a wasp-waist system will radiate to both the lower and higher trophic levels, impacting the entire ecosystem (Cury et al., 2000).

Estuaries are also an important waypoint for anadromous fishes. The term anadromy refers to a life-history strategy where certain marine fishes move into freshwater tributaries during the spawning season, and later return to the ocean to forage and grow (Braga, 2020; Puijenbroek et al., 2019). Anadromous species act as energy conduits, cycling nutrients from coastal waters into freshwater and terrestrial environments through carcass and gonad deposition (Kope, 2001; Samways et al., 2018). These species encounter many physiological challenges as they transition between habitats, and are vulnerable to habitat degradation resulting from human activities and climate variation (Kope, 2001; Puijenbroek et al., 2019). Ultimately, the use of various environments increases their susceptibility to both climate and anthropogenic stressors (Couillard et al., 2017; Possamai et al., 2021; Ramos et al., 2015)

Of the over 20 species that reside within Lake Melville and Goose Bay, only three species are pelagic: capelin (*mallotus* villosus), sand lance (*Ammodytes americanus*), and rainbow smelt (*Osmerus mordax*) (McCarthy, 2018; Small et al., in preparation). Of the three, rainbow smelt is the most abundant and widespread forage fish within Lake Melville and Goose Bay (McCarthy, 2018). During baseline fyke and gillnet surveys conducted in Lake Melville and Goose Bay in 1998, rainbow smelt made up 31% of the total catch (McCarthy, 2018). Current trends show a decline in trophic intermediates, as well as anadromous fishes in the northwestern Atlantic Ocean, which is reportedly due to habitat degradation and warming temperatures (Chase et al., 2019; Puijenbroek et al., 2019). Although there is a lack of data to assess any change in abundance of anadromous and forage fishes within Lake Melville, the area is experiencing a warm weather anomaly (Finnis & Bell, 2015; Kamula, 2020). Similarly, the area is under increasing anthropogenic stress due riverine exploitation for hydroelectric power (Durkalec et al., 2016; Kamula, 2020; McCarthy, 2018; McCarthy, 2009; Schartup et al., 2015). Thus, there exists a need to investigate how these processes impact key trophic intermediates within the Lake Melville system.

*1.4 Study species: Rainbow smelt (*Osmerus mordax*)*

Rainbow smelt (Fig. 4) is a small pelagic anadromous or freshwater fish species found throughout the northwest Atlantic Ocean and is well adapted for life in cold-water environments (Bradbury et al., 2006, 2008). The terms rainbow smelt and smelt are used interchangeably within this document to refer to the species. Smelt are often found under the ice and avoid freezing by maintaining antifreeze proteins and producing glycerol (Driedzic & Ewart, 2004; Hanson & Courtenay, 2020). Their range extends along the Atlantic Coast from Massachusetts, USA, to coastal Labrador, Canada (O'Brien et al., 2012; O'Malley et al., 2017), and they have also been introduced in the Laurentian Great Lakes and surrounding watersheds (i.e. Lake Champlain) (Dobosenski, 2020; O'Brien et al., 2012; O'Malley et al., 2017), while their introduction to many North American lakes has led to further dispersal into the Hudson Bay watershed (i.e. James Bay, Canada) (COSEWIC, 2018). Due to the relatively fast warming of the North Atlantic and introduction, their geographic range has experienced a northward retreat of approximately 500 km in the last 200 years, with the southern extent of their distribution previously extending to New Jersey (i.e. Delaware River), USA (Chase et al., 2019; Kovach, 2013; O'Malley et al., 2017). In landlocked populations, such as in the Great Lakes, rainbow smelt have also seen a decline in abundance and recruitment, showing a 15% decrease in biomass since the 20th century, which has led to cascading impacts on local food web dynamics (Feiner et al., 2015). Although smelt have historically supported commercial and recreational fisheries in Canada and the United States (Chase et al., 2019; Dobosenski, 2020; Hanson & Courtenay, 2020; O'Malley et al., 2017), both their abundance and harvest has declined rapidly over recent decades (Chase et al., 2019). Smelt are currently listed as a species of concern in U.S waters (Kovach, 2013), while many regions in Canada, such as the south shore St. Lawrence Estuary, have seen rapid declines in the last decades (Enterline et al., 2012). Overall, management practices have been limited by an underlying lack of information on the life history, diets and response to external pressures (i.e. anthropogenic or environmental) of rainbow smelt (Hanson & Courtenay, 2020).

Anadromous rainbow smelt live in nearshore coastal waters (Enterline et al., 2020) but move to freshwater tributaries near the time of ice break-up to spawn (Chase et al., 2019; Enterline et al., 2020; Kovach, 2013). Spawning occurs above tidal influence during nighttime hours and lasts an average of 10 days (Bradbury et al., 2006, 2008; Chase et al., 2019; Enterline et al., 2020; O'Brien et al., 2012; Rupp, 1959). Females are broadcast spawners and spend up to 4 days on the spawning grounds depositing small adhesive eggs, while males remain for up to 9 days tending to multiple females (Chase et al., 2019; Enterline et al., 2020). After spawning, the surviving adults move back into coastal waters, where they feed and grow (Chase et al., 2019; Enterline et al., 2020; McCarthy, 2018). However, there is limited information on the dispersion and habitat use of smelt during their adult phase (Kovach, 2013).

After hatching, larvae move downstream into the estuary where they remain in the low salinity surface layer (salinity < 5) (Laprise & Dodson, 1989). Larval smelt retention above the halocline confers protection from cannibalistic conspecifics and other predatory species, as they remain in the more saline waters below (Hanson & Courtenay, 2020; O'Brien et al., 2012; Simonin et al., 2016; Stritzel Thomson et al., 2011). After a period of 1-7 days, yolk sac reabsorption occurs and larvae begin to feed on plankton and, after a period of 90 days, larvae enter the juvenile stage

(Bradbury et al., 2004, 2006; Sirois & Dodson, 2000). While larval smelt feed primarily on zooplankton and small shrimp (i.e mysids), adult smelt feed on sand lance (*Ammodytes americanus),* amphipods, and often cannibalize larval rainbow smelt (Hanson & Courtenay, 2020; McCarthy, 2018; Stritzel Thomson et al., 2011). Adult smelt are also an important prey item for most estuarine piscivores including gadids (e.g., cod species), flatfish (e.g., winter flounder), and salmonids (e.g., brook trout) and are the primary prey found in the stomachs of ringed seals (*Pusa hipsida*) sampled after whelping within Lake Melville (Bradbury et al. 2004; Boldt et al. 2018; McCarthy, 2018).

1.5 Variability in phenology

The rainbow smelt exhibits variability in its growth rate, maturation age, life span, spawning time, and hatch date across its geographic range (Chase et al., 2019). Along the Atlantic Coast, there exists a latitudinal or thermal gradient, where southern populations live for shorter periods, grow faster, and mature earlier than more northern populations (O'Malley et al., 2017). Because rainbow smelt are exothermic, the Temperature-Size Rule may explain this variation, which theorizes that lower temperatures at higher latitudes result in slower metabolic rates, in turn slowing growth and delaying age of maturation to larger sizes (Angilletta, 2009; Forster & Hirst, 2012). The Lake Melville population is no exception, exhibiting slower growth and later maturation than its southern relatives. Lake Melville smelt are documented as maturing after the age of 3 (McCarthy, 2009), while the age of maturity within landlocked and southern populations has been documented as occurring within the first year (Chase et al., 2019; O'Brien et al., 2012). Lake Melville smelt are also among the oldest living populations, reaching ages of up to 8 years and lengths of up to 250 mm (McCarthy, 2018). By comparison, in more southern populations, smelt rarely exceed the age of 4 or 5 years and reach similar total lengths in their life span (Chase et al., 2019).

Spawning and hatching periods also show a high degree of latitudinal variability with populations in Maine, USA, beginning spawning in late February and March (Ayer et al., 2005), populations in the Great Lakes starting in April (O'Brien et al., 2012; Simonin et al., 2016), and populations in Newfoundland starting as late as June (Bradbury et al., 2004). This variability is likely linked to variability in temperature across latitudes as spawning occurs near the time of ice break-up, when temperatures reach 3-4°C (O'Brien et al., 2012; Rupp, 1959). Thus, a delay in the onset of warmer conditions may promote later spawning at higher latitudes. Subsequent hatch dates vary depending on water temperature as well, with larvae hatching after a period of 10-32 days (O'Brien et al., 2012) or an average of 156.5 degree days (i.e. the number of days for which average daily temperature sums up to 156.5 degrees) after spawning (Gagnon, 2005).

In rainbow smelt, abiotic factors like temperature and salinity impact larval growth. While observing smelt larvae reared *in vitro* over a period of 77 days, Ayer et al., (2005) observed faster growth rates in actively feeding smelt larvae when temperatures were higher (20°C vs. 15°C) as well as when salinities were lower (2% vs. 20%). Larval growth may also be influenced by the overall length of the growing season. While studying Atlantic silverside (*Menidia menidia*) *in vitro*, Conover & Present (1990) found evidence to support a counter-gradient or "latitudinal compensation" growth pattern, whereby more northern larvae grow faster in order to compensate for shorter growing seasons that prevail at higher latitudes (Conover & Present, 1990). However, growth could also be influenced by other environmental conditions such as food availability and predation (Arendt & Reznick, 2005)

1.6 The importance of early life stages for the recruitment of pelagic fishes

Mortality during the early life stages can occur as a product of starvation, dispersion to unsuitable habitat, or predation (O'Brien et al., 2012; Sirois & Dodson, 2000). Prey-driven mechanisms, such as Hjort's (1914) "critical period hypothesis" suggest that starvation is the main factor driving variability in larval recruitment, while Cushing's (1969) "match-mismatch hypothesis" suggests that the temporal overlap between prey abundance (*i.e.* plankton blooms) and larval hatch drives recruitment success. Other theories suggest that prey availability is not as critical to recruitment as once proposed. Iles and Sinclair (1982) theorized that larval recruitment is dependent on adults spawning in favourable areas when conditions are suitable for larval retention, rather than levels of available prey (Houde, 2008). Furthermore, although predation is generally not explicitly specified as a mechanism for controlling larval recruitment, size-selective mortality of the early life stages of fish is often a consequence of predation (Houde, 2008). Faster growing larvae are exposed to predation for shorter periods of time during vulnerable life stages, the "stage-duration hypothesis" (Cushing, 1990), while faster growing larvae tend to be bigger, giving them an inherent advantage over smaller individuals within the same cohort, the "bigger is better" hypothesis (Miller et al., 1988). Fast larval growth can also reduce the risk of mortality by starvation or dispersion as faster growing larvae would exhibit higher feeding rates and better swimming capabilities (Sirois & Dodson, 2000). Ultimately, it is believed that fast growth is selected for when surpassing some minimum size threshold decreases the risk of mortality (Arendt & Reznick, 2005).

Larval survival is one of the main factors driving the recruitment of forage fish (Boldt et al., 2019; Leggett & Deblois, 1994) and their survival is likely linked to more than one of the above mechanisms (Sirois & Dodson, 2000). Thus, any changes to the natural environment (either biotic or abiotic) may have detrimental effects on recruitment into the population as well as total population abundance (Drinkwater & Frank, 1994). Given that survival of larvae is linked to life history processes such as spawning, hatching and growth, it is important that we understand all three to assess the impact of the Muskrat Falls dam on the survival of rainbow smelt in Lake Melville.

1.7 Otolithometry

Otoliths, which are calcium carbonate structures within the inner ears, provide key information on growth of fishes (Houde, 2008; Sirois & Dodson, 2000). Similar to trees, which form annual growth rings, fish otoliths are often used to determine the age and date of formation (Campana, 2001). Age determination from calcified structures such as otoliths forms the basis of all rate calculations in fisheries science (Campana, 2001). Age determination via otolith analysis can occur on one of two scales. Annual aging is used mainly for harvest calculations and population studies, while daily aging targets early life stages recruitment and larval fish studies (Campana, 2001; Pannella, 1971). However, despite their differences, both are governed by similar analyses and sources of error such as a process error (i.e. not all axes of a bony structure show a complete age record) or a subjectivity error (i.e. high variability in age estimates among readers) (Campana, 2001). There are also other structures that encode age information. Fin rays, vertebrae and scales, for instance, also encode age data (Campana, 2001), though unlike otoliths they show signs of resorption under stress or with increased age (O'Malley et al., 2017; Stevenson & Campana, 1992).

The examination of otolith microstructure can provide insight into the growth and survival of early life stages of fish, in particular for rainbow smelt (Fig. 5) (Sirois & Dodson, 2000). Otoliths have been well studied in a variety of fish species since the discovery of annual rings in the late 19th century, and daily increments within annuli have become increasingly popular for determining growth rates, hatch dates, and age of larval fishes since their discovery in the 1970's (Pannella, 1971; Stevenson & Campana, 1992). When analyzing temperate water fishes, Pannella (1971) observed approximately 360 fine increments within the annuli, which he postulated to be daily growth increments. Since this discovery, this information has been useful in determining age and timing of life history events for larval fishes (Stevenson & Campana, 1992). Increment counts provide age information, while increment widths can be used to determine previous size-at-age using back-calculation procedures (Campana, 1990; Sirois & Dodson, 2000). Furthermore, range of hatch dates can be estimated from the age of the larvae and the date of catch and have been used to examine periods of successful hatching (e.g. Sirois & Dodson, 2000). Data encoded within the otolith provide important information for the understanding and management of fish populations.

1.8 Rationale and research objectives

The majority of life history processes of anadromous fishes are closely synchronized with seasonal cycles in environmental conditions and productivity (i.e. temperature change or blooms) (Ayer et al., 2005; Clarke et al., 2008). Thus, a modification to the natural flow regime of rivers and estuaries may disrupt life history processes and impact the survival of anadromous fish species (Drinkwater & Frank, 1994). The reduction of spring freshwater inflow into Lake Melville due to the operation of the Muskrat Falls project in the near-future could result in changes to thermal and salinity regimes as well as food availability (Clarke et al., 2008; Fuller et al., 2015; Puijenbroek et al., 2019), which can impact the growth and survival of larvae (Fuller et al., 2015). The alteration of the natural flow regime may also impact water column stability; less freshwater input in the summer may lead to a decrease in the depth of the halocline within Lake Melville, which smelt larvae use as a refuge from predators as well as for its surplus of available prey (Durkalec et al., 2016; Simonin et al., 2016; Small et al., in preparation). In addition, the higher than normal winter run-off may lead to warmer water temperatures and a shortening of the seasonal ice period within Lake Melville (McCarthy, 2018), which can result in subtle changes in the timing of spawning and subsequent hatching for smelt (Clarke et al., 2008). Lake Melville has also been experiencing a warm weather anomaly since the late 1990's (Finnis & Bell, 2015), which may also impact water temperatures within the estuary and can have cascading impacts on the timing and length of the ice season. Rainbow smelt are currently listed as one of the top five wild-caught food sources for local communities in Lake Melville, being consumed roughly once per week (Wells, 2016). They are also a key trophic intermediate providing forage for many commercially and culturally important species residing within Lake Melville, such as ringed seals and brook trout (McCarthy, 2009, 2018). Given the importance of the freshwater refuge for rainbow smelt larvae in spring and summer, changes in the seasonality of the freshwater regime could alter the recruitment of the species and, in turn, have cascading impacts on lower and higher trophic levels as well as local communities.

The current study examines the life history of anadromous rainbow smelt in Lake Melville, Labrador. More specifically, I quantify the hatch dates and growth rate of rainbow smelt larvae to determine how temperature and salinity drive these processes. The growth, maturation, spawning period, and age structure of adult rainbow smelt are also documented. The significance of the data presented herein is two-fold. Firstly, these data contribute to the relative scarcity of information on the life history processes of rainbow smelt in this region, which represents the Northernmost extent of the species' range. These gaps in basic life history information hinder data-driven management decisions on population status and vulnerability. Secondly, this study provides important baseline information which can be referenced in future studies examining the impact of hydroelectric dam operation on the life history of rainbow smelt.

