by

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Author's Declaration

This thesis consists of material all of which I authored or co-authored: see Statement of Contributions included in the thesis. This is a true copy of the thesis, including any required final revisions, as accepted by my examiners.

I understand that my thesis may be made electronically available to the public.

Statement of Contributions

I participated in the collection of field samples from the Attawapiskat River in fall of 2015 with local community members. First Nations fishers, consultants, and researchers from Laurentian University collected all remaining fish and invertebrate samples. I prepared otoliths for otolith microchemical analysis, and analyzed the otoliths with the assistance of Dr. Heidi Swanson and Dr. Panseok Yang. I reduced all otolith microchemical data, took photos of each otolith, and generated otolith microchemical profile plots for each fish. Image overlays were completed by myself and members of the Swanson Lab (Alexandra Crichton and Amy Nguyen). The age of each fish was determined by the Ontario Ministry of Natural Resources and Forestry. I assessed age of first migration for each fish, and visually classified each fish as migratory or non-migratory. Water chemistry data were obtained from the Ontario Ministry of Environment and Climate Change, and fish data prior to 2014 were obtained from the Ontario Ministry of Natural Resources and Forestry. Maps were created by Angela Graham. For fish collected in 2014-2016, I prepared and weighed samples for stable isotope analysis, with the assistance of lab volunteers and Shyann Hang. I completed all stable isotope mixing model analyses.

Abstract

Many northern fishes display plasticity in life history and trophic ecology that can influence productivity of fisheries and bioaccumulation of contaminants, such as mercury. Cisco (Coregonus artedi), Lake Whitefish (Coregonus clupeaformis), and Northern Pike (Esox lucius) are important subsistence food fishes to Aboriginal communities on the west coast of Hudson Bay, and our understanding of the life history of these fishes is incomplete. In this study, I investigated life history and trophic ecology of Cisco, Lake Whitefish, and Northern Pike from three rivers of the Hudson Bay Lowlands. Fish of each species were classified as either nonmigratory or migratory using otolith microchemistry profiles, and results indicated clear use of marine habitats by Cisco and Lake Whitefish. Whereas use of brackish-water habitats is welldocumented for Northern Pike in the Baltic Sea, I present the first data indicating possible use of brackish habitats by Northern Pike in North America. The majority of Cisco (99 %) and Lake Whitefish (92 %) were classified as migratory, whereas the majority of Northern Pike (70 %) were classified as non-migratory. A mixing model (MixSIAR) applied to stable isotope ratios of sulphur (δ^{34} S) was used to determine proportional dietary contribution of prey from marine and freshwater-derived sources for each fish species in each river. The majority of the diet of migratory Cisco (76 to 85 %) and Lake Whitefish (59 to 75 %) was composed of marine-derived nutrients/prey. Both migratory and non-migratory Northern Pike were reliant on marine-derived nutrients/prey. I estimated that up to 40 % of non-migratory Northern Pike diets were derived from marine sources; this is evidence that non-migratory Northern Pike were feeding on marinederived resources (possibly anadromous Cisco and Lake Whitefish). Results of this study will enable better predictions of changes in species-specific life history due to climate-induced shifts in temperature and/or productivity in northern rivers and oceans. In combination with

contaminant data, my results can be used to better understand how fish life history influences contaminant bioaccumulation both now and in the future.

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List of Abbreviations

ANOVA Analysis of variance

Ca Calcium

CI Credible interval

HBL Hudson Bay Lowlands

HDPE High density polyethylene

HNO₃ Nitric acid

LA-ICP-MS Laser ablation inductively coupled plasma mass spectrometry

MCMC Markov Chain Monte Carlo

NIST National institute of standards and technology

OMNRF Ontario Ministry of Natural Resources and Forestry

OMOECC Ontario Ministry of Environment and Climate Change

SINLab Stable Isotopes in Nature Laboratory

Sr Strontium

[Sr] Strontium concentration

Sr:Ca Strontium to calcium ratio

VCDT Vienna Canyon Diablo Triolite

List of Symbols

δ^{13} C	Stable isotope ratio of carbon, relative to an international standard
$\delta^{15} N$	Stable isotope ratio of nitrogen, relative to an international standard
$\delta^{34}S$	Stable isotope ratio of sulphur, relative to an international standard

CHAPTER ONE - INTRODUCTION

1.1 Organism Life History

Life history comprises the events in an organism's life that influence survival and reproduction (fitness). Understanding life history helps resource managers and scientists predict habitat use by an organism at different life stages/times of the year, and provides information necessary for population conservation and management. Important aspects of life history are reviewed by Stearns (1976), and include number and size of young, age of maturity, trade-offs between maturity and mortality, and variation in these traits among an individual's offspring. Life history theory can be used to explain why particular life history traits may have evolved in a species or population of interest. Life history traits often display a large degree of plasticity, as a result of interactions between genetics and environmental conditions (Metcalfe, 1993). Variations in life history exist both among and within species and populations; within a population, some individuals may display an alternative life history strategy that results in differences in reproductive tactics (e.g., territorial or opportunistic mating behaviour in males), migration, and/or developmental timing (Metcalfe, 1993). Migrations, such as those observed in fish and birds, are important aspects of life history that can affect size and age of maturity, and therefore timing of reproduction (Roff, 1988). Migrations can also affect the number and size of offspring produced (e.g., Kinnison et al., 2001; Loewen, Gillis, & Tallman, 2010).

1.2 Fish migrations

Migrations are a directed movement of animals from one habitat to another, with regular returns to the first habitat (Northcote, 1978). Migratory movements are often displayed by the majority of individuals in a population, and fish migrate to feed, spawn, avoid environments unsuitable for year-round habitation, increase reproductive success, and to increase a species' range (Northcote, 1978).

There are many different types of fish migrations. Diadromous migrations involve the general movement of fish between freshwater and marine environments. Anadromous, catadromous, and amphidromous migrations are all types of diadromous migrations. Anadromous migrations involve the movement from natal freshwater habitats to marine habitats for feeding, with a return to freshwater habitats for spawning (Myers, 1949). Catadromous migrations involve the movement from natal marine habitats to freshwater habitats for feeding, and a return to marine habitats for spawning (Myers, 1949). Amphidromous migrations are the migration of fish between freshwater and marine waters at a specific life stage for purposes other than reproduction (Myers, 1949). It has been postulated that diadromous migrations are an evolutionary result of/response to differences in food availability between marine and freshwater environments, and that diadromy evolved to allow fish to gain access to regions of higher productivity (Gross, 1987). Recent evidence, however, indicates that this theory may not be supported by data for all fish species (e.g., many species of the order Clupeiformes), and that other factors, such as predation, competition, temperature tolerances, allocation of energy, environmental conditions, and invasion of fish into freshwaters after the Pleistocene ice age may have influenced the evolution of diadromy; differences in productivity may in fact explain anadromy in only a small portion of anadromous species (Morinville and Rasmussen, 2003; Olsson et al. 2006; McDowall, 2008; Bloom & Lovejoy, 2014). Diadromy has also been proposed to have evolved from the fitness advantage gained by marine fishes when eggs are laid and incubated in relatively safer freshwater environments (Dodson, Laroche, & Lecomte, 2009).