Chapter 2: Hatching, growth, and maturation of rainbow smelt (*Osmerus mordax*) at the northern limit of their distribution range (Lake Melville, Labrador)

Abstract

Rainbow smelt (*Osmerus mordax*) is a small anadromous fish found throughout the northwest Atlantic Ocean, from the northeast coast of the United States to Labrador, Canada. In Lake Melville, Labrador, smelt represents the main forage species and is harvested as part of a recreational and subsistence fisheries. Despite the ecological and cultural importance of rainbow smelt in Lake Melville, many aspects of its life history remain unknown. In particular, the importance of hydrography for the early life stages needs to be documented as a large hydroelectric project is being completed and could impact its life history. Here, we examine the spawning, hatching period, measure larval growth as well as the age structure, growth, and age at maturation of adult rainbow smelt. Trawl surveys in conjunction with CTD profiles suggest that larval smelt abundance is negatively correlated with temperature, while otolith back-calculation indicates that larval growth rate is up to 3.33 times faster than that of more southern regions, which is hypothesized to be a result of the shorter growth season prevailing at high latitudes. In contrast to early life stages, our findings confirm that adult rainbow smelt grow slower, mature later, and live longer in northern populations compared to southern populations, which is likely due to lower metabolic rate in colder waters prevailing at high latitudes. Our results do not indicate any environmental impacts to rainbow smelt populations, but provide the first measurements of rainbow smelt phenology at the northernmost limit of their distribution range.

2.1 Introduction

The rainbow smelt (*Osmerus mordax*) is a small pelagic fish species found throughout the northwest Atlantic Ocean (Bradbury et al., 2006, 2008; Chase et al., 2019). Due to its variability in life history strategies, it can be found in both coastal and freshwater habitats ranging from Massachusetts, USA, up to coastal Labrador, Canada, while also extending through the Laurentian Great Lakes and many other freshwater bodies (i.e. Lake Champlain) (Dobosenski, 2020; O'Brien et al., 2012; O'Malley et al., 2017). Within its coastal populations, the rainbow smelt is anadromous moving inland to spawn in freshwater tributaries just ahead of tide (Bradbury et al., 2006; Enterline et al., 2020). After hatching, its larvae are carried by currents into the receiving waters downstream where they transition from yolk reserves to exogenous feeding—approximately 7 days after hatching (Bradbury et al., 2006; Sirois et al., 1998). During this period, larvae remain within the epilimnion where they feed and grow (Laprise & Dodson, 1989; Simonin et al., 2016).

Within the seasonally ice-covered Lake Melville, the largest estuary of coastal Labrador, rainbow smelt dominates the forage fish assemblage (Dobosenski, 2020; Hanson & Courtenay, 2020; Paterson et al., 2020) funneling energy from lower trophic levels to top predators, such as gadids, salmonids, flatfish and ringed seals (McCarthy, 2018). In addition to being one of the main prey of brook trout and salmon, both of which are harvested in Lake Melville, a winter recreational and subsistence fisheries directly target rainbow smelt, and smelt have been listed as one of the top five species consumed by local communities within the Lake Melville region (Wells, 2016). Despite their ecological and cultural importance in the region, most aspects of the early life ecology of smelt in Lake Melville remain unknown.

Both anthropogenic and climate change are impacting the hydrography of Lake Melville. Its main tributary, the Churchill River, was first harnessed for hydroelectric power generation in the 1970's (Bobbit & Akenhead, 1982; Durkalec et al., 2016; Kamula, 2020). Since then, the flow volume has remained close to pre-construction values of approximately 1700 m^3 s^{-1}, but the seasonal variation in flow has been altered significantly with a marked increase in freshwater being released in winter and less freshwater flowing in the spring and summer (Durkalec et al., 2016; Kamula, 2020). The completion of the second phase of hydroelectric development within the Churchill River, the Muskrat Falls dam, in 2021-2022 has the potential to further 'flatten' the seasonal freshwater inflow into Lake Melville (Clarke et al., 2008; Durkalec et al., 2016). This may cause the shortening of seasonal ice cover on a scale of weeks, while downstream seasonal temperature variation has the potential to lessen by up to two times its pre-construction variation (McCarthy, 2009). This alteration of the freshwater flow regime may also impact the temperature and salinity regimes, water column stability, and the intensity of vertical mixing within Lake Melville (Durkalec et al., 2016). Potential changes in the hydrography of Lake Melville can further be exacerbated by the warm weather anomaly prevailing in the region since the 1990's (Finnis & Bell, 2015; Kamula, 2020).

Larval survival is one of the main factors driving the recruitment of forage fish (Boldt et al., 2019; Leggett & Deblois, 1994), including rainbow smelt (Feiner et al., 2015; Sirois & Dodson, 2000). Larval rainbow smelt remain in the low salinity surface layer and exploit its surplus of available prey items (Sirois & Dodson, 2000). The stratification also confers protection from predators, such as adult rainbow smelt remaining in the deeper saltier waters, based on differing temperature and salinity requirements (Simonin et al., 2016). Given the importance of this freshwater refuge for rainbow smelt larvae in spring and summer, changes in the seasonality of the freshwater regime could alter the recruitment of the species and, in turn, have cascading impacts on lower and higher trophic levels.

Here, we examine the life history of rainbow smelt in Lake Melville. More specifically, we quantify the hatch dates and growth rates of rainbow smelt larvae in 2018 and 2019 to determine how temperature and salinity drive these processes. The growth, maturation, and age structure of adult rainbow smelt are also documented. Ultimately, we test the correlation between life history processes of rainbow smelt and hydrography to assess their vulnerability to anthropogenic and climatic changes at the northern limit of their distribution range.

2.2 Materials and Methods

Study area

Goose Bay and Lake Melville, collectively referred to as the Lake Melville System (LMS), are located in Central Labrador, Canada. Lake Melville is a semi-enclosed, seasonally ice covered estuarine fjard that connects to the Labrador Sea in the East and to Goose Bay in the West via two narrow, shallow glacial sills which limit the exchange of seawater (Durkalec et al., 2016; Kamula, 2020; McCarthy, 2018). Lake Melville is classified as a fjard and not a fjord because of its low topographical relief and irregular bathymetry (Kamula, 2020). The majority of fresh water that enters the LMS comes through 4 rivers: Goose, Northwest, Kenamu and Churchill (Durkalec et al., 2016; Kamula, 2020). The Churchill River, which flows into Goose Bay in the West, provides the majority (1700 m^3s^{-1}) of freshwater to the system (Kamula, 2020). A defining characteristic of the LMS is the consistent low-salinity surface layer that persists year round to depths of 10-20 m (Kamula, 2020; McCarthy, 2009).

Due to logistical constraints and based on the prediction that the potential impacts of the Muskrat Falls Project would be most prominent within Goose Bay and Upper Lake Melville, sampling effort was localized within this region. Sampling was conducted from June 29th to July 12th in 2018 and July 4th to July 14th in 2019 at ten stations which were distributed across the study area to create a cross-section between Goose Bay and Lake Melville (Fig. 6).

Field sampling

Salinity and temperature profiles were taken at each stations using a calibrated Sontek Cast Away-CTD in 2018 and an RBR Concerto in 2019. Temperature and salinity were averaged within the top 10 meters at each station because rainbow smelt larvae were aggregated around 10 m in the freshwater layer (Tiffany Small, Memorial University, unpublished data). Larval smelt were collected within the top 10 m from each of the ten stations during oblique tows and using a Sea-Gear bongo net (diameter = 28 cm, mesh size = 335μm) towed at 2 knots for 20 minutes. Due to inclement weather, two stations within Lake Melville were not sampled in 2018. Some larvae (n=58) were also collected during vertical tows, which were deployed at each station from the maximum depth of the water column to the surface. All larvae were sorted and preserved in 95% ethanol. Number of larvae from the oblique tows at each station was recorded during the sorting process and the ethanol solution was changed one day after first preservation to prevent samples from becoming acidic (Sirois & Dodson, 2000). Larval abundance (A) at each station i was estimated as the number of larvae caught divided by the volume of water filtered through the bongo net (individuals·100m^{-3}) using the following equation:

$$A_i = n_i/(\frac{V_f}{100})$$

Where n_i is the number of larvae, and V_f is the estimated volume of water filtered through the bongo net during a given oblique tow. Volume filtered was estimated using the equation:

$$V_f = 2(\pi r^2 \Delta x)$$

Where r is the radius of the net, and Δx is the distance, which is in turn, equal to the vessel speed (v) multiplied by the duration of the oblique tow (Δt). Hence, volume filtered can also be expressed as:

$$V_f = 2(\pi r^2(\Delta t \cdot v))$$

Each of the volumes filtered was multiplied by 2 to include both nets. A 100% filtration efficiency was assumed, which might result in conservative abundance estimates.

Adult rainbow smelt were collected (n=201) by local fishers with a fishing rod through the ice in February and March during the 2019 and 2020 recreational and subsistence ice fisheries. Additional samples (n=67) were collected in August and September by Wood Group plc. during their 2019 net surveys (Fig. 6). The latter samples were collected using 15 m four paneled experimental gill nets (Mesh sizes: 5.1, 7.6, 10.2 and 12.7 cm). The nets were deployed for a period of at least 16 hours, to ensure that they were fishing during dusk and dawn periods.

Environmental data

Sea surface temperature (SST) data over the study period were collected by the department of environment and climate change, Newfoundland and Labrador, as part of their Methylmercury monitoring program (*Methylmercury Monitoring in the Muskrat Falls Reservoir, Churchill River, Goose Bay, Lake Melville*, n.d.) at a depth of 1 m from the surface. A cubic spline was fit to the data to interpolate missing data points and the temperature time series produced was used to estimate the SST at first hatch and to determine the spawning period, which was estimated as occurring 156.5 degree days before the hatching period (Gagnon, 2005). This number of degree days represents the average incubation period from six studies within North America. Because spawning is believed to begin when waters reach temperatures of 3-4°C (O'Brien et al., 2012), a threshold was set to exclude dates where temperatures were less than 3°C as the first day of the spawning period. Proportion of ice cover was determined by using daily ice data obtained by Canadian Ice Services (CIS) and allowed for testing whether spawning within Lake Melville occured near the date of ice breakup (O'Brien et al., 2012; Rupp, 1959). For this study, ice breakup dates were calculated as the first day where ice concentration reached <50% within the study area (e.g. Bouchard et al., 2021) and the optimal growth window for young-of-year smelt was calculated as the period from first hatching to the day of first ice formation (first appearance of ice in the study area). Ice concentration was calculated by dividing the area of ice coverage by the total study area. These data were then plotted to show the periods of spawning, hatching and growth for both years.

Otolith analysis

A subsample of 200 larvae were selected to represent the size frequency distribution of all the larvae collected (5-13 mm). A minimum of 10 representatives from each station were selected from the 2019 sampling period (n=152), while additional representatives were taken from the 2018 field season (n =48). To account for the possibility that capelin larvae may have been caught in addition to rainbow smelt larvae, preanal myomere counts for each specimen were taken (Fahay, 2007). No capelin were found during this process. Standard length of each larva was measured using a camera connected to an image analysis system and no correction for shrinkage resulting from the preservation process was made (Sirois et al., 1998). Sagittal otoliths were removed with a pair of fine needles and mounted on a microscope slide using thermoplastic glue. Otoliths were then measured using an image analysis system connected to a light microscope (1000x magnification). The core radius, otolith radius, and width of every increment were measured for each otolith using calibrated ImageJ software. The age in days was inferred from the number of increment widths measured per otolith (Stevenson & Campana, 1992). All otoliths were measured twice in a random order, 3 months apart and any otoliths with a discrepancy in number of increments greater than 10% were excluded from further analyses (Sirois & Dodson, 2000). A coefficient of variation (CV) was calculated in order to assess aging precision (Campana, 2001). Hatch dates were determined for each larva by subtracting the number of daily increments (age in days) from the corresponding date of capture and the frequency of hatch per day was plotted to show when the majority of smelt hatched in 2018 and 2019.

Sagittal otoliths from 267 adult rainbow smelt were analyzed at The Campana Lab at the University of Iceland. Otoliths were immersed in ethanol just prior to imaging, sulcus side down. While under a Leica S8 APO stereomicroscope at 16-40x magnification using reflected light, the growth increment sequence was digitally photographed at a resolution of 5760 x 3600 with an Olympus DP74 digital video camera. Calibrated CellSens software was used to measure otolith length along the long axis; the precision of repeated measurements was ±0.3%. Age interpretations were made from the digital image, which seldom required image enhancement. Known-age otoliths were not available, nor have age validation results been published for this species. Ageing precision was quantified using the coefficient of variation (Campana, 2001).

Whole otoliths of long-lived fishes can often underestimate age (Campana et al., 1990). To determine if otolith sections would be more suitable for ageing than whole otoliths, three large otoliths were embedded and sectioned after whole-otolith ageing. Otoliths were individually embedded in a slow-drying hard epoxy (Araldite epoxy GY502 and hardener HY956 in a 5:1 weight ratio). Sections through the core (~650 µm thickness) were prepared with a single cut using twin blades separated by a spacer on an Isomet low-speed diamond-bladed saw. The sections were subsequently mounted on a standard microscope slide and lightly coated with ethanol just prior to imaging. Sections were aged without prior comparison to the matching whole otolith image. Growth bands were visible in both the sectioned and whole otoliths. In general, whole otoliths were clear and easy to read, although the innermost one or two growth bands were challenging to see in larger otoliths. There was no indication that growth band formation ceased to form on lateral margins, or become obscured in thick otoliths when observed whole, thus the decision was made to use whole otoliths during the aging process. In addition, the relationship between fish length and otolith length for adult smelt was calculated.

Growth rates

A linear regression was performed using the observed measurements (Standard Length and Age) for both seasons (2018 and 2019) and an average growth rate ($mm \cdot d^{-1}$) was calculated. In addition, the biological intercept (BI) method (Campana, 1990) was used to back-calculate length at age (L_t) using the following equation:

$$L_t = L_c + (O_t - O_c)(L_c - L_0)(O_c - O_o)^{-1}$$

Where L is the standard length at capture (L_c), and O is the otolith radius at capture (O_c). A length at the biological intercept (L_0) of 5.81 mm was adapted from Sirois et al., (1998) and otolith radius at the biological intercept (O_0) was estimated from the observed core radius on the otoliths of each individual larva (Leclerc et al., 2011; Sirois et al., 1998).

The Von Bertalanffy growth function (VBGF) was applied to adult fish, ranging in age from 1 to 8 years, to assess variation in the growth rates and size-at-age of males and females. The Von Bertalanffy growth equation is expressed as:

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

Where $E[L][t]$ is the length at age t, L_∞ is the average asymptotic length, K is the growth rate coefficient and t_0 is the time where length is equal to zero (Hopkins, 1992).

Gonad analysis

Gonads from each fish were removed, weighed, and imaged with a digital Single Lense Reflex (SLR) camera (resolution of 6000 x 4000). Each individual was characterized as mature or immature based on GSI percentage (100 x gonad mass/total mass) and gonad images following the methodology from Hagstrøm Bucholtz et al., (2008). Samples collected in August and September were staged as mature or immature by Wood plc using gsi, colour and texture. Proportion of mature individuals for both sexes combined within each age cohort was calculated and the age of maturation was determined based on age from otoliths. Similarly, the proportion of mature individuals within age of maturity is described here as the age where 50% of the adult population is sexually mature (A_{50}) (Wheeler et al., 2009). Similarly, proportion of mature individuals for both combined sexes within successive length classes (ΔL=2mm) was determined to also calculate the length at which 50% of the population was mature (L_{50}). Values of Fulton's condition factor were calculated as $K=(TW/TL^3)\cdot 100,000$ (Chase et al., 2019) to provide general trends of physical condition within the population.

Statistical analyses

Mean temperature and salinity of the top ten meters for each station were calculated and a two-way ANOVA was conducted in R 4.1.2 to assess the correlation between larval abundance with these variables. Abundance data were log transformed to fit a normal distribution (Shapiro-wilks, p-value=0.488). A paired t-test was used to test difference in mean larval abundance between years as well as between Goose Bay and Lake Melville. Ordinary kriging was used to visually represent the surface temperature across the study area. Variogram models were chosen based on the "fit.variogram" function of the "gstat" package in R-studio (V 4.1.0). Gaussian (temperature) and spherical (salinity) models provided the best fit.

2.3 Results

Hydrography

Bottom depth at each station varied from 30 to 100 m, with a mean of 51 m (Table 1). The average temperature within the top ten meters was 9.9 (± 1.1) ℃ in 2018 and 11.4 (± 1.4) ℃ in 2019, while the average salinity within the top ten meters was 4.12 (± 3.1) pss and 1.2 (± 1.1) pss in 2018 and 2019, respectively (Fig. 7; Table 1). Freshwater persisted until a depth range of 10-15 meters, depending on station, and a sharp pycnocline was observed at all stations at these depths. Atlantic water with average temperature and salinity of 3.3 (± 1.8) ℃ and 18.1 (± 4.3) pss in 2018 and 4.5 (± 2.5) ℃ and 15.9 (± 4.8) pss in 2019 laid below the pycnocline. Ice breakup within the study area occurred on May 31st for both years, while ice formation (>0%) occurred on November 10th, 2018 and November 14th, 2019.