Fish migrations are complex, and fishes may not fit perfectly into one of the above-defined categories; a continuum of migratory strategies is often displayed among species (McDowall,

1987; see Quinn & Leggett, 1987). As a result, I will herein refer to 'migrations' as a general term to describe movements of fish between freshwater and marine/brackish environments.

Migrations to sea have both costs and benefits for individual fitness, and fish will only migrate if there is a net benefit to individual fitness (Gross, 1987; Jonsson & Jonsson 1993). Benefits of migrating to sea include increased growth and reproduction via access to habitats with higher productivity (Gross, 1987), and decreased parasite loads (Bouillon & Dempson, 1989). However, migrations are energetically expensive (Gross, 1987); fish that migrate to sea must either osmoregulate or osmotolerate. In addition, migrating fish expend extra swimming energy when migrating (Gross, 1987), especially when the two habitats between which a fish is migrating are geographically distant. Migrating fish may also face increased risks of disease and predation in a new environment (Gross, 1987).

1.2.1 Anadromy

Anadromy is the downstream migration of fish from freshwaters to marine waters for feeding, and subsequent upstream migration to freshwaters for spawning (McDowall, 1987). At northern latitudes, an anadromous life history strategy is thought to confer a fitness advantage because freshwaters tend to be relatively unproductive compared to marine environments (Gross, 1987; Gross, Coleman, & McDowall, 1988). Anadromous life histories are more common in temperate and northern regions, whereas catadromous life histories are more common in tropical regions. Previous researchers have stated that this geographic difference in prevalence likely reflects relatively high productivity in northern marine waters (compared to freshwater) and tropical freshwaters (compared to marine) (McDowall, 1987; Gross, Coleman, & McDowall, 1988). There are, however, a number of other factors that may lead to anadromous behaviour, such as predation, competition, temperature tolerances, energy allocation differences, and

environmental conditions (Morinville and Rasmussen, 2003; Olsson et al. 2006; McDowall, 2008; Bloom & Lovejoy, 2014).

Some fishes, such as Chum Salmon (*Oncorhynchus keta*, Walbaum, 1792), are obligatory anadromous (Rounsefell, 1958), and therefore must make migrations to complete their life cycle. Other fish species are facultatively anadromous, and migrations are not essential. Populations of facultatively anadromous fishes may display partial migration, where only some individuals migrate (Gross, 1987; Hicks, Closs, & Swearer, 2010). For example, some individual Brown Trout (*Salmo trutta*, Linnaeus 1758) are anadromous, while others remain in freshwaters (Jonsson, 1985).

Partial migration (partial anadromy is one example of partial migration) is thought to be a conditional life history strategy where differences among individuals in life history tactics are not strictly genetically controlled, but affected by an interaction between the state (e.g., size) of the individual (Gross & Repka, 1998) and the conditions of the environment (e.g., Jonsson & Jonsson, 1993). In at least some species of partially anadromous fishes, females, regardless of whether they are anadromous or freshwater residents, are able to produce both freshwater resident and anadromous progeny (e.g., Zimmerman & Reeves, 2000; Courter et al., 2013).

The proportion of anadromous individuals within a partially anadromous population can be influenced by environmental conditions such as food availability (Nordeng, 1983; Olsson et al., 2006), sex (see Jonsson & Jonsson, 1993), and the relative productivity of freshwater natal habitats compared to accessible marine habitats (Gross et al., 1988). With higher nutrient availability in northern marine waters relative to freshwaters, anadromous fish often grow more quickly, have higher fecundity, and have larger size-at-age (Gross, 1987) than freshwater-residents of the same species (e.g., Rikardsen et al., 2000).

Anadromous fishes use marine environments to varying degrees. The term 'semi-anadromy' is used to describe fishes that migrate to marine environments, but that do not migrate to full strength seawater. Instead, semi-anadromous fishes migrate to brackish waters, or waters with salinity higher than freshwater, but lower than that of seawater (Reist & Chang-Kue, 1997). Migrations may be limited to brackish waters because of limits in the physiological ability to tolerate higher salinity (see Kissinger et al., 2016). Size-related salinity tolerance (e.g., Conte & Wagner, 1965; McCormick & Naiman, Robert, 1984) in addition to time of first feeding (e.g., Metcalfe & Thorpe, 1992), growth and feeding rates (e.g., Forseth et al., 1999), and climate conditions throughout early fish development (e.g., Josnsson, Jonsson, & Hansen, 2005) can affect size and age of first migration for migratory fishes. Since larger organisms may be subject to lower rates of mortality as a result of salinity stress (Northcote, 1978), some populations of freshwater-hatching fish, such as a group of Coho Salmon in Alaska, remain in freshwater to increase body size before beginning marine migrations (e.g., Drucker, 1972). McCormick (1994) reports on size-related salinity tolerance in a number of salmonid species.

1.3 Techniques for Studying Fish Migration

Fish migrations can be investigated with a variety of techniques, including telemetry, direct observation, mark-recapture, otolith microchemistry, and stable isotope analysis; all of these methods have associated advantages and disadvantages. Fish telemetry is a relatively direct but invasive method for studying fish migrations. Telemetry studies require surgery to insert tags into the body of the fish (see Lucas & Baras, 2000). These tags transmit or store data, and can indicate when fish are in close proximity to a receiver, allowing fish location to be mapped, or can store fish position information that can be mapped after tag retrieval (see Lucas & Baras,

2000). Tags used in telemetry studies are expensive, can be shed from the organism, have a limited battery life, and data quality is influenced by type and quantity of receivers as well as several environmental factors (see Lucas & Baras, 2000). However, telemetry data can be of very high temporal and spatial resolution (see Lucas & Baras, 2000).

Fish observation and mark-recapture studies are advantageous as fish are disturbed and manipulated less than in telemetry studies, but these methods are limited by the ability to recapture fish that were originally tagged or observed in the study (see Lucas & Baras, 2000). Observational and mark-recapture methods are only effective when fish are actively examined; information on fish movement before and after sampling periods is not available. Indirect methods of determining fish migration history, such as stable isotope analysis of fish tissue and otolith microchemical analysis, often allow inference of fish movements over a longer period of time than direct observational methods. However, otolith microchemistry analysis requires sacrificing the fish, and effectiveness of the method can be influenced by many environmental factors. Otolith microchemistry and stable isotope analysis are discussed in more detail below.