Abundance, hatch date and growth rate of larval smelt

A total of 770 larvae from 2018 and 1129 larvae from 2019 were collected. There was no significant difference in mean abundance between 2018 (50±52 individuals·100m^{-3}) and 2019

(58±50 individuals·100m^{-3}) (paired t-test; p-value=0.72). Larval abundance at each station varied from 14 to 169 individuals·100m^{-3} in 2018 and 10 to 127 individuals·100m^{-3} in 2019. Abundance was negatively correlated with temperature (two-way ANOVA; p-value=0.019) and was not correlated with salinity (two-way ANOVA, p-value=0.24), both averaged within the top ten meters of the water column. The correlation between abundance and temperature followed a linear model (Fig. 8). Abundance of larval smelt was higher in Upper Lake Melville than in Goose Bay (paired t-test; p-value=0.016) (Fig. 6) and reached 35.1 (±20.2) individuals·100m^{-3} in Goose Bay in 2018 and 16.6 (± 8.3) individuals·100m^{-3} in 2019, while average abundance in Upper Lake Melville was 65.6 (± 62.2) individuals·100m^{-3} in 2018 and 85.7 (± 42.6) individuals·100m^{-3} in 2019.

The age of larvae caught in 2018 ranged from 0 to 10 days and from 0 to 15 days in 2019. The aging precision between both independent readings was 3.6% and of the 200 larval otoliths analyzed 19 (9.5%) were removed from further analysis due to discrepancy in age determination that exceeded 10%. The back-calculated hatch dates varied between years with the earliest hatch dates being June 26th and June 22nd in 2018 and 2019, respectively, while the latest observed hatch date was July 11th for both years (Fig. 9). The date with the highest occurrence of hatch was June 29th in 2018 and July 10th in 2019 (Fig. 10). Estimated spawning periods ran from June 10th to 28th, 2018 and from June 3rd to 27th, 2019, based on an estimated embryonic period of 156.5 degree days (Gagnon, 2005). Using the interpolated SST values for the study area, temperature at first hatch was estimated as being 7.3°C and 8.9°C in 2018 and 2019, respectively. The growth season was estimated to vary from June 26th to November 10th in 2018 and June 22nd to November 14th in 2019, based on back-calculated hatch dates and ice concentration data (Fig. 9).

Standard Length (SL) of larval smelt ranged from 5.15-11.20 mm in 2018 and 4.94-13.10 mm in 2019. Average otolith increment width was 2.05 (±0.175) µm while the average hatch mark diameter was 9.56 (±1.05) µm. Average length of Age-0 fish was 5.65 (±0.41) mm in 2018 and 5.70 mm in 2019. The observed growth rate of larval smelt averaged 0.532 $\text{mm}\cdot\text{d}^{-1}$ (Linear regression, R^2=0.83), while the back-calculated growth rate averaged 0.471 $\text{mm}\cdot\text{d}^{-1}$ (R^2=0.99) for data pooled from both seasons. The estimated length at hatch (y-intercept) was 6.2 mm from the observed growth rates and 6.3 mm from the back-calculated trajectories (Fig. 11).

Age and growth rate of adult smelt

A total of 201 adult smelt were collected during the recreational and subsistence fishery and 66 during gill net surveys in 2019 and 2020. The age of adult smelts ranged from 1 to 8 years and, at 1.2%, the aging precision between independent readings was high (Campana, 1990). A linear relationship between fish length and otolith length was observed over the size distribution (Fig. 12) and can be used for growth back-calculation. The overall fitted linear regression ($P<0.001$, r2=0.88) was:

$$Len = 0.94 + 0.0327(Oto)$$

where *Len* is fork length (mm) and *Oto* is otolith length (µm). A biological intercept of Len=50 mm and Oto=1500 µm would be reasonable if the Biological Intercept method were to be used for growth back-calculation. Back-calculations to the early larval stage however, is not recommended as growth during this period exhibits a curvilinear relationship between fish length and otolith radius (Sirois & Dodson, 2000). The A_{50} for both combined sexes was 3.47 years and the L_{50} for both combined sexes was 131 mm (Fig. 13).

There was a clear check observed at a mean (±SE) otolith diameter of 1105±19 µm on fish aged as 1-year-old, but not on older fish (aged 2-8 years). We assumed that this check had merged distally with the first annulus in older fish. However, if this assumption were proven false then one year must be subtracted from all fish aged 2 or older. To validate this assumption, we attempted to collect age validation protocol for this species as well as known young-of-year fish from around the time of annulus formation with the intention of using their otolith radius as the expected diameter of the first true annulus in older fish (Campana, 2001). Unfortunately, we were unsuccessful in securing these data for the current study, but recommend this approach for future research. Given that translucent zones typically form during the winter; the decision was made to count translucent edges as annuli on all fish sampled during the winter months. However, translucent margins were also present on some otoliths collected in the summer and fall. Where this translucent edge was clear, it was counted as an annulus. Yet, translucent edges were present in a small percentage (9%) of samples collected during summer and fall, and thus do not influence our overall conclusions.

Visual inspection of VBGF plots revealed clear sex differences in length-at-age and growth rate, occurring near the age of maturation (Fig. 14). Female average fork length was larger than that of males' for each age cohort after A_{50}. Thus, VBGF curves varied between males and females, with female L_∞=243.6, K=0.212 and $t_0=0.581$, and male L_∞=186.9, K=0.358 and t_0=0.274.

GSI varied by sex and time of year. In August, mean GSI (±SD) was 0.58 (±0.45) % increasing to 2.525 (±0.740) % in September, 14.80 (±2.17) % in February and 17.97 (±2.07) % in March for females, while males showed less variability with mean GSI being 0.59 (±0.26) % in August, 3.07 (±0.583) % in September, 2.25 (±0.599) % in February and 2.523 (±0.381) % in March (Fig. 15). Aged 1 juveniles and spent adults were only collected in August. Both males and females displayed asymmetry in size and location of the gonads. Fulton's condition factor ranged between 0.51 and 0.65, with a mean of 0.583 (±0.065) for individuals aged as 3 years or older (older that age of maturity). Individuals aged 1 and 2 years (younger than age of maturity) had an average factor of 0.388 (±0.095).

2.4 Discussion

Ecology of rainbow smelt at the northernmost limit of their range

Rainbow smelt hatch later within Lake Melville compared to southern regions. For comparison, in Lake Champlain, the St. Lawrence Estuary, and Lake Michigan the hatch period begins as early as May (Simonin et al., 2016; Sirois & Dodson, 2000; Tin & Jude, 1983). In Lake Melville, the hatch period of rainbow smelt began in late June, which is comparable to dates reported in other Newfoundland populations, where the water is colder and seasonal sea-ice is present. For example, anadromous rainbow smelt in the Salmonier River (Latitude: 47° N) hatched from early June to late July (Bradbury et al., 2006). Similarly, the estimated spawning period for Lake Melville smelt began in early June for both sampling years compared to February and March at the southern extent of their distributoin range (Chase et al., 2019). Rainbow smelt are known to align their reproductive cycle with seasonal change in temperature (Ayer et al., 2005; Chase et al., 2019; O'Brien et al., 2012). For example, they time their spawning runs with spring ice breakup when temperatures reach 3-4℃ (O'Brien et al., 2012; Rupp, 1959), and first hatch occurs 10-32 days (Ayer et al., 2005) or an average of 156.5 degree days (Gagnon, 2005) after spawning. Thus, it is expected that populations in colder, more northern regions such as that of Lake Melville would see delays in these processes to times when conditions are more favourable for survival. Within Lake Melville, otolith back–calculation also revealed that smelt hatching period began 4 days earlier in 2019, when SST was approximately 3 degrees higher, than in 2018. Given that incubation period is strongly correlated with temperature (Gagnon, 2005), these results are to be expected.

Rainbow smelt larvae exhibit faster growth than most other southern populations in North America. Studies conducted within Lake Huron and the St. Lawrence Estuary recorded growth rates ranging from 0.16 to 0.35 mm·d^{-1} (O'Brien et al., 2012; Sirois & Dodson, 2000). Our results were comparable to those of smelt larvae from Lake Champlain, where Simonin et al., (2016) observed an average growth rate of 0.57 mm·d^{-1}. Because rapid growth is believed to occur when surpassing some minimum size threshold decreases the risk of mortality (Arendt & Reznick, 2005), variability in larval smelt growth across regions is likely due to different selective pressures (Sirois & Dodson, 2000). A shorter growth season within Lake Melville, coupled with selection for a maximal size for overwinter survival, likely selects for faster growth during the larval stage (Conover & Present, 1990). With the early onset of ice formation in Labrador (Nov 10-14), Lake Melville smelt larvae have a shorter window for attaining a suitable size (ca. 111 days post-hatch), which is critical for survival and subsequent recruitment (Arendt & Reznick, 2005; Sirois & Dodson, 2000).

Larger and faster growing larvae are less susceptible to risk of predation, starvation and dispersion from favorable nursery habitats (Sirois & Dodson, 2000) suggesting that factors such as predation, food availability or drift may contribute to the fast growth of larvae. For example, Arendt & Reznick (2005) found that in high predation, high resource areas, fast growth was selected for in guppies (*Poecilia reticulata*), whereas in low predation, low resource areas selection for slower growth occurred. Within Lake Melville, rainbow smelt larvae aggregate near the pycnocline in summer, where zooplankton abundance is also high (Tiffany Small, Memorial University, unpublished data). The high growth rates of larvae in the Lake Melville System may thus indicate a surplus of available energy resources (Sirois & Dodson, 2000), and the strong stratification of the lake may provide an abundance of prey for smelt larvae after yolk reabsorption. Additionally, Lake Melville smelt have a suit of predators including birds, salmonids and gadids (McCarthy, 2009), and fast growth may be selected for as size refuge from these predators (Arendt & Reznick, 2005). Future research should aim to understand how predator-prey interactions influence growth of larval smelt, including within Lake Melville.

Since temperature is an important driver for metabolic rate, somatic growth, developmental time and subsequent ontogenetic transitions (i.e. metamorphosis and maturation) (Angilletta, 2009), variations in growth and maturation across the rainbow smelt's entire geographic range are likely due to variation in thermal gradients (Trip et al., 2014). Typically, age and size at maturation increase with decreasing temperature (Kuparinen et al., 2011), thus it is expected that these life history traits will occur later at the northern extent of the smelt's range, where temperatures are colder and metabolic rates are slower. In contrast to larval smelt, adult smelt grew slower than more southern populations; living longer and achieving comparable sizes to that of the average maximum length in North America over a longer period of time (see table 1 in Chase et al., 2019). Lake Melville smelt reached fork lengths of up to 221 mm and ages of up to 8 years, whereas more southern populations achieved similar lengths in roughly 3-4 years (Chase et al., 2019). Our findings on the age of maturity were consistent with previous reports suggesting that Lake Melville smelt mature after the age of 3, with a L_{50} of approximately 131 mm (McCarthy, 2009). In contrast, spawning runs in more southern regions have been comprised of individuals as young as 1 year, with a length of maturity of 126 mm (Chase et al., 2019; O'Malley et al., 2017). Fulton's condition factor showed similar trends to that of Chase et al., (2019), ranging between 0.5 and 0.65 for mature individuals and less than 0.5 for immature individuals. Our observations thus support the body of evidence suggesting that rainbow smelt follow the Temperature-Size Rule.

Potential effects from climate and anthropogenic change

The abundance of larvae within Lake Melville was higher at locations with lower temperature (8.0℃ in 2018 and 9.5℃ in 2019, respectively). This possibly suggests that larval survival was higher at stations with lower temperatures and would be consistent with rainbow smelt being a cold-water species that inhabits waters ranging from 9 to14℃ (Ayer et al., 2005). However, Ayer et al., (2005) observed that rainbow smelt reared *in vitro* had similar survival rates across a wide range of temperatures (5 to 20℃). As larvae were only a few days old and not yet motile, they potentially occupied the different sampling stations due to drift rather than active preference. The variation in abundance between stations could also be driven by variation in predator and prey abundance rather than direct physiological impact on smelt larvae ((Cushing, 1990; Houde, 2008; Simonin et al., 2016)). Alternatively, temperature may not be determining abundance through survival and variation in larval abundance may be driven by differing spawning locations.

With the Lake Melville region experiencing a warm weather anomaly since the 1990's (Finnis & Bell, 2015; Kamula, 2020), climate change could negatively impact larval growth, which could have implications on larval survival and subsequent recruitment (Cushing, 1969, 1990; Hjort, 1914; Houde, 2008; Iles & Sinclair, 1982; Miller et al., 1988). Larval growth has been shown to increase with an increase in temperature (Ayer et al., 2005) and the warmer climate may improve growth of rainbow smelt larvae. That being said, it may be possible that rainbow smelt will adapt to some extent to warmer waters if food availability remains adequate at those temperatures.

In addition to climate change, the operation of the Muskrat Falls hydroelectric dam has the potential to modify the spatial and temporal thermal regime of the downstream Lake Melville. For example, Archer (2008) observed a thermal influence from the Kielder Dam, UK, as far as 60 km downstream from the main reservoir with temperatures being lower than normal in the spring and summer but higher than normal in the fall. This cold water intrusion during the larval growth stage may decrease the rate at which larvae grow increasing their susceptibility to size-selective mortality. Hydropeaking within the Churchill River may lead to the potential shortening of ice cover within Lake Melville (McCarthy, 2009) and may also cause a dampening of temperature variability (lower summer maxima, higher winter minima) (Casado et al., 2013; Clarke et al., 2008). This change to the natural hydrography may impact the timing of life history processes that rely on thermal/salinity cues (i.e. migration and spawning) (Clarke et al., 2008). The impacts on Lake Melville rainbow smelt due to thermal and flow regime shifts could range from a subtle alteration in timing of life history processes to possible physiological changes (i.e. oocyte and germ cell development, growth rate) (Li et al., 2021).

2.5 Conclusion

The rainbow smelt population of upper Lake Melville is well adapted to the cold environment and short productive period prevailing at high latitudes. It exhibits a faster growth rate during the larval stages but a lower growth rate, older age at maturity and longer life span than southern populations. We observed higher larval abundance at lower temperatures, which suggests that climate warming could negatively impact the abundance of rainbow smelt in the region. We also observed no significant difference in larval abundance within Lake Melville between 2018 and 2019, despite being more saline in 2018 (4.12 (± 3.1)) and warmer in 2019 (11.4 (± 1.4) ℃), which may indicate a certain level of resilience to fluctuations in temperature and salinity. However, since temperature has been known to influence growth (Ayer et al., 2005), and larval growth has been hypothesized as being a major influence on mortality and recruitment (Cushing, 1969, 1990; Hjort, 1914; Houde, 2008; Iles & Sinclair, 1982; Miller et al., 1988), variation in temperature my lead to subsequent impacts on larval survival. However, the negative climate impacts could be dampened by plasticity in the ecology of the species, which is well adapted to a large variation of temperatures over its distribution range. The new hydroelectric facility could also contribute to changes in growth and subsequent abundance by reducing the gradient of the strong pycnocline where both smelt larvae and zooplankton prey accumulate. In any case, any change that may indirectly impact larval survival and, ultimately, recruitment, of rainbow smelt in Lake Melville would have cascading impacts on the whole ecosystem as the species funnels energy between zooplankton and higher order predators (i.e. salmonids, seals, seabirds) (Dobosenski, 2020). Although we do not predict negative impacts to rainbow smelt populations in the short- to mid-term based on our results, it is critical to continue monitoring the physiology and abundance of rainbow smelt in upper Lake Melville for any confounding factors that could impact rainbow smelt populations.

Chapter 3: General Conclusion

Larval rainbow smelt are well adapted to the variable environmental conditions and short productive period that prevail within Lake Melville. They exhibit a faster growth rate than more southern populations, which is likely selected for because of a shorter growth season and a minimum size requirement for overwinter survival. However, other mechanisms may also contribute to fast larval growth, such as a surplus of available prey within the low salinity surface layer or high predation pressure (size-selective mortality). With limited age data having been collected from 2018, no conclusion can be drawn as to the impacts that varying temperatures and salinities have on larval growth. However, previous research suggests that in warmer, less saline conditions, larval smelt grow faster than in colder more saline conditions (Ayer et al., 2005). The data presented herein do, however, provide important baseline information, which can be used to assess the survival of larvae in the future. For example, Small et al., (in preparation) found that the spring bloom, indicated by relative concentrations of chlorophyll-*a*, occurred in early June in 2020. High chlorophyll-*a* concentrations persisted until mid-July. High chlorophyll-*a* concentrations have been linked to increases in overall zooplankton biomass (Lyngsgaard et al., 2017). Therefore, if we assume that previous years were characterized by similar peaks in relative chlorophyll-*a* concentrations, then our data suggest that rainbow smelt hatch coincides with a period of high prey abundance.

The operation of the Muskrat falls dam may shorten the ice period and lessen temperature variability within Lake Melville, which could have impacts on the timing of life history processes such as spawning and hatching as well as prey availability due to destabilization of the strong pycnocline (Durkalec et al., 2016; McCarthy, 2018). If prey-driven mechanisms, such as those proposed by Hjort (1914) and Cushing (1969), impact the survival of larvae then a decline in primary and secondary productivities or alteration to the temporal overlap between the spring bloom and hatching period would be expected to negatively impact survival of smelt. Our findings also suggest that larval rainbow smelt grow faster in Lake Melville than in more southern regions. The expected influx of colder, saltier waters during the summer months due to Muskrat falls operation may not impact larval survival directly, but may decrease growth rates of larvae, leading to increased susceptibility to predation and starvation (Ayer et al., 2005). If size-selective mechanisms, such as those proposed by Miller (1988) and Cushing (1990), were the main driver for survival then a slowing of larval growth rates may negatively impact survival of smelt within Lake Melville. Thus, this baseline information on timing of life history processes and growth is important for future work aimed at assessing how these factors drive survival of larval smelt within Lake Melville. Although it is currently unclear what impacts the Muskrat Falls dam will have on survival, our data suggest larval rainbow smelt have a certain level of tolerance to fluctuations in temperature and salinity, as abundance was not significantly different between 2018 and 2019, despite being 1.5 ℃ warmer in 2019 and 2.9 pss saltier in 2018.

Growth and maturity of rainbow smelt follows the temperature size rule, which states that in more northern, colder climates, exothermic fish experience slower growth rates and later maturation (Forster & Hirst, 2012). Our findings are also similar to those of previous studies conducted within Lake Melville, which found that rainbow smelt ranged in age from 1 to 8 years and matured after the age of 3 (McCarthy, 2018). Furthermore, our asymptotic lengths of 231.5 mm and 182.1 mm for females and males respectively, were similar to that of other studies across North America (Chase et al., 2019). It is unclear how the operation of a new hydroelectric dam and climate change will impact the growth, maturation and age structure of Lake Melville rainbow smelt, but given that they show plasticity in these processes across their entire geographic range, Lake Melville smelt may be capable of adapting to a changing environment within the estuary, at least within the coming years.

The back-calculated hatch period showed a correlation with temperature, beginning earlier in June 2019, when temperatures were warmer (7.9℃ vs. 5.2℃). Given that temperature impacts the timing of key life history events such as spawning and migration, the operation of a new hydroelectric dam in the region, which could result in colder and saltier waters entering the estuary in spring-summer, is expected to delay ice-break up by approximately one week (McCarthy, 2009). This delay in warm-up and subsequent ice break-up may lead to subtle shifts in spawning and hatching timings to periods where temperatures are warmer, and later in the season.

Due to the plasticity in life history and physiological processes that rainbow smelt exhibit across their entire geographic range, a single population cannot be used to inform management practices for another. Thus, insights into the regionally specific processes that drive recruitment, growth and survival are key for the development of a management framework for that region. Future research should aim to use stomach content analysis of both smelt and their predators, to assess predator-prey interactions within this system and how these relationships contribute to the perceived fast growth of larval rainbow smelt. Furthermore, it is critical to continue monitoring the ontogeny and abundance of rainbow smelt in upper Lake Melville in response to the operation of Muskrat Falls Project. By continuing to monitor the hydrography of Lake Melville and collect information on growth and timing of life history processes in rainbow smelt, a longer time series containing pertinent information on their response to changes in environmental conditions may emerge, setting the framework for future management practices.

In the future, studies such as this should aim to sample larval smelt over a longer portion of the growing season to allow for more comprehensive growth rate analyses. It is likely that, with a longer sampling period, representatives from the entire hatching period would have been collected. Thus, information on variation in growth as it pertains to early and late hatching larvae as well as variation in growth during the larval stage in general could have been assessed. Future studies should also include turbidity measures (i.e. concentration of suspended sediments) in spring-summer in their analysis as it has been suggested that within the estuarine turbidity maximum (i.e. where suspended particle concentrations are highest) larval smelt abundance is highest as it provides refuge from predators while not adversely impacting feeding success (Sirois & Dodson, 2000).

This study provides baseline information which can be referenced in future studies examining the impact of hydroelectric dam operation on the life history of rainbow smelt and, in turn, ecosystem health more broadly, due to the species' ecological importance. These data also contribute to the relative scarcity of information on the life history processes and growth of rainbow smelt in this region.

References

Angilletta Jr, M. (2009). *Thermal adaptation: A theoretical and empirical synthesis* (1st ed.). Oxford University Press.

Archer, D. (2008). *The influence of river regulation at Kielder Water on the thermal regime of the River North Tyne*. BHS 10th National Hydrology Symposium, Exeter University.

Arendt, J. D., & Reznick, D. N. (2005). Evolution of juvenile growth rates in female guppies (Poecilia reticulata): Predator regime or resource level? *Proceedings of the Royal Society B: Biological Sciences*, *272*(1560), 333–337. https://doi.org/10.1098/rspb.2004.2899

Ayer, M., Benton, C., King, W., Kneebone, J., Elzey, S., Toran, M., Grange, K., & Berlinsky, D. (2005). Development of Practical Culture Methods for Rainbow Smelt Larvae. *North American Journal of Aquaculture*, *67*(3). https://doi.org/10.1577/A04-064.1

Bakun, A. (2006). Wasp-waist populations and marine ecosystem dynamics: Navigating the "predator pit" topographies. *Progress in Oceanography*, *68*(2–4), 271–288. https://doi.org/10.1016/j.pocean.2006.02.004

Bengtsson, L., Herschy, R. W., & Fairbridge, R. W. (Eds.). (2012). *Encyclopedia of Lakes and Reservoirs*. Springer Netherlands. https://doi.org/10.1007/978-1-4020-4410-6

Bobbit, J., & Akenhead, S. (1982). *Influence of Controlled Discharge from the Churchill River on the Oceanography of Groswater Bay, Labrador* (No. 1097). Government of Canada, Fisheries and Oceans.

Boldt, J. L., Thompson, M., Rooper, C. N., Hay, D. E., Schweigert, J. F., Quinn II, T. J., Cleary, J. S., & Neville, C. M. (2019). Bottom-up and top-down control of small pelagic forage fish: Factors affecting age-0 herring in the Strait of Georgia, British Columbia. *Mar Ecol Prog Ser*.

Bouchard, C., Charbogne, A., Baumgartner, F., & Maes, S. M. (2021). West Greenland ichthyoplankton and how melting glaciers could allow Arctic cod larvae to survive extreme summer temperatures. *Arctic Science*, *7*(1), 217–239. https://doi.org/10.1139/as-2020-0019

Bradbury, I. R., Campana, S. E., & Bentzen, P. (2008). Otolith elemental composition and adult tagging reveal spawning site fidelity and estuarine dependency in rainbow smelt. *Marine Ecology Progress Series*, *368*. https://doi.org/10.3354/meps07583

Bradbury, I. R., Campana, S. E., Bentzen, P., & Snelgrove, P. V. R. (2004). Synchronized Hatch and Its Ecological Significance in Rainbow Smelt Osmerus mordax in St. Mary's Bay, Newfoundland. *Limnology and Oceanography*, *49*.

Bradbury, I. R., Gardiner, K., Snelgrove, P. V. R., Campana, S. E., Bentzen, P., & Guan, L. (2006). Larval transport, vertical distribution, and localized recruitment in anadromous rainbow smelt (*Osmerus mordax*). *Canadian Journal of Fisheries and Aquatic Sciences*, *63*(12), 2822–2836. https://doi.org/10.1139/f06-164

Braga, H. O. (2020). The role of local ecological knowledge for the conservation and sustainable fisheries of the sea lamprey (Petromyzon marinus Linnaeus, 1758) in the Iberian Peninsula. *Ocean and Coastal Management*, *198*, 13.

Campana, S. E. (1990). How Reliable are Growth Back-Calculations Based on Otoliths? *Canadian Journal of Fisheries and Aquatic Sciences*, *47*(11), 2219–2227. https://doi.org/10.1139/f90-246

Campana, S. E. (2001). Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. *Journal of Fish Biology*, *59*(2). https://doi.org/10.1111/j.1095-8649.2001.tb00127.x

Campana, S. E., Zwanenburg, K. C. T., & Smith, J. N. (1990). ^{210} Pb/ ^{226} Ra Determination of Longevity in Redfish. *Canadian Journal of Fisheries and Aquatic Sciences*, *47*(1), 163–165. https://doi.org/10.1139/f90-017

Casado, A., Hannah, D. M., Peiry, J.-L., & Campo, A. M. (2013). Influence of dam-induced hydrological regulation on summer water temperature: Sauce Grande River, Argentina: Dam effects on summer river temperature. *Ecohydrology*, *6*(4), 523–535. https://doi.org/10.1002/eco.1375

Chase, B. C., Elzey, S. P., turner, S. M., & Ayer, M. H. (2019). Fecundity and reproductive life history of anadromous rainbow smelt (Osmerus mordax) in coastal waters of Massachusetts. *Fisheries Bulletin*, *117*.

Clarke, K. D., Pratt, T. C., Randall, R. G., & Smokorowski, K. E. (2008). *Validation of the Flow Management Pathway: Effects of Altered Flow on Fish Habitat and Fishes Downstream from a Hydropower Dam.* (Canadian Technical Report of Fisheries and Aquatic Sciences 2784, p. 118). Fisheries and Oceans Canada.

Conover, D. O., & Present, T. M. C. (1990). Countergradient variation in growth rate: Compensation for length of the growing season among Atlantic silversides from different latitudes. *Oecologia*, *83*(3), 316–324. https://doi.org/10.1007/BF00317554

COSEWIC. (2018). *COSEWIC Assessment and Status Report on the Rainbow Smelt Osmerus mordax, Lake utopia large-bodied population and the Lake Utopia small-bodied population, in Canada* (p. 54). Committee on the Status of Endangered wildlife in Canada. http://www.registrelepsararegistry.gc.ca/default.asp?lang=en&n=24F7211B-1

Couillard, C. M., Ouellet, P., Verreault, G., Senneville, S., St-Onge-Drouin, S., & Lefaivre, D. (2017). Effect of Decadal Changes in Freshwater Flows and Temperature on the Larvae of two Forage Fish Species in Coastal Nurseries of the St. Lawrence Estuary. *Estuaries and Coasts*, *40*(1), 268–285. https://doi.org/10.1007/s12237-016-0144-7

Cury, P., Bakun, A., Crawford, R. J. M., Jarre, A., Quinones, R. A., Shannon, L. J., & Verheye, H. M. (2000). Small pelagics in upwelling systems: Patterns of interaction and structural changes in ‘‘wasp-waist’’ ecosystems. *Journal of Marine Sciences*, *57*, 16.

Cushing, D. H. (1969). The regularity of the spawning season in some fishes. *J. Cons. Int. Explor. Mer*, *33*, 81–92.

Cushing, D. H. (1990). Plankton Production and Year-class Strength in Fish Populations: An Update of the Match/Mismatch Hypothesis. In *Advances in Marine Biology* (Vol. 26, pp. 249–293). Elsevier. https://doi.org/10.1016/S0065-2881(08)60202-3

Dobosenski, J. A. (2020). Investigating population genetics of invasive rainbow smelt in the Great Lakes Region. *Journal of Great Lakes Research*, *46*, 382–390.

Driedzic, W. R., & Ewart, K. V. (2004). Control of glycerol production by rainbow smelt (Osmerus mordax) to provide freeze resistance and allow foraging at low winter temperatures. *Comparative Biochemistry and Physiology Part B: Biochemistry and Molecular Biology*, *139*(3), 347–357. https://doi.org/10.1016/j.cbpc.2004.04.007

Drinkwater, K. F., & Frank, K. T. (1994). Effects of river regulation and diversion on marine fish and invertebrates. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *4*(2). https://doi.org/10.1002/aqc.3270040205

Durkalec, A., Sheldon, T., & Bell, T. (2016). *Lake Melville: Avativut, Kanuittailinnivut (our environment, our health)*. Scientific Report. Nain, NL. Nunatsiavut Government.

Dyer, K. (2001). Estuarine Circulation. In *Encyclopedia of Ocean Sciences* (pp. 846–852). Elsevier. https://doi.org/10.1006/rwos.2001.0077

Enterline, C. L., Chase, B. C., Carloni, J. M., & Mills, K. E. (2012). Anadromous Rainbow Smelt in the U.S. Gulf of Maine. *Maine Department of Marine Resources*, 100.

Enterline, C. L., Elzey, S. P., Chase, B. C., & Ayer, M. H. (2020). Quantifying Within-Season Repeat Spawning by Rainbow Smelt with Implications for Comparing Sex Ratios and Survey Catches among Runs. *Transactions of the American Fisheries Society*, *149*, 27–42.

Fahay, M. P. (2007). *Early Stages of Fishes in the Western North Atlantic Ocean* (Vol. 1).

Feiner, Z. S., Bunnell, D. B., Höök, T. O., Madenjian, C. P., Warner, D. M., & Collingsworth, P. D. (2015). Non-stationary recruitment dynamics of rainbow smelt: The influence of environmental variables and variation in size structure and length-at-maturation. *Journal of Great Lakes Research*, *41*(1), 246–258. https://doi.org/10.1016/j.jglr.2014.11.029

Finnis, J., & Bell, T. (2015). An analysis of recent observed climate trends andvariability in Labrador. *The Canadian Geographer*, *59*(2). https://doi.org/10.1111/cag.12155

Forster, J., & Hirst, A. G. (2012). The temperature-size rule emerges from ontogenetic differences between growth and development rates: Ontogenetic differences between growth and development rates. *Functional Ecology*, *26*(2), 483–492. https://doi.org/10.1111/j.1365-2435.2011.01958.x

Fuller, M. R., Doyle, M. W., & Strayer, D. L. (2015). Causes and consequences of habitat fragmentation in river networks: River fragmentation. *Annals of the New York Academy of Sciences*, *1355*(1). https://doi.org/10.1111/nyas.12853

Gagnon, K. (2005). *Distribution et abondance des larves d'éperlan arc-en-ciel (Osmerus mordax) au lac Saint-Jean /*. Université du Québec à Chicoutimi. https://doi.org/10.1522/24115225

Geyer, W. R., Trowbridge, J. H., & Bowen, M. M. (2000). The Dynamics of a Partially Mixed Estuary*. *Journal of Physical Oceanography*, *30*(8), 2035–2048. https://doi.org/10.1175/1520-0485(2000)030<2035:TDOAPM>2.0.CO;2

Hagstrøm Bucholtz, R., Tomkiewicz, J., & Dalskov, J. (2008). *Manual to determine gonadal maturity of herring (Clupea harengus L.)* (DTU Aqua-report 197-08; DTU Aqua-Report, p. 45). Charlottenlund: National Institute of Aquatic Resources.

Hanson, J. M., & Courtenay, S. C. (2020). Data Recovery from Old Filing Cabinets: Seasonal Diets of the Most Common Demersal Fishes in the Miramichi River Estuary (Atlantic Canada), 1991–1993. *Northeastern Naturalist*, *27*(3), 34.

Hjort, J. (1914). Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. *Rapp. P.-V. Reun. Cons. Int. Explo. Mer*, *20*, 1–228.

Hopkins, K. D. (1992). Reporting Fish Growth: A Review of the Basics. *Journal of the World Aquaculture Society*, *23*(3). https://doi.org/10.1111/j.1749-7345.1992.tb00766.x

Houde, E. D. (2008). Emerging from Hjort's Shadow. *Journal of Northwest Atlantic Fishery Science*, *41*, 53–70. https://doi.org/10.2960/J.v41.m634

Hunt, G. L., & McKinnell, S. (2006). Interplay between top-down, bottom-up, and wasp-waist control in marine ecosystems. *Progress in Oceanography*, *68*(2–4), 115–124. https://doi.org/10.1016/j.pocean.2006.02.008

Iles, T. D., & Sinclair, M. (1982). Atlantic Herring: Discreteness and Abundance. *Science*, *215*, 627–633. https://doi.org/doi:10.1126/science.215.4533.627

Kamula, C. M. (2020). Sediment and particulate organic carbon budgets of a subarctic estuarine fjard_ Lake Melville, Labrador. *Marine Geology*, *424*, 14.

Kope, R. G. (2001). Salmon Fisheries, Pacific. *Encyclobedia of Ocean Sciences*, *5*, 2461–2472.

Kovach, A. I. (2013). Identifying the spatial scale of population structure in anadromous rainbow smelt (Osmerus mordax). *Fisheries Research*, 12.