1.3.1 Otolith Microchemistry

The term 'otolith microchemistry' is used to describe analyses of trace elemental concentrations in otoliths (Panfili et al., 2002). Analyzing the elemental composition of fish otoliths can lend insight into fish life history (Panfili et al., 2002). Otoliths are bones of the inner ear in teleost fishes which are involved in hearing and balance (Campana, 1999). Otoliths have an annular growth structure (annuli) much like tree rings (Panfili et al., 2002), and are not resorbed. These bones are composed mainly of calcium carbonate, however, trace elements from the environment can be incorporated into the matrix of the otolith and used as tracers of habitat use (Panfili et al., 2002). Otoliths can thus provide a record of the conditions to which a fish was

exposed throughout its entire life (see Campana & Neilson, 1985); as a fish is exposed to different elements in the water, these elements are taken up over the gills or through the intestines into the blood plasma, where they are transported to the endolymphatic fluid surrounding the otoliths, and incorporated into the otolith (Campana, 1999). The contribution of elements in diet and water to the concentration of elements in otoliths differs among species, but it is generally accepted that water is the main source of elements taken up into otoliths (e.g., Walther & Thorrold, 2006; Webb, Woodcock, & Gillanders, 2012; Doubleday et al., 2013). The authors of one study, however, reported that up to 70 % of otolith Sr in Atlantic Salmon was from dietary sources (Kennedy et al., 2000).

Calcium (Ca) and strontium (Sr) have the same valence and similar atomic radii, and as a result, Sr can be incorporated in otoliths in place of Ca (Radtke et al., 1996; Kennedy et al., 2000; Doubleday et al., 2014). Because Sr:Ca ratios increase with salinity, fish that migrate to sea experience higher salinities and have higher Sr:Ca ratios in their otoliths compared to fish that remain in low salinity waters (e.g., Macdonald & Crook, 2010).

The relationship between elemental concentrations in water and elemental concentrations in otoliths varies among species, and is influenced by many factors (reviewed in Sturrock et al., 2012; see Campana (1999) for details on elemental discrimination at interfaces along the route of uptake). An important assumption of otolith microchemistry is that there is a positive relationship between the elemental concentration in water and the elemental concentration in otoliths. While a positive relationship between Sr concentrations (or Sr:Ca) in water and Sr concentrations (or Sr:Ca) in otoliths has been examined and determined for a number of species (e.g., Zimmerman, 2005; Walther & Thorrold, 2006; Bath et al. 2000; Engstedt, Koch-Schmidt, & Larsson, 2012), it has not been validated for every species on which otolith microchemistry is

conducted. However, it is generally assumed that this positive relationship between otolith elemental concentration and elemental concentrations in water is applicable to other fish species. When lab trials have been performed on the species of interest, otolith Sr concentrations and Sr:Ca ratios can allow for differentiation between use of freshwater, brackish, and marine environments (Zimmerman, 2005).

There are several methods for determining concentrations of elements in otoliths. One of the most commonly employed techniques, and the one used in this thesis, is laser ablation-inductively coupled plasma mass spectrometry (LA-ICP-MS) (Ludsin, Fryer, & Gagnon, 2006). Laser ablation ICP-MS is a relatively fast and effective technique for analyzing a large number of elements and otoliths (Pracheil et al., 2014). Transverse sections of otoliths are prepared to expose annuli, and a laser is used to ablate material from the exposed surface. The ablated material is then delivered to an ICP-MS, where the concentrations of the elements in the otolith can be determined. Material can be sampled along a continuous transect from the otolith core to the outer edge, at specific points within the otolith, or only within the otolith core, depending on the time period in the life of a fish that is of interest.

1.3.2 Stable Isotopes

Anadromous and freshwater-resident life history forms of fish can often be differentiated by examining stable isotope ratios in fish tissue; stable sulphur (δ^{34} S), carbon, (δ^{13} C), and nitrogen (δ^{15} N) isotope ratios are often higher in anadromous fish relative to freshwater resident fish (e.g., Doucett, Hooper, & Power, 1999; Swanson & Kidd, 2010). Stable isotope ratios can provide information regarding fish feeding habits over a period of between four to eight months, up to approximately one year (e.g., Hesslein, Hallard, & Ramlal, 1993; Buchheister and Latour, 2010; Franssen et al. 2017). Freshwater and marine food sources are especially well differentiated with

the use of stable isotopes of sulphur, as δ^{34} S ratios are higher in marine environments than in freshwater environments (Peterson & Fry, 1987), and sulphur fractionates little with trophic transfer (see McCutchan et al. 2003). Carbon isotopes fractionate minimally through dietary assimilation (Rounick & Winterbourn, 1986; Peterson & Fry, 1987), and are most often used to differentiate between nearshore (benthic) and offshore (pelagic) carbon sources in freshwater environments (France, 1995). Ratios of δ^{13} C have also been shown to be higher (less negative) in anadromous fish than in resident fish (e.g., Doucett, Hooper, & Power 1999), and thus can be useful in studies of life history and migration. Nitrogen isotopes fractionate with each trophic transfer, and are most often used to determine relative trophic position (Minagawa & Wada, 1984). Similar to δ^{13} C, δ^{15} N ratios are often higher in anadromous fish than in resident fish, and can be useful in studies of fish life history and migration (e.g., Doucett, Hooper, & Power 1999). Since isotope ratios at the bottom of the food chain can differ among sites, previous authors have recognized the importance of accounting for differences in δ^{15} N and δ^{34} S at the bottom of the food chain (Rounick & Winterbourn, 1986; Cabana & Rasmussen, 1996; Swanson et al., 2011).

If migrating fish are feeding in isotopically distinct habitats, stable isotope ratios can be used to estimate proportional contributions of different prey sources to a migrating consumer with mixing models (e.g., Phillips & Gregg, 2001). Linear mixing models, such as IsoError (Phillips, Newsome, & Gregg 2005) can be applied to isotope data and used to estimate proportional contributions of different food sources (dietary endmembers) to consumer diets. Linear models do not account for the large amount of uncertainty that is often observed in endmember isotope ratios or fractionation factors, however. Bayesian mixing models applied to stable isotope data are a more recent advance that allow incorporation of prior information (such as results of gut content analysis), and/or estimates of uncertainty in isotope ratios of sources (endmembers), the

mixture (consumer), and isotope fractionation (Moore & Semmens, 2008; see Phillips et al., 2014).

1.4 Study Area: The Hudson Bay – James Bay Region of Canada

1.4.1 Geography of the Hudson Bay – James Bay Region

Hudson and James Bay are located in northern central Canada, and are connected to the Arctic Ocean through Foxe Basin and the Arctic Archipelago. Hudson Bay has a surface area of more than 1 000 000 km² (Ingram & Prinseberg, 1998), and James Bay has a surface area of 67 000 km² (El-Sabh & Koutitonsky, 1977). Water circulation in Hudson and James Bay is driven by temperature and salinity-driven density differences between incoming water from the Arctic Ocean and freshwaters entering the bays, as well as by wind (Ingram & Prinseberg, 1998). Water from the Arctic Ocean travels through Foxe Basin and enters Hudson Bay, where it then circulates around the Bay in a counter clockwise direction. Some of this water travels into and counter clockwise around James Bay. The water then re-enters Hudson Bay before exiting into Hudson Strait (Ingram & Prinseberg, 1998). The estimated water residence time in Hudson and James Bay combined is between one and two years (Ingram & Prinseberg, 1998), and is 10 months in James Bay (El-Sabh & Koutitonsky, 1977). There are 35 large rivers that drain into Hudson and James Bay, and of these, there are 12 major rivers in the Hudson Bay Lowlands. These are, in order of decreasing discharge: the Nelson, La Grande, Moose, Eastmain, Albany, Rupert, Severn, Churchill, Winisk, Attawapiskat, Harricana, and Ekwan rivers (Déry et al., 2005). Discharge of the above-named rivers ranges from 94.24 km³ year⁻¹ in the Nelson River to 2.76 km³ year⁻¹ in the Ekwan River (Déry et al., 2005). Many of these rivers have associated coastal First Nations communities. The large freshwater inputs of these and other rivers leads to

the waters of Hudson and James Bay having lower salinity than the nearby Arctic Ocean (discussed in detail below).