Krvavica, N., Gotovac, H., & Lončar, G. (2021). Salt-wedge dynamics in microtidal Neretva River estuary. *Regional Studies in Marine Science*, *43*, 101713. https://doi.org/10.1016/j.rsma.2021.101713

Kuparinen, A., Cano, J. M., Loehr, J., Herczeg, G., Gonda, A., & Merilä, J. (2011). Fish age at maturation is influenced by temperature independently of growth. *Oecologia*, *167*(2), 435–443. https://doi.org/10.1007/s00442-011-1989-x

L. Trip, E. D., Clements, K. D., Raubenheimer, D., & Choat, J. H. (2014). Temperature-related variation in growth rate, size, maturation and life span in a marine herbivorous fish over a latitudinal gradient. *Journal of Animal Ecology*, *83*(4), 866–875. https://doi.org/10.1111/1365-2656.12183

Laprise, R., & Dodson, J. J. (1989). Ontogenetic changes in the longitudinal distribution of two species of larval fish in a turbid well-mixed estuary. *Journal of Fish Biology*, *35*, 9.

Leclerc, V., Sirois, P., & Bérubé, P. (2011). Impact of forest harvesting on larval and juvenile growth of yellow perch (Perca flavescens) in boreal lakes. *Boreal Environment Research*, *16*, 417–429.

Leggett, W. C., & Deblois, E. (1994). Recruitment in Marine Fishes: Is it Regulated by Starvation and Predation in the Egg and Larval Stages? *Netherlands Journal of Sea Research*, *32*(2).

Li, M., Schartup, A. T., Valberg, A. P., Ewald, J. D., Krabbenhoft, D. P., Yin, R., Balcom, P. H., & Sunderland, E. M. (2016). Environmental Origins of Methylmercury Accumulated in Subarctic Estuarine Fish Indicated by Mercury Stable Isotopes. *Environ. Sci. Technol.*

Li, T., Mo, K., Wang, J., Chen, Q., Zhang, J., Zeng, C., Zhang, H., & Yang, P. (2021). Mismatch between critical and accumulated temperature following river damming impacts fish spawning. *Science of The Total Environment*, *756*, 144052. https://doi.org/10.1016/j.scitotenv.2020.144052

Lu, Z., deYoung, B., & Foley, J. (2013). *Physics and Physical Oceanography Data Report*. Memorial University of Newfoundland.

Lyngsgaard, M. M., Markager, S., Richardson, K., Møller, E. F., & Jakobsen, H. H. (2017). How Well Does Chlorophyll Explain the Seasonal Variation in Phytoplankton Activity? *Estuaries and Coasts*, *40*(5), 1263–1275. https://doi.org/10.1007/s12237-017-0215-4

McCarthy, J. (2009). *Habitat Qualification* (No. 3; Fish and Fish Habitat). AMEC Earth and Environment.

McCarthy, J. (2018). *Predicted Increases in Fish Methylmercury Muscle Tissue Concentrations in Goose Bay and Lake Melville* (p. 102). Wood Environment and Infrastructure Solutions.

McLusky, D. S., & Elliott, M. (2004). *The Estuarine Ecosystem: Ecology, Threats and Management* (3rd ed.). Oxford University Press.

Methylmercury Monitoring in the Muskrat Falls Reservoir, Churchill River, Goose Bay, Lake Melville. (n.d.). Environment and Climate Change. https://www.gov.nl.ca/ecc/methylmercury-mrf/

Miller, T. J., Crowder, L. B., Rice, J. A., & Marschall, E. A. (1988). Larval Size and Recruitment Mechanisms in Fishes: Toward a Conceptual Framework. *Canadian Journal of Fisheries and Aquatic Sciences*, *45*(9), 1657–1670. https://doi.org/10.1139/f88-197

Nielsen, S. L., Banta, G. T., & Pedersen, M. F. (Eds.). (2004). *Estuarine Nutrient Cycling: The Influence of Primary Producers: The Fate of Nutrients and Biomass*. Springer Netherlands. https://doi.org/10.1007/978-1-4020-3021-5

O'Brien, T. P., Taylor, W. W., Briggs, A. S., & Roseman, E. F. (2012). Influence of water temperature on rainbow smelt spawning and early life history dynamics in St. Martin Bay, Lake Huron. *Journal of Great Lakes Research*, *38*(4), 776–785. https://doi.org/10.1016/j.jglr.2012.09.017

O'Malley, A. J., Enterline, C., & Zydlewski, J. (2017). Size and Age Structure of Anadromous and Landlocked Populations of Rainbow Smelt. *North American Journal of Fisheries Management*, *37*(2), 326–336. https://doi.org/10.1080/02755947.2016.1264508

Pannella, G. (1971). Fish Otoliths: Daily Growth Layers and Periodical Patterns. *Science*, *173*(4002), 1124–1127. https://doi.org/10.1126/science.173.4002.1124

Paterson, G., Di Pierdomenico, L. L., & Haffner, G. D. (2020). Basin-Specific Pollutant Bioaccumulation Patterns Define Lake Huron Forage Fish. *Environmental Toxicology and Chemistry*, *39*(9), 1712–1723. https://doi.org/10.1002/etc.4794

Petts, G. E. (1984). Sedimentation within a regulated river. *Earth Surface Processes and Landforms*, *9*(2), 125–134. https://doi.org/10.1002/esp.3290090204

Possamai, B., Hoeinghaus, D. J., & Garcia, A. M. (2021). Environmental factors drive interannual variation in estuarine food-chain length. *Estuarine, Coastal and Shelf Science*, *252*, 107241. https://doi.org/10.1016/j.ecss.2021.107241

Puijenbroek, P. J. T. M., Buijse, A. D., Kraak, M. H. S., & Verdonschot, P. F. M. (2019). Species and river specific effects of river fragmentation on European anadromous fish species. *River Research and Applications*, *35*(1). https://doi.org/10.1002/rra.3386

Ramos, S., Cabral, H., & Elliott, M. (2015). Do fish larvae have advantages over adults and other components for assessing estuarine ecological quality? *Ecological Indicators*, *55*, 74–85. https://doi.org/10.1016/j.ecolind.2015.03.005

Rupp, R. S. (1959). Variation in the Life History of the American Smelt in Inland Waters of Maine. *Transactions of the American Fisheries Society*, *88*(4), 241–252. https://doi.org/10.1577/1548-8659(1959)88[241:VITLHO]2.0.CO;2

Samways, K. M., Soto, D. X., & Cunjak, R. A. (2018). Aquatic food-web dynamics following incorporation of nutrients derived from Atlantic anadromous fishes: Nutrients from anadromous fishes. *Journal of Fish Biology*, *92*(2), 399–419. https://doi.org/10.1111/jfb.13519

Schartup, A. T., Balcom, P. H., Soerensen, A. L., Gosnell, K. J., Calder, R. S. D., Mason, R. P., & Sunderland, E. M. (2015). Freshwater discharges drive high levels of methylmercury in Arctic marine biota. *Proceedings of the National Academy of Science of the United States of America*, 6.

Simonin, P. W., Parrish, D. L., Rudstam, L. G., Pientka, B., & Sullivan, P. J. (2016). Interactions between Hatch Dates, Growth Rates, and Mortality of Age-0 Native Rainbow Smelt and Nonnative Alewife in Lake Champlain. *Transactions of the American Fisheries Society*, *145*, 649–656.

Sirois, P., & Dodson, J. (2000). Critical periods and growth-dependent survival of larvae of an estuarine fish, the rainbow smelt Osmerus mordax. *Marine Ecology Progress Series*, *203*, 233–245. https://doi.org/10.3354/meps203233

Sirois, P., Lecomte, F., & Dodson, J. (1998). An otolith-based back-calculation method to account for time-varying growth rate in rainbow smelt (Osmerus mordax) larvae. *Canadian Journal of Fisheris and Aquatic Sciences*, *55*(12).

Small, T., Sutton, J., Clement, marie, Cyr, F., Bernatchez, L., McCarthy, J., & Geoffroy, M. (2021). How hydrology structures the abundance, distribution and ontogenic segregation of pelagic fish in a sub-arctic estuary. *In Prep*.

Stevenson, D. K., & Campana, S. E. (1992). *Otolith Microstructure Examination and Analysis* (Canadian Special Publication of Fisheries and Aquatic Sciences 117, p. 126). Fisheries and Oceans.

Stritzel Thomson, J. L., Parrish, D. L., Parker-Stetter, S. L., Rudstam, L. G., & Sullivan, P. J. (2011). Growth rates of rainbow smelt in Lake Champlain: Effects of density and diet: Growth rates of rainbow smelt. *Ecology of Freshwater Fish*, *20*(4), 503–512. https://doi.org/10.1111/j.1600-0633.2010.00472.x

Sun, Y. (2020). Disentangling effects of river inflow and marine diffusion in shaping the planktonic communities in a heavily polluted estuary. *Environmental Pollution*, 12.

Tin, H. T., & Jude, D. J. (1983). Distribution and Growth of Larval Smelt in Eastern Lake Michigan, 1978-198. *Transactions of the American Fisheries Society*, *112*, 517–524.

Vanalderweireldt, L., Winkler, G., Forget-Lacoursière, E. L., Mingelbier, M., & Sirois, P. (2020). Habitat use by early life stages of the re-established striped bass and conspecific fish species along the St.

Lawrence estuary. *Estuarine, Coastal and Shelf Science*, *237*, 106696. https://doi.org/10.1016/j.ecss.2020.106696

Wells, J. (2016). *Final Baseline Human Health Risk Assessment: Lower Churchill Hydroelectric Generation Project*. Dillon Consulting.

Wheeler, J. P., Purchase, C. F., Macdonald, P. D. M., Fill, R., Jacks, L., Wang, H., & Ye, C. (2009). Temporal changes in maturation, mean length-at-age, and condition of spring-spawning Atlantic herring (Clupea harengus) in Newfoundland waters. *ICES Journal of Marine Science*, *66*(8), 1800–1807. https://doi.org/10.1093/icesjms/fsp117

Figures

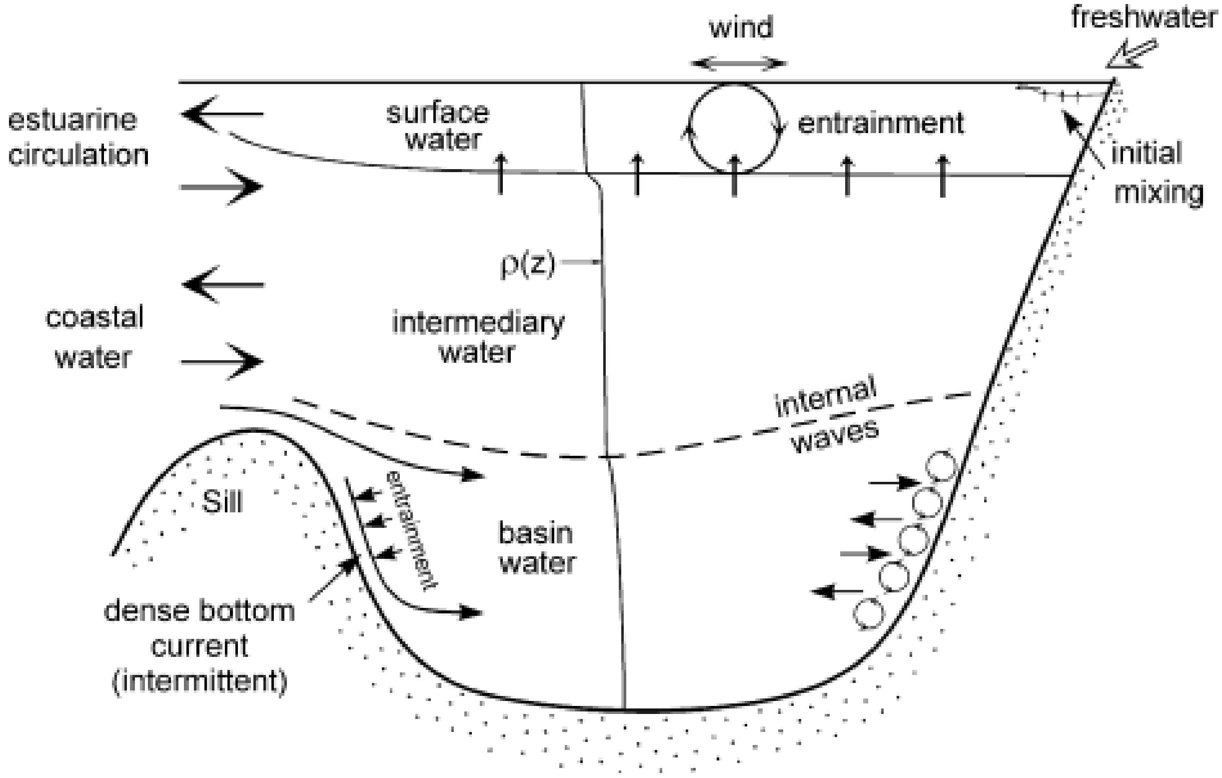

Figure 1. Water masses, physical processes, and circulation modes in fjords. The vertical density distribution is shown by ρ(z). Mixing in the basin water occurs essentially at the bottom boundaries (Bengtsson et al., 2012).

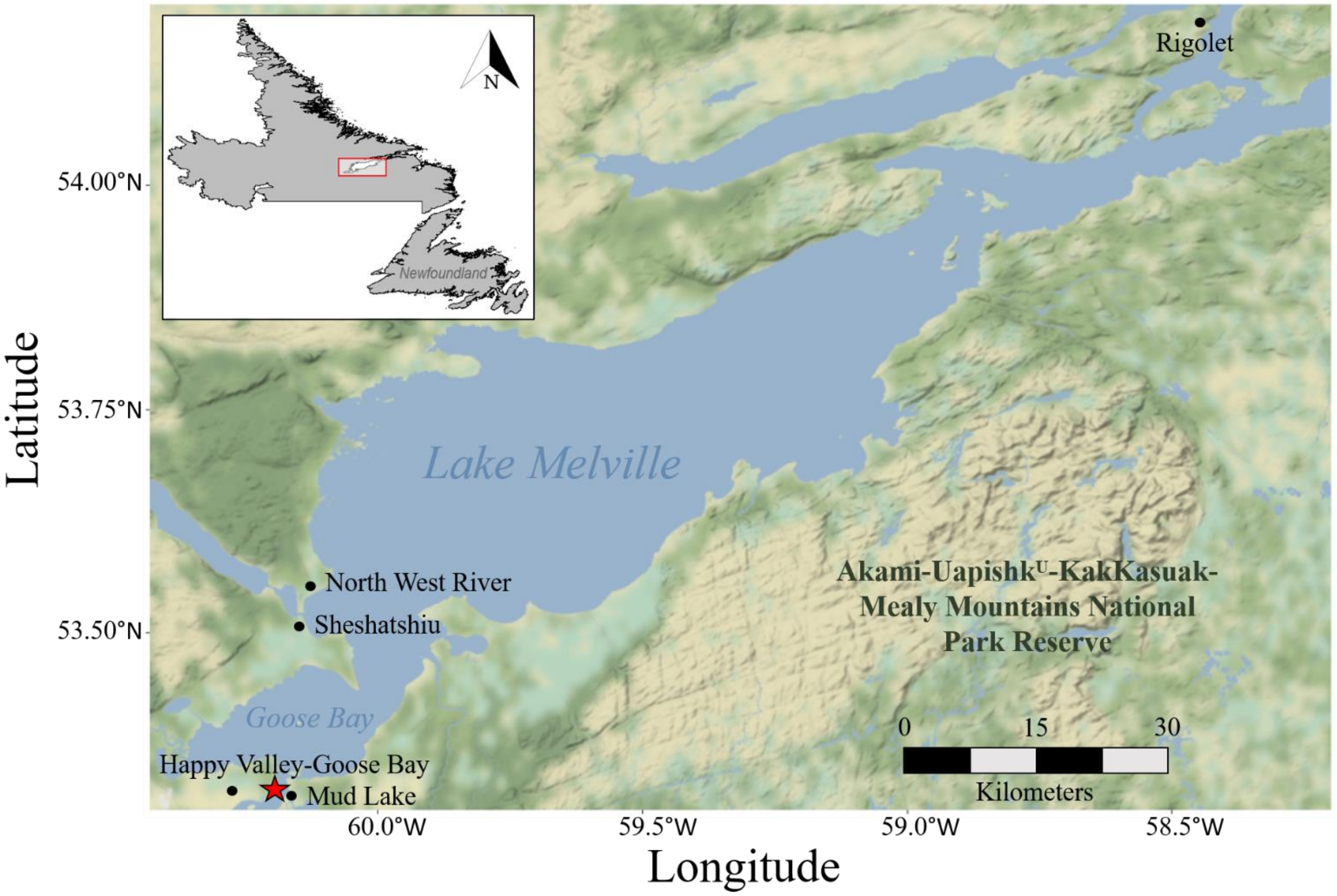

Figure 2. Map of Lake Melville, Labrador denoting the five local communities; Happy Valley-Goose Bay, Mud Lake, Sheshatshiu, North West River and Rigolet. The mouth of the Churchill River (red star) flows between Happy Valley-Goose Bay and Mud Lake. To the east of Lake Melville is the Mealy Mountains National Park Reserve.

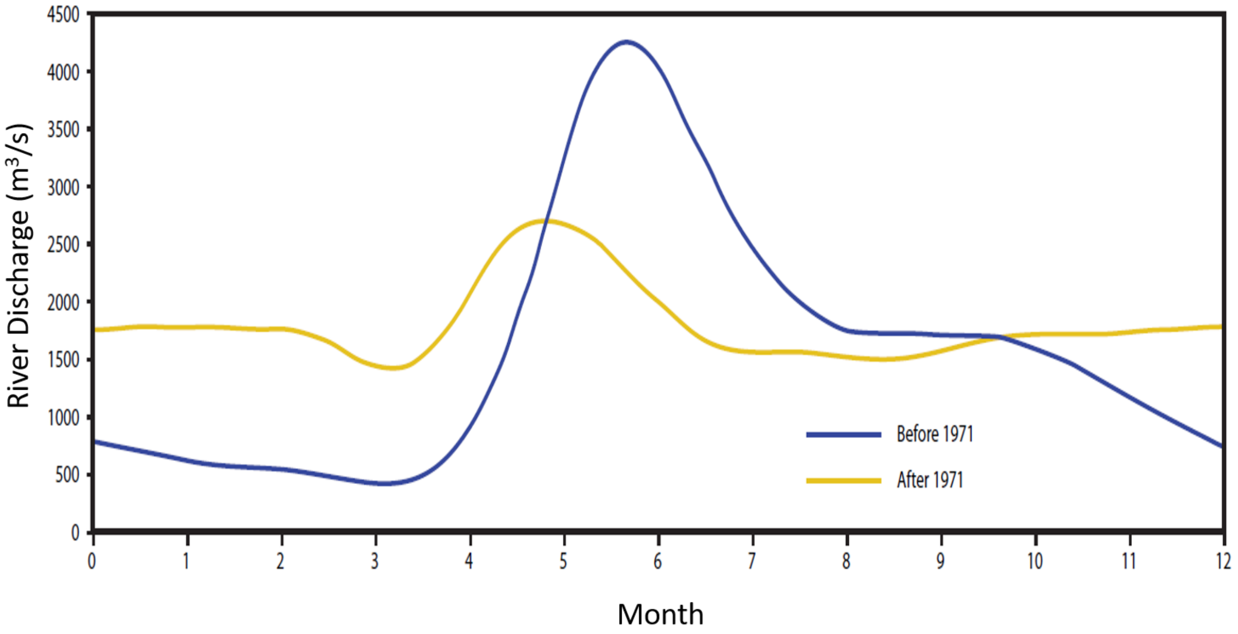

Figure 3. Variation in river discharge from the Churchill River due to the impact of the Upper Churchill hydroelectric facilities built in 1971. The figure shows the monthly mean Churchill River discharge calculated for two periods of time: before (blue curve) and after (yellow curve) 1971 (Durkalec et al., 2016).

Figure 4. Adult (top) and larval (bottom) rainbow smelt sampled from Lake Melville, Labrador, Canada.

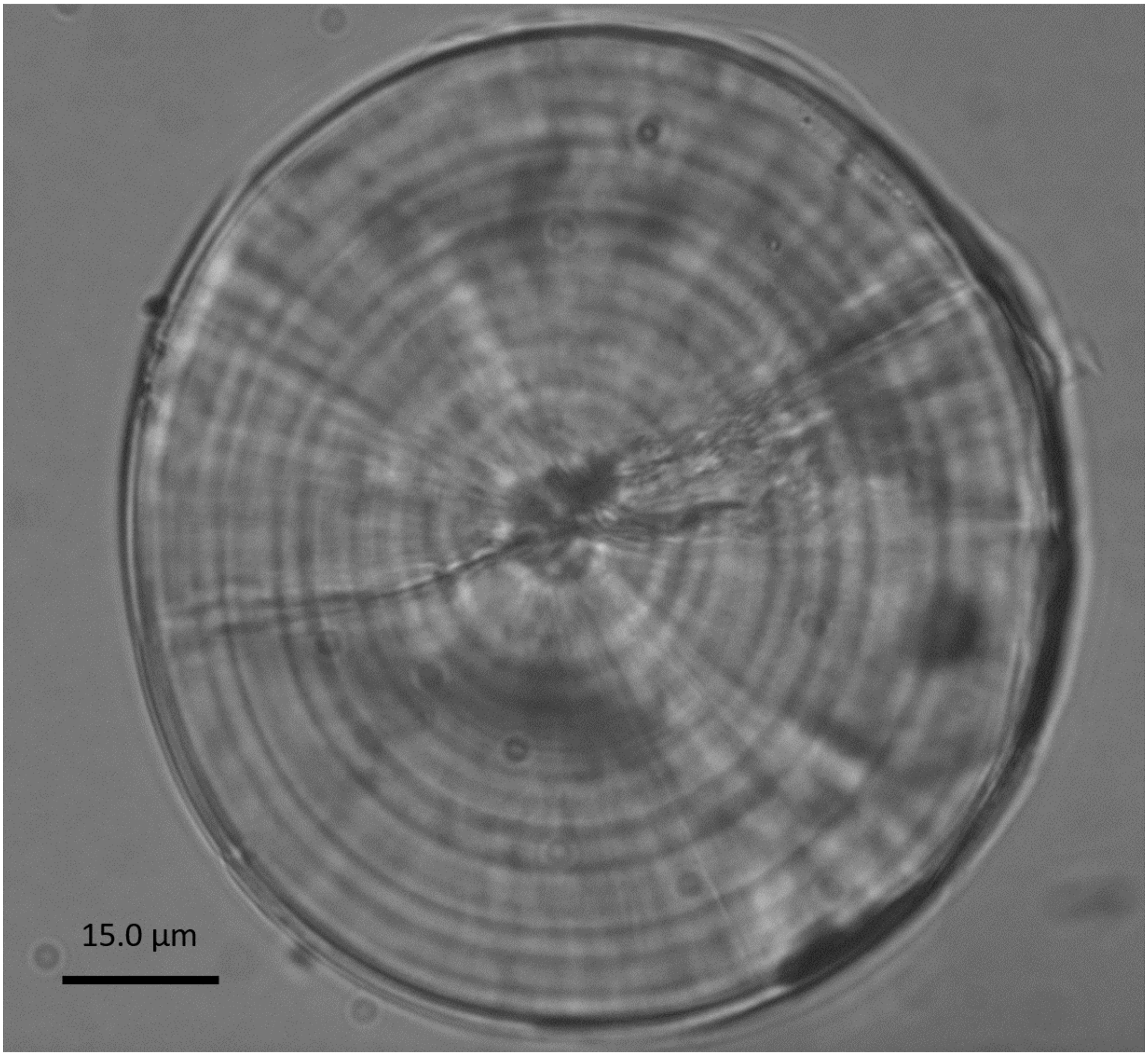

Figure 5. Larval rainbow smelt (RS007) otolith as viewed under a light microscope at 1000x magnification. This larva was 12.33 mm long and aged as 11 days old.

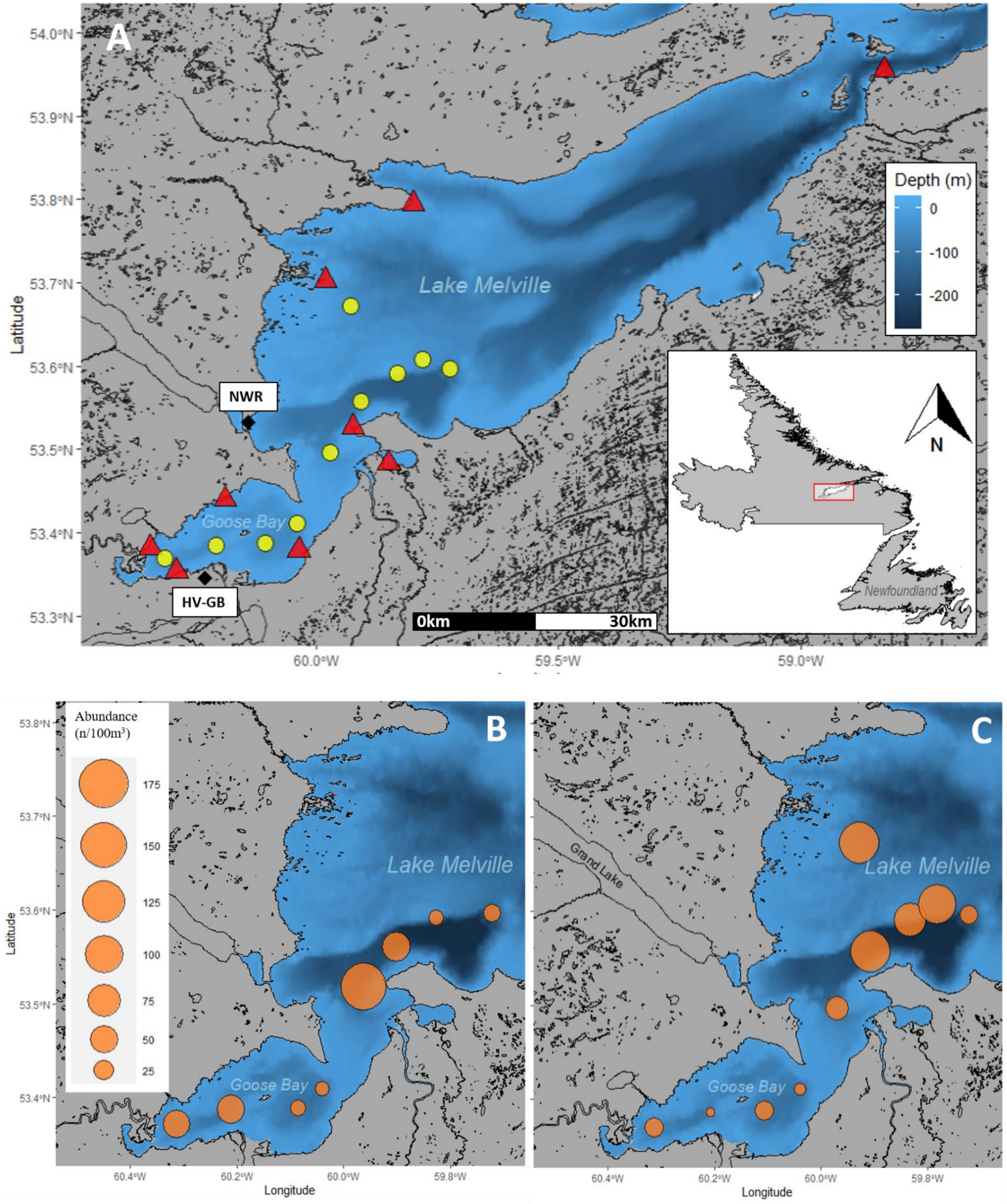
A
54.0°N
53.9°N
53.8°N
53.7°N
53.6°N
53.5°N
53.4°N
53.3°N
Latitude
Lake Melville
Goose Bay
NWR
HV-GB
Depth (m)
0
-100
-200
N
Newfoundland
0km
30km
60.0°W
59.5°W
59.0°W
B
Abundance (n/100m³)
175
150
125
100
75
50
25
53.8°N
53.7°N
53.6°N
53.5°N
53.4°N
Latitude
Lake Melville
Goose Bay
60.4°W
60.2°W
60.0°W
59.8°W
Longitude
C
Grand Lake
Lake Melville
Goose Bay
60.4°W
60.2°W
60.0°W
59.8°W
Longitude

Figure 6. (a) Map of Lake Melville, Labrador. Yellow circles represent stations where larval smelt were sampled (2018-2019) and red triangles represent stations where adult smelt were sampled (2019-2020); (b) Abundance of larval rainbow smelt by station in 2018; and (c) Abundance of larval rainbow smelt by station in 2019.

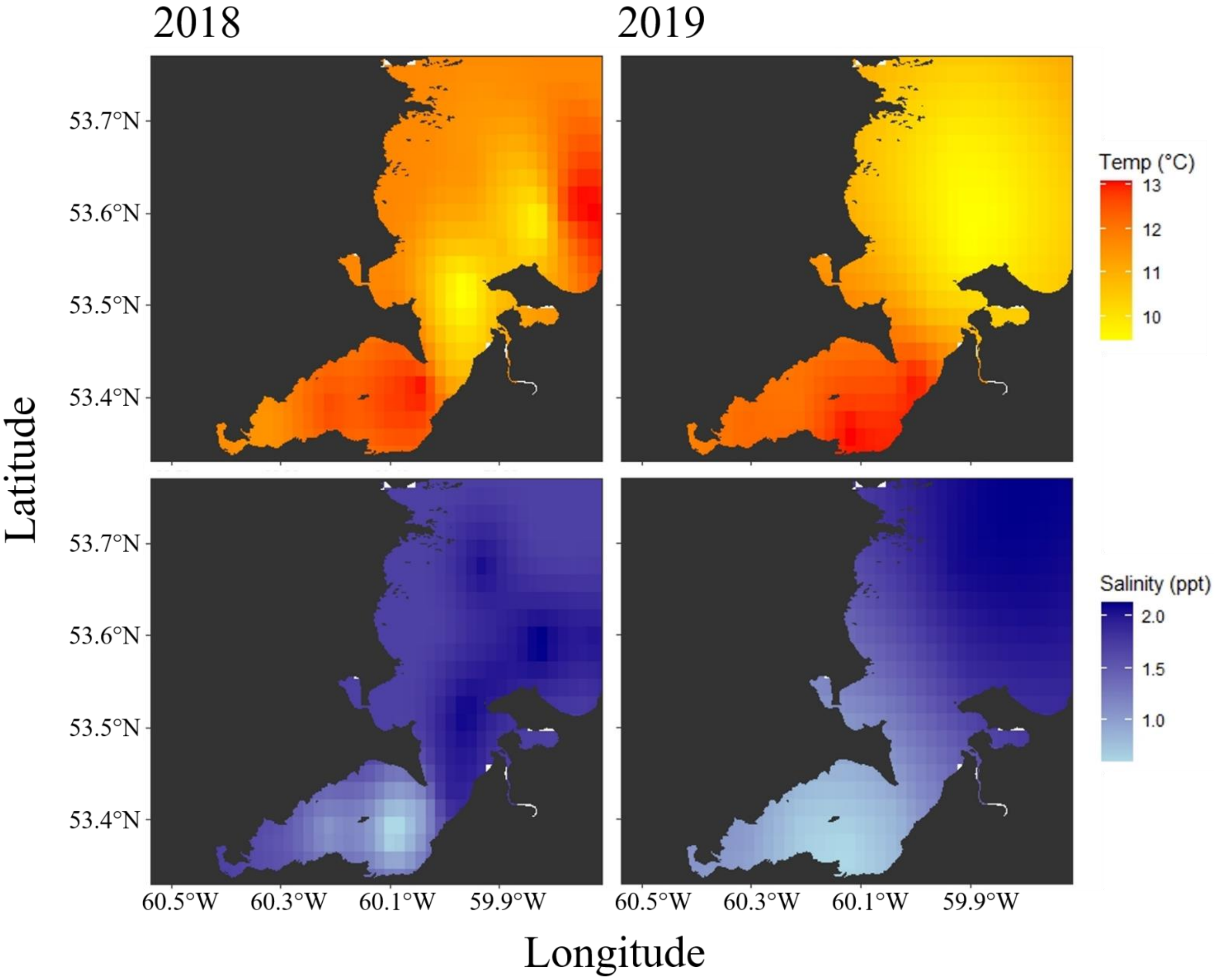

Figure 7. Surface temperature (top) and salinity (bottom) of Lake Melville and Goose Bay during field seasons in 2018 and 2019.