The Hudson Bay Lowlands (HBL) comprise an area of approximately 474 000 km² on the west side of Hudson and James Bay. The lowlands are located in the Far North of Ontario and Manitoba, extend from 51°N to 65°N latitude (Rouse, 1991), and are bounded on the east at approximately 78°W and on the west at approximately 96°W. The Lowlands are named as such because elevation is less than 200 m above sea level (Rouse, 1991). Isostatic depression of the Hudson Bay area by the Laurentide Ice Sheet allowed the Tyrell Sea to advance into the present day Hudson Bay Lowlands between 7000 to 8000 years ago (Lee, 1960). The Tyrell Sea covered the region with marine sediments of low permeability, leading to a poorly drained landscape with a low topographic gradient (ranging from 0.65 to 1 m·km⁻¹) (Riley, 2011). Poor drainage and low topographic gradient help maintain wet conditions and facilitated the development of extensive peatland deposits that cover the surface of the Lowlands. Peat has accumulated so that it is now approximately 2 m thick over much of the interior (Riley, 2011). The landscape is largely composed of peatlands in the form of bogs and fens, with many pools and ponds throughout (McCrea & Fischer, 1986). The Hudson Bay Lowlands is the world's second largest semicontinuous wetland and peatland after the Siberian Lowlands (Gorham, 1991; Glooschenko et al., 1994). These peatlands are globally significant stores of carbon, and this large pool of organic matter is effective at sequestering atmospherically-deposited nutrients as well as pollutants (Rydberg, et al., 2010; Stewart & Lockhart, 2005).

The temperature of the HBL region has historically been moderated by seasonal ice covering the bay. Ice used to remain into the summer months, producing a cooling effect on the surrounding land (Rouse, 1991) and making the HBL region cooler than other regions at the

same latitude. In the mid-1990s, the surface air temperature of the Hudson Bay area began to significantly increase (Hochheim & Barber, 2010), and the extent of ice coverage on the Bay has significantly decreased, modifying regional climate (Hochheim & Barber, 2010).

1.4.2 Salinity of Hudson and James Bay

As a result of the large freshwater inputs from inflowing rivers, the salinity of Hudson and James Bay do not reach the full salinity of seawater, which is ~33 to 35 parts per thousand. Surface salinity of Hudson Bay during the summer ranges from approximately 23 to 30 parts per thousand (Prinsenberg, 1978). The salinity of Hudson and James Bay is higher in winter than in summer, as salt is eliminated from winter sea ice (Ingram & Prinseberg, 1998). Large freshwater riverine inputs in James Bay result in lower salinity compared to Hudson Bay (Ingram & Prinseberg, 1998); the surface salinity of James Bay ranges from 20 to 30 parts per thousand in winter and from 10 to 31 parts per thousand in summer (Prinsenberg, 1978; Ingram & Prinseberg, 1998). As a result of the counter clockwise water circulation pattern and large freshwater riverine inputs, eastern James Bay is less saline than western James Bay. The same is true for Hudson Bay; salinity in eastern Hudson Bay ranges from 24 to 28 parts per thousand whereas salinity in western Hudson Bay ranges from 28 to 30 parts per thousand (Lapoussiere et al., 2009).

1.4.3 Fish Life History in the Hudson Bay – James Bay Region

A number of anadromous and freshwater-resident subsistence food fishes are present in the HBL, including Brook Trout (*Salvelinus fontinalis*, Mitchill, 1818), Lake Whitefish (*Coregonus clupeaformis*, Mitchill 1818), Cisco (*Coregonus artedi*, Leseur, 1818), Longnose Sucker (*Catostomus catostomus*, Forster, 1773), Arctic Char (*Salvelinus alpinus*, Linnaeus, 1758),

Walleye (*Sander vitreus*, Mitchill, 1818), Northern Pike (*Esox lucius*, Linnaeus, 1758), Lake Sturgeon (*Acipenser fulvescens*, Rafinesque, 1817), White Sucker (*Catostomus commersonii*, Lacépède, 1803), and Burbot (*Lota lota*, Linnaeus, 1758) (Berkes et al., 1994; Stewart & Lockhart, 2004). The characteristics and life history of Cisco, Lake Whitefish, and Northern Pike are explored more fully below, as these are some of the species targeted by First Nations fishers in coastal rivers of the HBL, and are the species included in this study.

1.4.3.1 Cisco

Cisco has several other common names, including lake herring, lake cisco, or tullibee (Scott & Crossman, 1973). Cisco can be found in lakes throughout much of Canada, from Alberta and the Northwest Territories through to Quebec, as well as in north central and eastern United States (Scott & Crossman, 1973), and in both lakes and coastal rivers around Hudson and James Bay, where it can tolerate the coastal salt water (Ryder, Scott, & Crossman, 1973; Scott & Crossman, 1973). Riverine Cisco are smaller in size than lacustrine Cisco from the same region (e.g., Blackie, Vecsei, & Cott, 2012). Cisco are pelagic planktivores (Scott & Crossman, 1973) that in freshwater feed mainly on zooplankton and insect larvae (see Scott & Crossman, 1973; Milne, Shuter, & Sprules, 2005). Anadromous Cisco eat small marine fishes, krill, and amphipods, depending on the time of year (Greendale & Hunter, 1978).

Cisco of coastal rivers migrate annually to marine waters in the summer months after the ice has broken up, and return to rivers in the fall. Researchers working in eastern James Bay have previously described migratory behaviour in anadromous Cisco (Morin, Dodson, & Power, 1981). Adult Cisco have been observed in James Bay at least 15 to 20 km north of the mouth of the river in which they overwinter (Dodson, Lambert, and Bernatchez, 1985). In Northern Ontario, most Cisco migrate upriver and spawn in the fall (~September) (Dymond, 1943; Ryder,

Scorr, & Crossman, 1973), although some populations have been observed to migrate in September but delay spawning until November (Dodson et al., 1985). In more southern regions, such as the Great Lakes, Cisco spawn as late as December (see Scott & Crossman, 1973).

Allopatric populations of spring and fall spawning Cisco have also been identified in a Quebec drainage system (Henault & Fortin, 1989; Pariseau, Dumont, & Migneault, 1999), where morphometric and genetic differences existed between these two groups (Henault & Fortin, 1989; Turgeon & Bernatchez, 2001). Cisco are iteroparous and therefore spawn multiple times throughout their lives, however, Cisco do not necessarily spawn each year once they have reached sexual maturity (e.g., Morin, Dodson, & Power, 1982).

Detailed data are not available for western James and Hudson Bay, however, in eastern James and Hudson Bay, Cisco hatch early in the spring (May), when water temperatures are relatively cool (< 8 °C) (Ochman & Dodson, 1982). Riverine larval Cisco are then passively transported downstream shortly after ice break up (Ochman & Dodson, 1982). Similar transportation of larvae shortly after hatch by water currents has been documented in Lake Superior by Oyadomari & Auer (2008). Larval Cisco appear to be tolerant of a wide range of salinities, and have been observed at salinities of 4 parts per thousand or less (Ochman & Dodson, 1982), and up to 15 parts per thousand in Hudson Bay (Ponton, Gagne, & Fortier, 1993).

Cisco are important to the subsistence fishery of the Hudson and James Bay Lowlands region. Many people do not differentiate between Cisco and Lake Whitefish, as they look very similar, and in some communities, Cisco is referred to as the small or little whitefish (personal communication, Bill Keller, Laurentian University, Sudbury, ON). As a result, Cisco are often consumed interchangeably with Lake Whitefish.

1.4.3.2 Lake Whitefish

Lake Whitefish has several other names, including common whitefish and Great Lakes whitefish (Scott & Crossman, 1973). Lake Whitefish is distributed in lakes and coastal rivers throughout almost all of Canada and Alaska, and has an approximate northern limit of Cambridge Bay (Scott & Crossman, 1973). This species is found in coastal rivers and mid- to large-sized lakes of the Hudson Bay Lowlands area (Ryder et al., 1973). Lake Whitefish are primarily benthivorous, although they also feed on plankton, insect larvae, fish eggs, molluscs, and fish, depending on the time of year (Greendale & Hunter, 1978; see Scott & Crossman, 1973).

Lake Whitefish of coastal rivers in the Northwest Territories, Ungava Bay and Hudson Bay regions are known to be anadromous (Scott & Crossman, 1973). Some coastal populations in the Hudson Bay region are composed of anadromous and freshwater-resident individuals (Michael Power, University of Waterloo, unpublished data). Anadromous Lake Whitefish migrate to marine waters each summer after the ice has broken up and return to rivers in the fall.

Researchers working in eastern James Bay have described this migratory behaviour (Morin, Dodson, and Power, 1981), and, similar to Cisco, Lake Whitefish have been found in summer in James Bay at locations 15-20 km north of the mouth of the river in which they overwinter (Dodson, Lambert, & Bernatchez, 1985). In the Hudson Bay Lowlands region, Lake Whitefish migrate upstream to spawn in rivers between late August and September (Ryder et al., 1973; Dodson et al., 1985), but spawning can occur later in more southerly regions (e.g., Hart, 1931). Lake Whitefish in eastern James and Hudson Bay hatch in rivers early in the spring (May), when water temperatures are still relatively cool (< 8 °C) (Ochman & Dodson, 1982). Similar to Cisco, riverine larval Lake Whitefish are passively transported downstream within two weeks of ice

break up (Ochman & Dodson, 1982). The European Whitefish (*Coregonus lavaretus*, Linnaeus, 1758) was shown in the laboratory to have the potential to move ~80 km within a day this way (Lindroth, 1957). Larval Lake Whitefish have been observed at the surface of the water at salinities of 4 parts per thousand or less (Ochman & Dodson, 1982), but at salinities up to 15 parts per thousand in Hudson Bay (Ponton et al., 1993).

1.4.3.3 Northern Pike

Northern Pike is a cool water (Casselman & Lewis, 1996), piscivorous fish species that is widely distributed throughout freshwaters of North America and Eurasia (Scott & Crossman, 1973). In northern North America, Northern Pike are found from Alaska to Labrador, and the species' distribution extends south into much of the central and eastern United States (Scott & Crossman, 1973). This wide distribution encompasses a large latitudinal gradient, indicating that Northern Pike can exist in a range of environmental conditions, despite being classified as a cool water species (see Inskip, 1982). Northern Pike preferentially inhabit calm water over fast moving water, and prefer shallow, vegetated areas (Scott & Crossman, 1973). In the spring, fish move to locations with shallow, sheltered, flooded vegetation to spawn (see Casselman & Lewis, 1996). Adult Pike are generalist, opportunistic feeders consuming a variety of prey including fish, frogs, crayfish, and small mammals (Scott & Crossman, 1973). Northern Pike spawn in spring, after ice melt, and eggs generally hatch within ~12 to 14 days (Scott & Crossman, 1973). Young Northern Pike remain in the spawning location for ~6 to 10 days after hatch (see Scott and Crossman, 1973).

Northern Pike have classically been considered a freshwater fish species that displays a large range in patterns of fish movement. Within freshwaters of Denmark, researchers showed that while some individuals were sedentary, others moved up to ~2 km within a six hour time period

(Jepsen et al., 2001). Recent research has identified that a molecular precursor associated with osmoregulation, and therefore anadromy, developed in teleost fishes prior to development of Salmonidae (Dalziel et al. 2014). As Northern Pike is a member of the Esociformes family, which has been proposed to be a sister group of Salmonidae (Ramsden et al. 2003), these molecular findings indicate that it may be possible for Northern Pike to tolerate higher-salinity environments (Dalziel et al. 2014), despite being primarily classified as a freshwater fish species.

Northern Pike are generally thought to be able to survive salinities up to 18 parts per thousand (Dahl, 1961 (in Danish) referenced in Jacobsen et al., 2007). Northern Pike have commonly been observed in saline waters with salinities of ~ 6 to 12 parts per thousand (e.g., Westin & Limburg, 2002; Engstedt et al., 2010; Jacobsen et al., 2017), but it is not uncommon for them to be found in waters with salinities of up to ~ 15 parts per thousand (Schlumpberger, 1966 (in Russian) referenced in Jacobsen et al., 2007; see Inskip, 1982; Müller & Berg, 1982; see Engstedt et al., 2014). Some evidence suggests that Northern Pike have even been observed in areas with salinities that may be as high as 25 parts per thousand (see Engstedt et al., 2014). Juvenile Northern Pike are also able to tolerate saline waters; studies have shown that fry can survive direct transfer from freshwater to brackish waters of 11 parts per thousand, and gradually increasing salinity up to 13.2 parts per thousand, however, salinity tolerance decreases with increasing water temperature (Jacobsen et al., 2007; Jørgensen et al., 2010). Northern Pike do not have the ability to osmoregulate when exposed to waters of salinity higher than that of the organism's blood, and therefore must osmotolerate (Oikari, 1978).