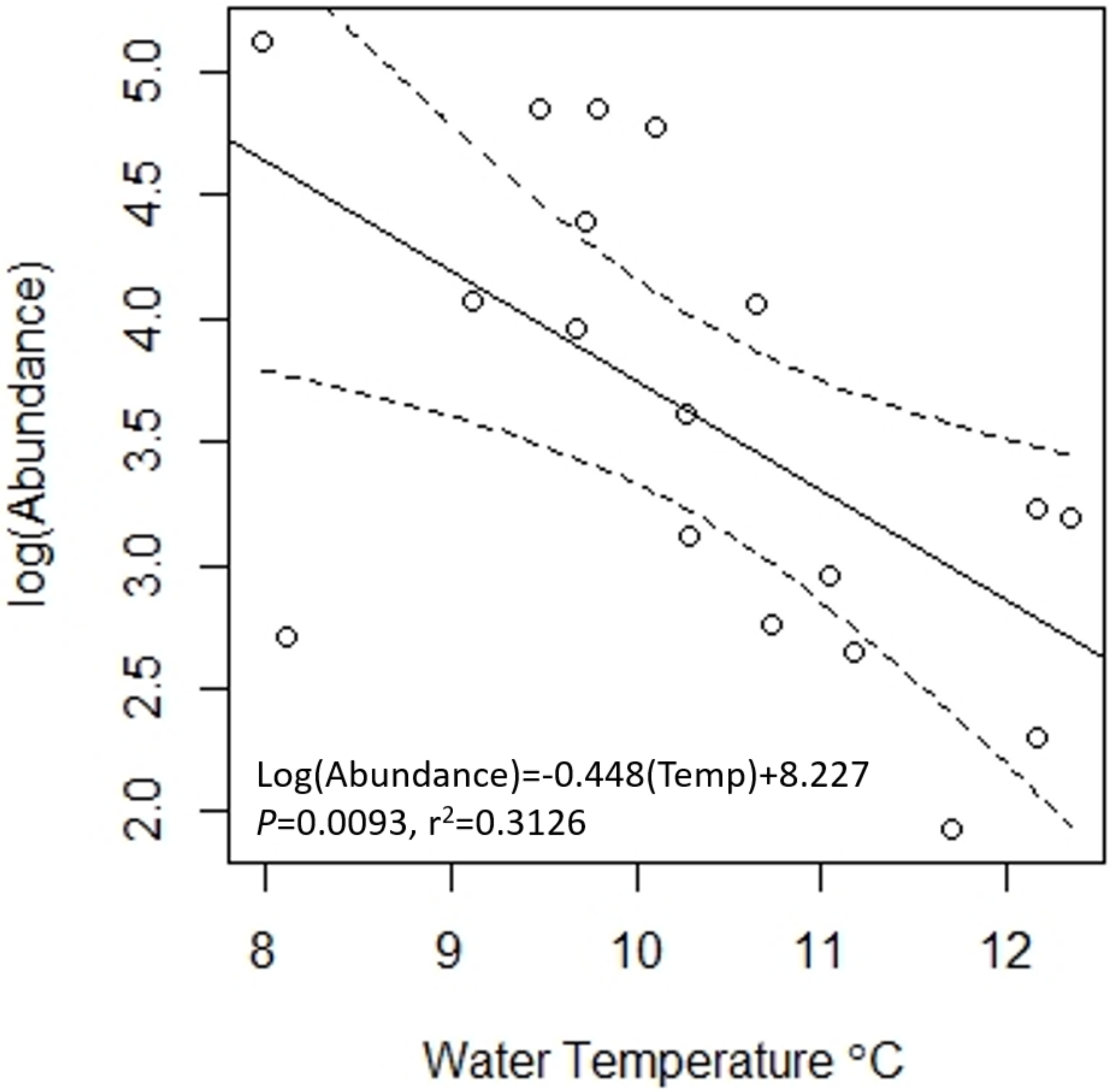

Figure 8. Abundance of larval rainbow smelt in relation to water averaged within the top ten meters of the water column. Solid lines indicate linear regression while dotted lines indicate the 95% confidence interval.

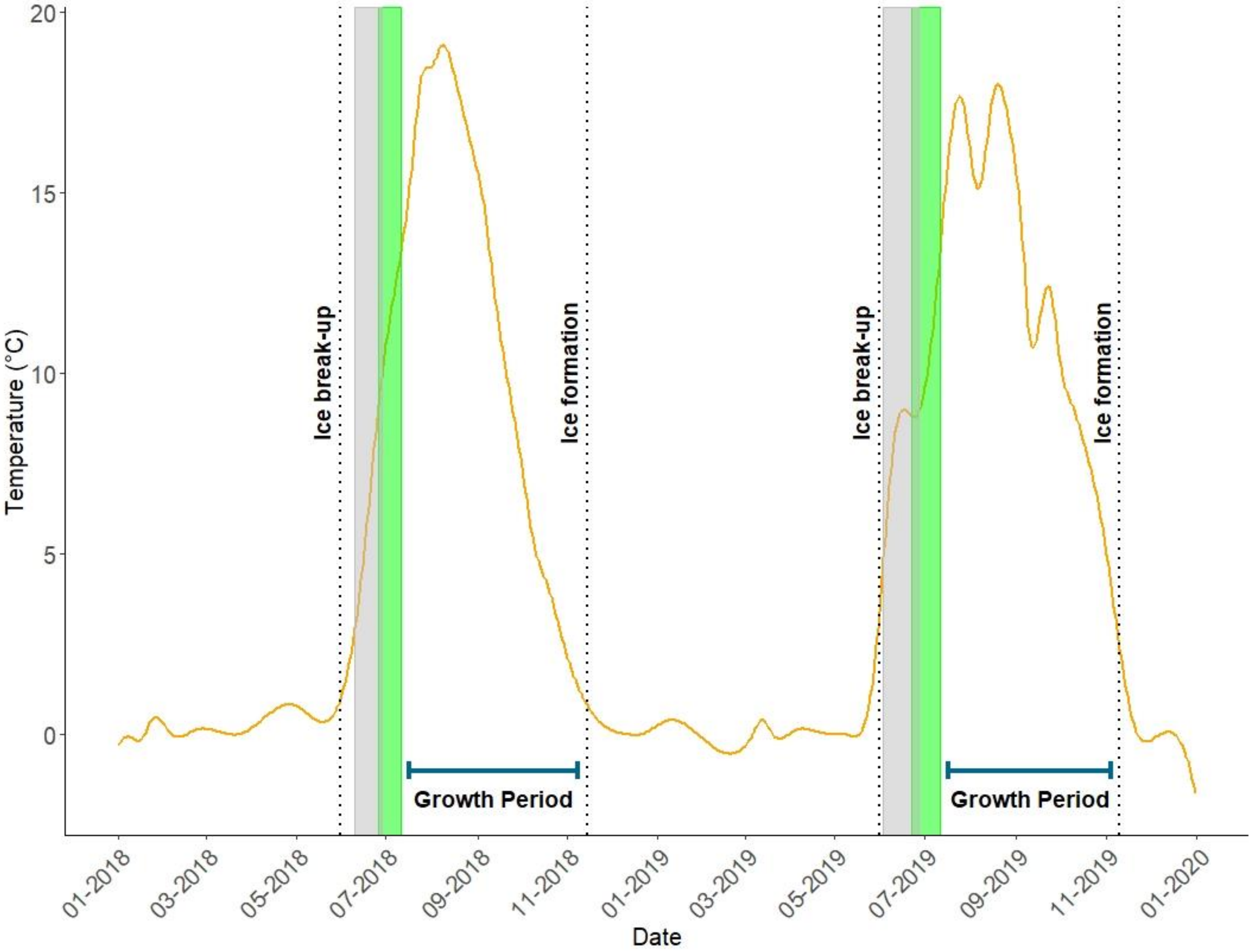

Figure 9. Hatching period (green) and estimated spawning period (grey) for rainbow smelt within Lake Melville and Goose Bay. Black dashed lines indicate ice break up (<50%) and ice formation (>0%), while the orange line indicates sea surface temperature.

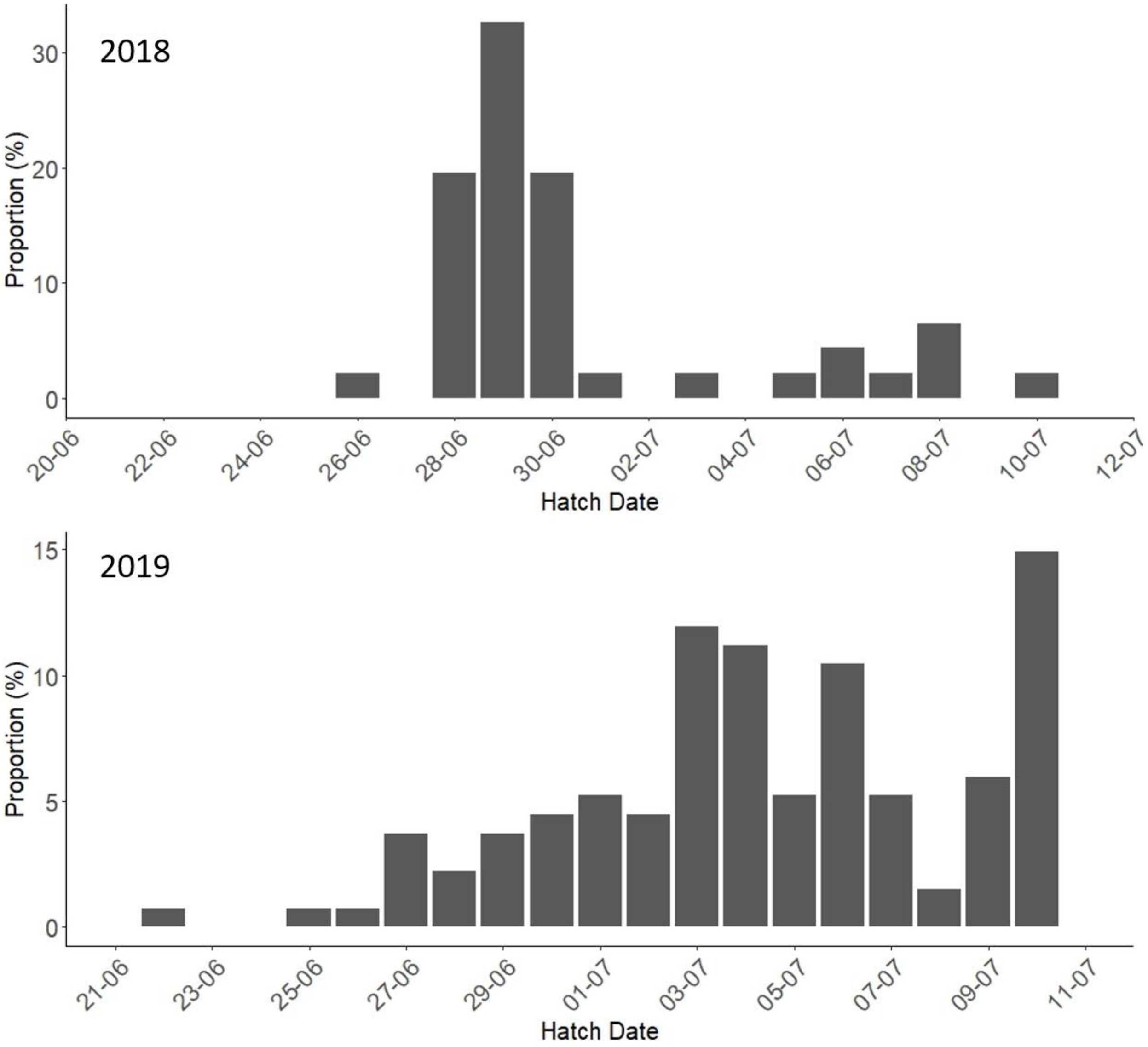

Figure 10. Frequency distribution of hatch for rainbow smelt caught in Lake Melville, Labrador in 2018 and 2019.

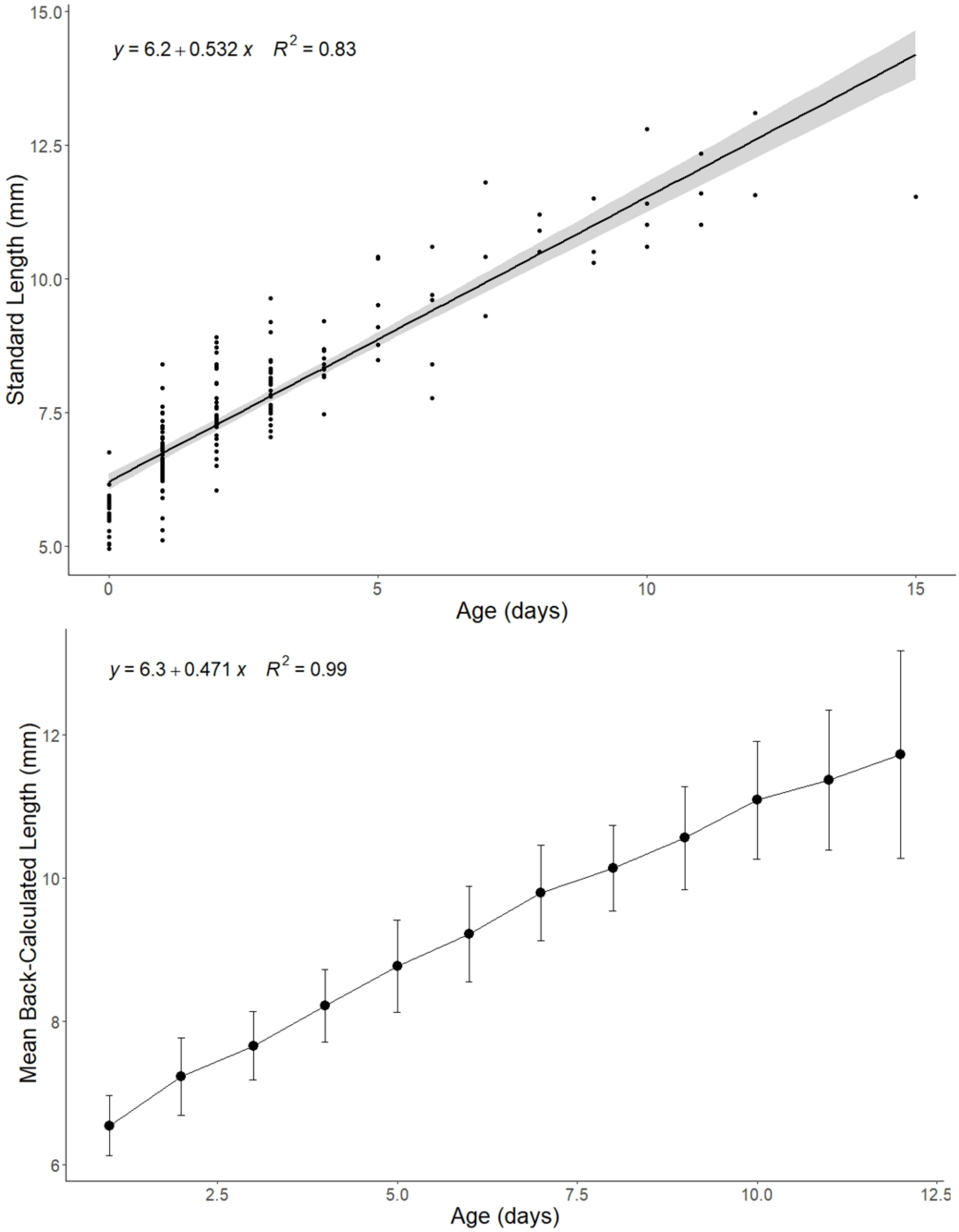

Figure 11. Observed growth rate (top) and back-calculated growth rate (bottom) for rainbow smelt larvae caught in Lake Melville Labrador in 2018 and 2019.