Northern Pike can exhibit natal homing in both freshwater and marine waters, as observed in the Baltic Sea, the Gulf of Bosnia, and a river in Finland (Müller & Berg, 1982; Vehanen et al., 2006; Engstedt, Engkvist, & Larsson, 2014). Although some Northern Pike live and spawn in

brackish waters of the Baltic Sea, some Northern Pike spawn in nearby freshwaters (Engstedt et al., 2010; Muller, 1986; Müller & Berg, 1982). The population thus exhibits breeding partial migration (Chapman et al., 2012), with sympatric populations of anadromous and brackish water-resident individuals overwintering together in brackish water, but breeding in freshwater and brackish habitats, respectively (Engstedt et al., 2010). Anadromous Northern Pike require freshwater to spawn, whereas marine/brackish residents spawn at salinities between 6.5 and 11 parts per thousand (Westin & Limburg, 2002; Jacobsen et al., 2017). An estimated 45 % to 82 % of Northern Pike in the Baltic Sea are thought to originate in freshwaters, depending on the geographic location (Engstedt et al., 2010; Rohtla et al., 2012). The progeny of anadromous Northern Pike in the Baltic Sea region migrate to sea after spending between one and several months in the freshwater environment in which they hatched (Engstedt et al., 2010; Nilsson, Engstedt, & Larsson, 2014). Migratory behaviour of Northern Pike, to my knowledge, has not been studied in North America.

1.5 Study Rationale

The Hudson Bay Lowlands region is already experiencing many of the effects of climate change, including decreased sea ice extent, increased precipitation, decreased permafrost extent, and increased surface warming, and these will only amplify in the future (Gagnon & Gough, 2005a, 2005b). Climate change may also impact aquatic primary productivity, fish growth, and anadromous migrations in fish (e.g., Reist et al., 2006; Wrona et al., 2006; Stern et al., 2012).

Since anadromous fishes rely on freshwater, estuarine, and marine habitats for growth, reproduction, and migration, they are particularly susceptible to effects of climate warming, as they may be influenced by change in any of these separate but connected environments (Gross,

1987; see Reist et al., 2006). If productivity of freshwater environments increases as a result of climate warming (see Reist et al., 2006, Wrona et al., 2006), anadromous fishes may remain in freshwater instead of migrating to sea (Gross, 1987) because the incentive to migrate for greater access to resources in the more productive marine environment may be diminished (Reist et al., 2006). As freshwater residents have been shown to have higher mercury concentrations than anadromous individuals of the same species (see Swanson and Kidd, 2010), changes in anadromy in this region could therefore have implications for exposure of humans to mercury through fish consumption.

1.6 Study Objectives

Given the importance of understanding anadromy in terms of fish ecology, management, and contaminant exposure and accumulation, the overall objective of my thesis research was to develop a better understanding of the life history and extent of anadromy in three subsistence fish species in three rivers (Severn, Winisk, and Attawapiskat) that drain the Hudson and James Bay Lowlands and flow into Hudson and James bays. Using a combination of otolith microchemistry (otolith strontium concentration ([Sr]) to trace use of marine vs freshwater habitat) and stable isotope analysis (δ^{34} S to trace reliance on marine or freshwater prey resources), my specific objectives and hypotheses were as follows:

Objective 1: To more fully describe aspects of the life history (e.g., age at first migration, proportion of migratory individuals) of Cisco and Lake Whitefish in each of the three study rivers in the Hudson Bay Lowlands.

Based on research conducted on rivers in Eastern James Bay, I hypothesized that the majority of Cisco and Lake Whitefish from rivers that flow into western James and Hudson Bay

would be migratory, and that they would migrate within their first year of life. I further hypothesized that prevalence of migratory individuals would be different among rivers, as a result of the salinity patterns and water currents within Hudson and James Bay, and the differences in productivity between fresh and marine waters that differ among rivers.

Objective 2: To investigate whether North American Northern Pike access marine/brackish environments, and if found to do so, to describe their life history (e.g., age at first migration, proportion of migratory individuals). To investigate this possible use of marine/brackish habitats, I used the Hudson Bay Lowlands as a model system where Northern Pike have access to

marine/brackish waters.

I hypothesized that some Northern Pike would migrate to marine/brackish waters in the Hudson Bay Lowlands, based on documented anadromous behaviour in the Baltic Sea. I hypothesized that the prevalence of anadromous individuals and life history of anadromous individuals would be different from that previously observed in the Baltic Sea, and because the salinity of Hudson and James Bay can exceed known salinity tolerances of Northern Pike, I predicted prevalence of anadromy to be lower in the Hudson Bay Lowlands than in the Baltic Sea. I further predicted that, unlike the Baltic Sea, there would be no evidence of brackish water resident individuals in the Hudson Bay Lowlands, as a result of higher salinity than in the Baltic Sea.

Objective 3: To examine the reliance of Cisco, Lake Whitefish, and Northern Pike on marinederived nutrients.

I hypothesized that in each of the three study species, isotope ratios (especially $\delta^{34}S$) would differ between individuals classified as migratory and non-migratory (based on otolith microchemistry results) reflecting different use of marine and freshwater habitats. I also

hypothesized that there would be differences in habitat use (as traced by isotopes) among species, due to differences in salinity tolerances among species. Given that isotope ratios are in general higher in marine environments than in freshwaters, I predicted that, within each species, migratory individuals would have significantly higher isotope ratios than non-migratory individuals. Based on the higher salinity of Hudson and James bays compared to the Baltic Sea, and the higher salinity tolerances of Cisco and Lake Whitefish compared to Northern Pike, I further predicted that migratory Cisco and Lake Whitefish would have higher δ^{34} S ratios than Northern Pike. I hypothesized that proportional contribution of marine-derived nutrients/prey to fish tissue would differ among species, and I predicted that stable isotope mixing models would indicate that migratory Cisco and Lake Whitefish had greater proportional contributions of marine derived nutrients/prey to diets than migratory Northern Pike. I also predicted that individuals of all species classified as non-migratory, if present, would have diets composed of entirely freshwater-derived nutrients/prey.

1.7 Expected Significance

My aim was to better understand fish life history in the HBL region. Climate change has the potential to increase freshwater productivity, which could reduce fitness benefits gained from migrating to sea, and result in fewer anadromous migrations and/or fewer anadromous individuals within partially migratory populations (Reist et al., 2006). Warming waters could also change interspecific interactions (e.g., competition, predation, parasitism) and consequently life history of northern fishes via a northward shift in the distribution of more southern fish species (see Reist et al., 2006). Diadromous species of fish are particularly susceptible to disturbances as they require two connected habitats for survival and reproduction (Gross, 1987). Understanding the use of multiple habitats by anadromous fishes will allow the creation and

implementation of conservation plans to ensure proper protection of all habitats used by migratory organisms, ultimately protecting migratory species that make use of multiple habitats. In addition, in combination with contaminant data, and the knowledge that life history influences contaminant bioaccumulation, this work will be used by researchers, local fishers, and policymakers to interpret variability in fish mercury concentrations and ensure safe fish consumption.

CHAPTER TWO - METHODS

2.1 Study Location

The Hudson Bay Lowlands (HBL) is an area of approximately 474 000 km² on the west side of Hudson and James Bay. The lowlands are located in the Far North of Ontario and Manitoba, extend from 51°N to 65°N latitude (Rouse, 1991), and are bounded on the east at approximately 78°W and on the west at approximately 96°W. The landscape of the Lowlands is largely composed of peatlands in the form of bogs and fens, with many pools and ponds throughout (McCrea & Fischer, 1986).

The rivers included in this study are the Severn, Winisk, and Attawapiskat rivers, the mouths of which are located on the western coast of Hudson and James bays, in the Hudson and James Bay Lowlands (Figure 1). These rivers were selected for study because they all have coastal First Nations communities and associated subsistence fisheries. The Severn, Winisk, and Attawapiskat rivers are a subset of 35 major rivers that drain into Hudson and James Bay, and have drainage basin sizes of approximately 102800, 67300, and 50500 km², and annual discharges of 21.20, 14.69, and 11.08 km³ year¹, respectively (Energy Mines and Resources Canada, 1985; Déry et al., 2005).

2.2 Sample Collection

2.2.1 Fish Collection and Processing

Species chosen for this study represent a valuable resource to subsistence fishers of the HBL, and the included species are: Northern Pike, Lake Whitefish, and Cisco. For each river, the target sample size was 20 fish of each species of interest from waters above tidal influence and 20 fish of each species from within the zone of tidal influence. This sampling strategy was employed to maximize the probability of capturing both non-migratory and migratory life history

types of each species in each river (if present). Collection of samples occurred via pre-existing government, First Nations, and industry sampling programs. Fish were captured through angling and gill netting. Multi-mesh benthic gill nets (28-127 mm mesh size, 0.9 m high, 24.8 m long; large mesh River Index Netting gillnets; Jones & Yunker, 2010) were used to capture fish in fall (September/October) 2011, 2013, 2014, and 2015. Some fish from the Winisk River were captured in June of 2011. Angling also occurred in fall 2015 to supplement sample sizes, particularly for Northern Pike. Table 1 outlines the sample sizes of each species of fish that were collected and analysed for otolith microchemistry and stable isotope ratios. Sampling locations are shown in Figure 2.

Upon capture, length (mm), weight (g), sex, and maturity were recorded for each fish. Stomach contents were also recorded, although, due to field sampling constraints, only coarse estimates of stomach contents were possible (i.e. fish, invertebrates, etc.). Skinless, dorsal muscle tissue was collected from each fish for stable isotope analysis, and stored in Whirl-Pak bags. Ageing structures (both sagittal otoliths, as well as cleithra for Northern Pike) were collected from each fish. Otoliths were cleaned in deionized water, dried, and stored in centrifuge tubes in advance of otolith microchemical and ageing analyses. Flesh was removed from cleithra using a cloth and warm water, and the structures were dried and stored in paper envelopes prior to ageing analysis.

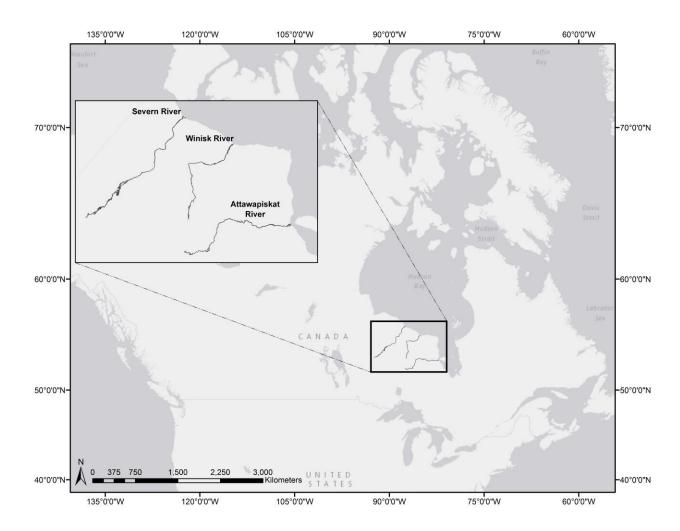


Figure 1. Map of the Severn, Winisk, and Attawapiskat rivers in the Hudson and James Bay Lowlands of the Far North of Ontario that are the sites of fish collection in this study. (Credit: Angela Graham).

Table 1. Sample sizes of fish collected and analyzed from above or within the zone of tidal influence of the Attawapiskat, Severn, and Winisk rivers. The aim was to capture both freshwater resident and migratory individuals of each species, from each river, if present.

	Cisco		Lake Whitefish		Northern Pike	
River	Upstream of tide	Tidal	Upstream of tide	Tidal	Upstream of tide	Tidal
Attawapiskat	8	25	16	31	20	21
Severn	20	26	22	20	35	3
Winisk	28	20	24	19	20	19

2.2.2 Baseline Organism Collection

To facilitate isotopic baseline correction (Post, 2002), clams (Unionidae and Sphaeriidae) and snails (Lymnaeidae, Planoribae, and Physidae) were collected from each river, when possible. Marine mussels (Mytilidae) were not ubiquitously available, and were collected opportunistically from near-shore marine waters northwest of the mouth of the Severn River. Logistical constraints prevented sampling of additional marine organisms for baseline analysis.

2.2.3 Water Sample Collection and Analysis

For otolith microchemistry to provide meaningful information regarding marine migrations, water chemistry must differ between freshwater and marine environments. Water samples were gathered from each river to determine background Sr:Ca ratios in the water, as ratios in water influence ratios in otoliths (Kraus & Secor, 2004), and Sr:Ca ratios and Sr concentrations in salmonid and Northern Pike otoliths correlate positively with salinity (Zimmerman, 2005; Engstedt, Koch-Schmidt, & Larsson, 2012). Water samples were collected in 2014 and 2015

from each river at sites above tidal influence, and in marine waters near the mouth of each of the Attawapiskat, Severn, and Winisk rivers (Figure 2).

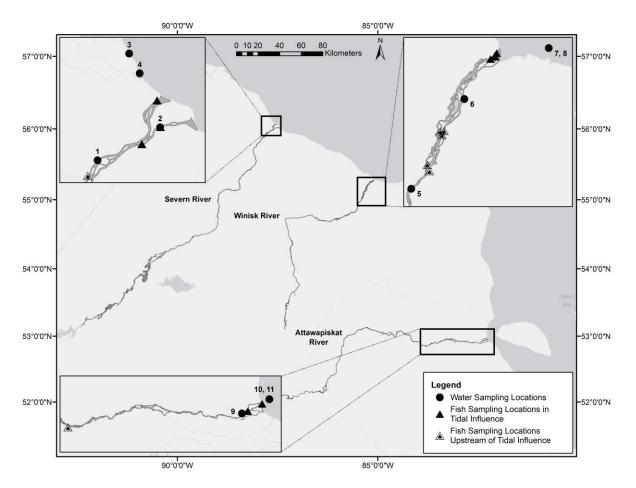


Figure 2. Locations of fish and water sampling in the Severn, Winisk, and Attawapiskat rivers. Water sampling locations are numbered, corresponding to numbers listed in Table 3 (results). (Credit: Angela Graham).