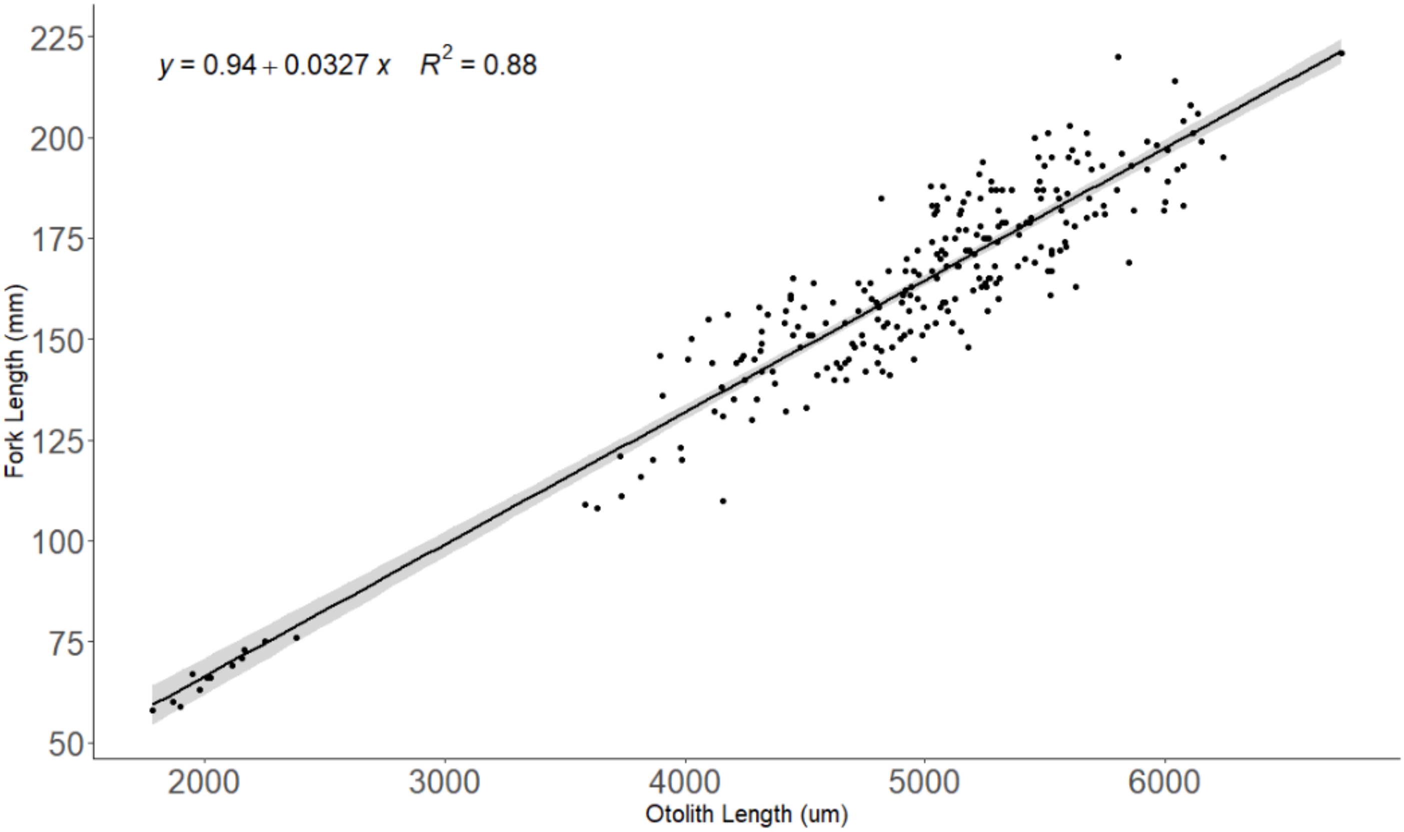

Figure 12. Linear relationship between rainbow smelt fork length and otolith diameter of adult smelt caught in 2019 and 2020.

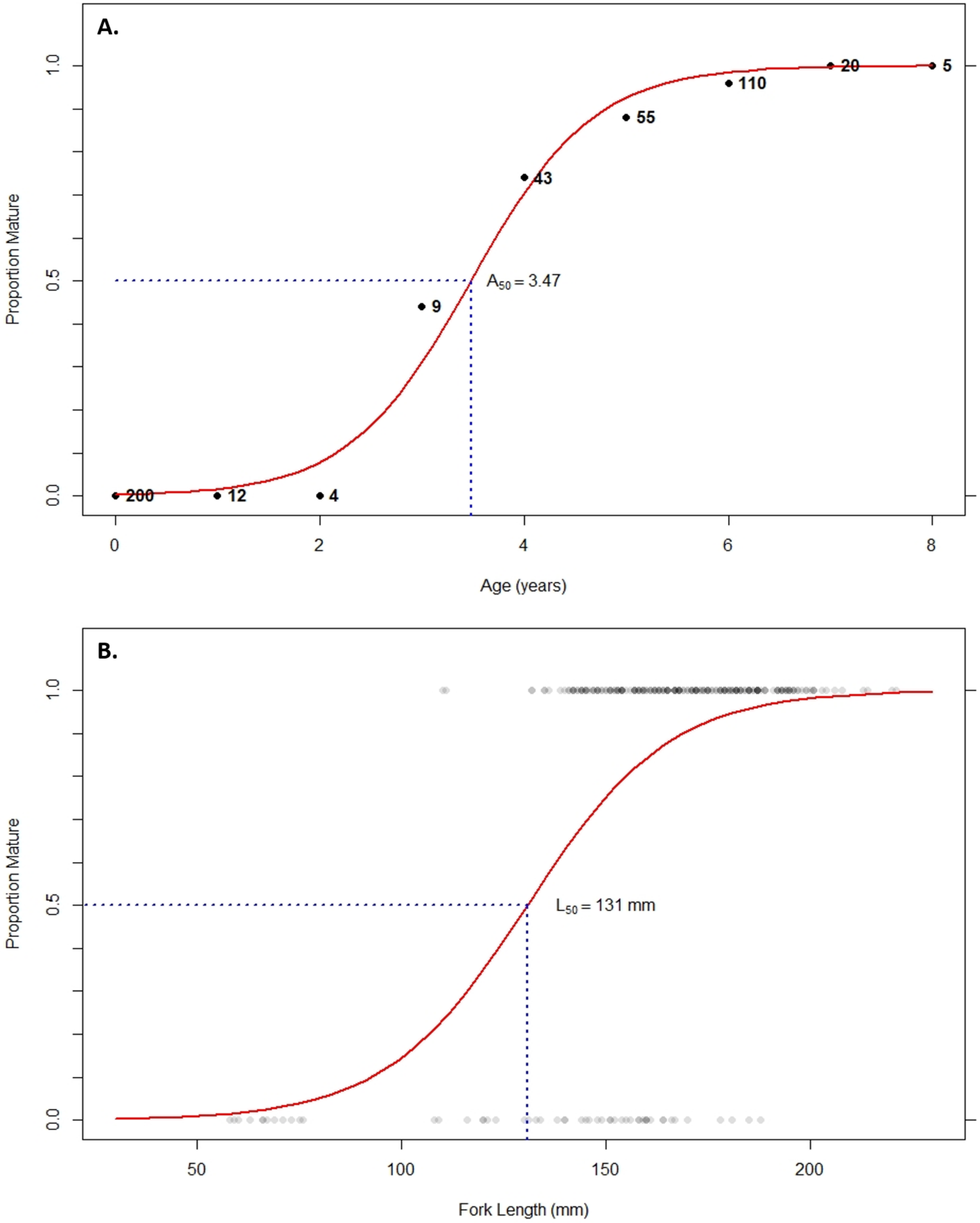

Figure 13. Age of maturity (A_{50}) and length of maturity (L_{50}) of the pooled male and female rainbow smelt gonadal data. Numbers equal the n values for each age cohort.

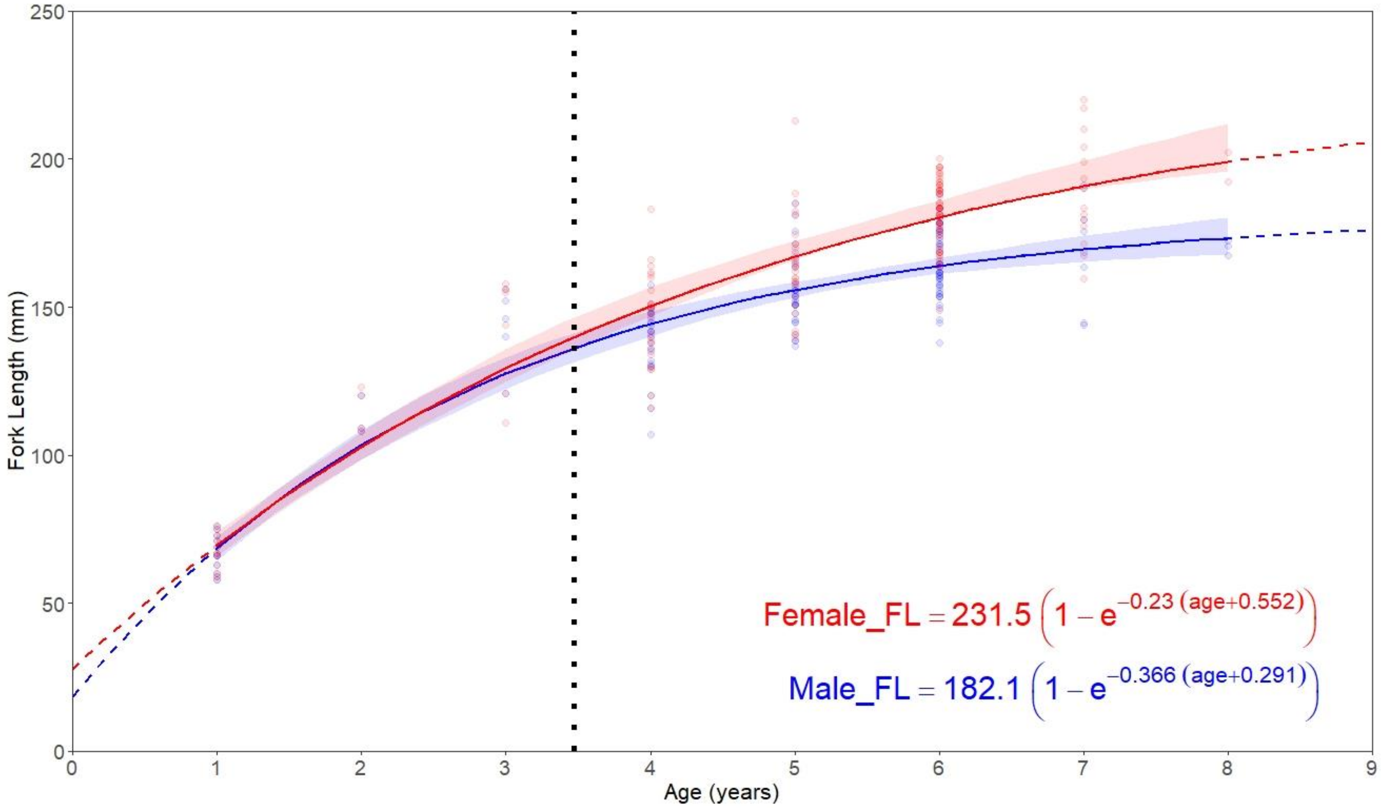

Figure 14. Von Bertalanffy growth curves for female (blue) and male (red) rainbow smelt caught within Lake Melville and Goose Bay, Labrador, during 2018 and 2019. The dashed black line indicates the calculated maturation age (A_{50}).

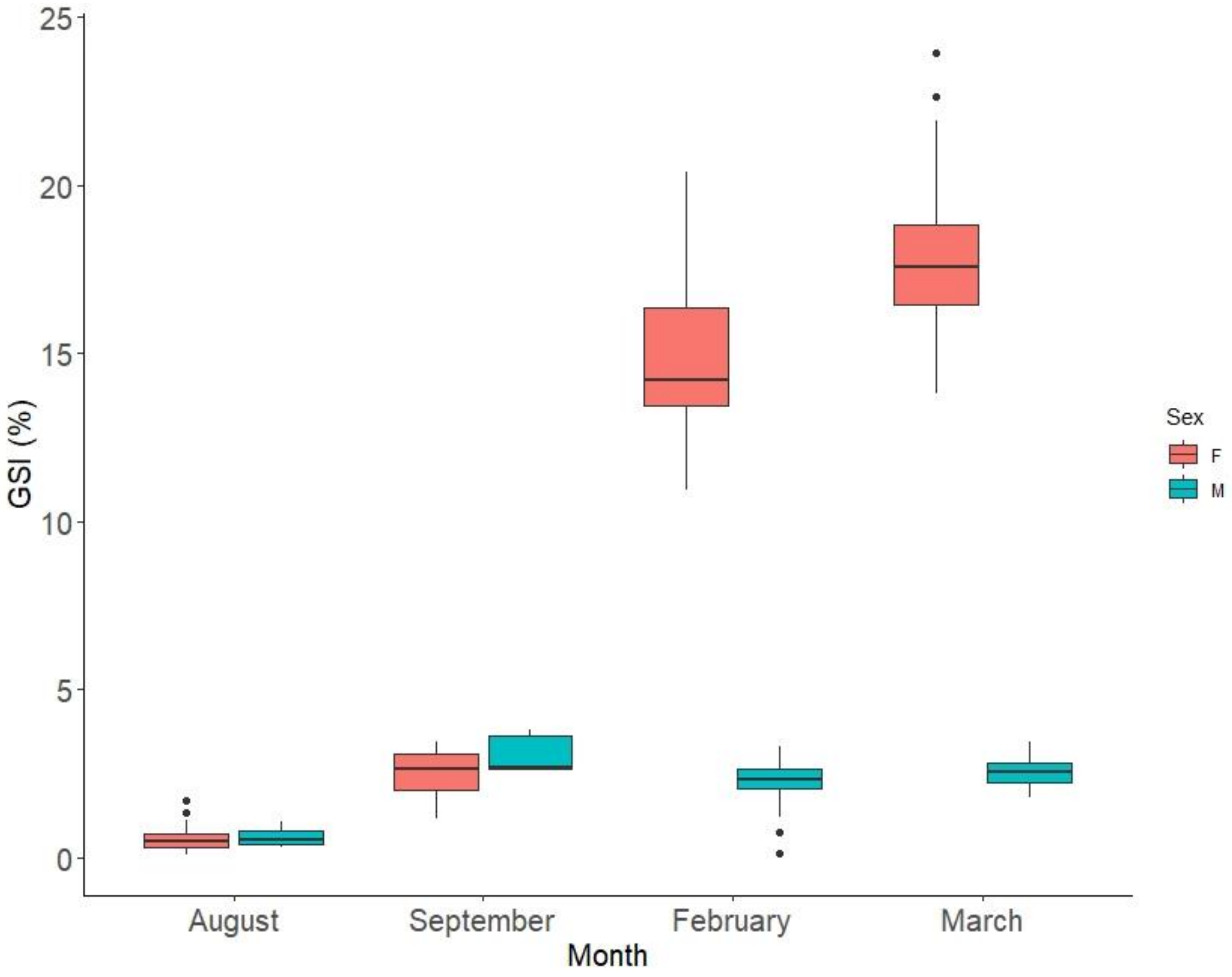

Figure 15. Gonadosomatic Index (GSI) of female (red) and male (blue) rainbow smelt as a function of month of capture during 2019 and 2020.

Tables

Table 1. General information collected for each station within Goose Bay and Lake Melville, Labrador.

ID	Location	Sampling Date	Latitude	Longitude	Depth (m)	Temperature (°C)	Salinity (pss)	Samples collected
1	Goose Bay	2018/07/09, 2019/07/09	53.3718	-60.3135	30	9.684, 12.164	2.083, 0.51	Larvae
2	Goose Bay	2018/06/30, 2019/07/10	53.3871	-60.2121	40	10.643, 11.704	0.649, 0.186	Larvae
3	Goose Bay	2018/07/01, 2019/07/07	53.3885	-60.0852	40	10.726, 12.346	0.236, 0.236	Larvae
4	Goose Bay	2018/07/02, 2019/07/07	53.4087	-60.0389	50	11.176, 12.158	0.512, 0.244	Larvae
5	Lake Melville	2018/07/10, 2019/07/04	53.5183	-59.9631	40	7.978 10.278	7.634, 0.799	Larvae
6	Lake Melville	2019/07/01, 2019/07/04	53.5602	-59.9013	100	9.121, 9.474	5.902, 2.1	Larvae
7	Lake Melville	2018/07/08, 2019/07/05	53.5921	-59.8261	65	8.111, 9.725	8.629, 2.422	Larvae
8	Lake Melville	2018/07/11 2019/07/11	53.6736	-59.9302	30	9.502, 9.798	6.701, 3.172	Larvae
9	Lake Melville	2018/07/11 2019/07/11	53.5484	-59.6405	39	11.037, 10.098	5.963, 2.738	Larvae
10	Lake Melville	2018/07/12, 2019/07/11	53.5965	-59.7217	80	11.045 10.292	6.296, 2.369	Larvae
11	Goose Bay	2019/02/01	53.3544	-60.2879	30			Adults
12	Goose Bay	2020/03/25	53.3797	-60.0354	30			Adults
13	Goose Bay	2020/03/13	53.3822	-60.3419	40			Adults
14	Goose Bay	2020/02/13	53.4402	-60.1877	40			Adults
15	Lake Melville	2019/10/09	53.4833	-59.8500	30			Adults
16	Lake Melville	2019/09/26	53.5271	-59.9239	50			Adults
17	Lake Melville	2019/08/27	53.7029	-59.9808	45			Adults
18	Lake Melville	2019/08/27	53.7949	-59.7992	40			Adults
19	Lake Melville	2019/08/27	53.9552	-58.8273	100			Adults