Freshwater samples were collected via surface grab, filtered with a 0.45 µm filter, and refrigerated or kept on ice prior to analysis. Analyses for Sr and Ca concentrations were conducted at the Ontario Ministry of Environment and Climate Change (OMOECC) Dorset Environmental Science Centre following the OMOECC MET3474 protocol for metals analysis. Marine water samples were collected via surface grab in 1 L bottles and kept cool on ice.

Samples were filtered with a 0.45 µm filter into a 250 mL HDPE bottle, acidified with 3 mL of HNO₃ and sent to ALS Environmental for analysis of Sr and Ca by ICP-MS. Strontium to calcium (Sr:Ca) molar ratios (mmol) were calculated for each water sampling location and compared between freshwater and marine waters.

2.3 Otolith Analysis

Otolith microchemical analyses were conducted on otoliths of each fish included in this study to examine fish life history and use of marine and freshwater habitats.

2.3.1 Otolith Preparation

One of each pair of cleaned and dried otoliths from each collected fish was prepared for analyses of otolith microchemistry using methods similar to that of Swanson et al. (2010). Otoliths that appeared crystalline were not selected for microchemical analysis, as vaterite inclusions in otoliths affect the concentration of elements (Gauldie, 1996). Clean, dry otoliths were embedded in Buehler EpoThin epoxy resin (Buehler, Lake Bluff, Illinois, USA) with the sulcus side facing up. Curing was facilitated by using a 50 °C drying oven for 48 hrs. Embedded otoliths were then examined, with the sulcus side down, under a dissecting microscope with reflected light. A transverse line was drawn through the core of the otolith to the outer edges to indicate where the otolith should be cut. In some cases, where otoliths had large abnormalities, particularly with otoliths of Northern Pike, these lines were angled significantly so that the line went through the longest axis of the otolith and all annuli would be included in the resulting cut section.

Otoliths were sectioned transversely using a Buehler Isomet low speed saw, with a saw speed of ~100 rpm. Sections were then mounted cut side down on sticky label paper within a 2.5 cm Lucite ring. These rings were backfilled with Buehler EpoThin epoxy resin and allowed to

cure in a 50 °C drying oven for 48 hrs. Rings were wet sanded with distilled water on 30 μm, 9 μm, and 6 μm polishing paper, and finally on a Buehler MetaServ 250 Single Grinder-Polisher polishing wheel with 0.05 μm alumina slurry at 350-400 rpm. Each otolith was imaged with a Leica M80 dissection microscope (Leica Microsystems, Wetzlar, Germany) with reflected light. Rings were then ultrasonically cleaned for 15 minutes in distilled water before being dried and stored in clean KimWipes.

2.3.2 Otolith Microchemistry

Laser ablation inductively coupled plasma mass spectrometry (LA-ICP-MS) was conducted at one of two laboratories, depending on laboratory availability. The first laboratory was located at the Department of Geological Sciences at the University of Manitoba, where a Thermo-Finnigan Element 2 inductively coupled plasma mass spectrometer (ICP-MS) (Thermo Fisher Scientific, Waltham, Massachusetts, USA) coupled to a Nd:YAG laser (Merchantek LUV 213, New Wave Research/Merchantek, Fremont, California, USA) was used. At the second laboratory, the W.M. Keck Collaboratory for Plasma Spectrometry at Oregon State University, a Thermo X-Series II Quadrupole ICP-MS (Thermo Fisher Scientific, Waltham, Massachusetts, USA) coupled to a Photon Machines Analyte G2 (Photon Machines, Bozeman, Montana, USA) 193 nm laser was used.

Laser and ICP-MS conditions as well as data acquisition settings were recorded, and are reported in Table 2. A 50 second warm up period before analysis of each otolith allowed acquisition of background concentrations and correction for instrument drift throughout a run. Calcium was used as an internal standard, and a glass standard, NIST 610 (National Institute of Standards and Technology) was used as an external standard to calculate elemental

concentrations within the otolith. The NIST 610 standard was analyzed at the start and end of every ring of otoliths (5-9 otoliths; approximately 1 hour of instrument time).

Table 2. Laser ablation, ICP-MS, and data acquisition settings for otolith microchemical analysis at both the Winnipeg and Oregon laser systems.

Laser conditions	Sector field ICP-MS with Nd:YAG laser (Winnipeg)	Quadrupole ICP-MS with Excimer laser (Oregon)
Spot size	30 μm	30 µm
Repetition rate	10 Hz	7-10 Hz
Laser scanning speed	2-5 μm·sec ⁻¹ *	3-5 µm·sec ⁻¹ *
Energy density on sample	~7-8 mJ·cm ⁻²	$5.2 \text{ mJ} \cdot \text{cm}^{-2}$
Incident pulse energy	~0.01 mJ	
ICP-MS conditions		
Plasma power	1280 W	1380 W
Cooling gas flow	14.4 L·min ⁻¹	13.0 L·min ⁻¹
Auxiliary gas flow	1.0 L·min ⁻¹	0.80 L·min ⁻¹
Sample gas (Ar)	1.1 L·min ⁻¹	0.99 L·min ⁻¹
Make-up gas (He)	0.67 L·min ⁻¹	0.2 L·min ⁻¹
Data acquisition		
Protocol	Time resolved	Time resolved
Scanning mode	BScan and	Sector only
	EScan	
Detector mode	Analog and	Counting
	counting	
Magnet settling time	1-300 µsec	N/A

^{*}Typically a scanning speed of 3 μ m·sec⁻¹ was used, but 5 μ m·sec⁻¹ was used with very large Northern Pike otoliths, and 2 μ m·sec⁻¹ was used for ventral transects of Northern Pike otoliths to increase spatial resolution.

2.3.3 Reduction of Mass Spectrometry Data

Laser ablation mass spectrometry data were reduced using the trace elements data reduction scheme within Iolite v. 2.3 (The University of Melborne), an application addition to Igor Pro v.

6.3.7.2 (WaveMetrics Inc., Portland, Oregon, USA). After data reduction, [Sr] (ppm) were plotted against distance from the otolith core (calculated as ablation time (sec) x ablation speed (µm/sec)) for each otolith using R Studio v. 3.3.1. Raw data were also smoothed in R Studio using a 10 point moving average (similar to smoothing done by Friedrich & Halden, 2010).

After sample ablation, images of the otoliths, including the laser ablation line, were captured using reflected light on a Leica M80 microscope with a Leica IC80 camera attachment (Leica Microsystems, Wetzlar, Germany). Plots of Sr concentration (ppm) throughout the fish's life (measured as distance from otolith core (μm)) were overlain onto the post-ablation images captured from each otolith.

2.3.4 Determination of Fish Age

Fish ages were determined at the Northwest Fisheries Ageing Lab (Ontario Ministry of Natural Resources and Forestry (OMNRF) in Dryden, Ontario. Ages determined by the OMNRF are traditionally read from 'cracked and burned' or polished thin sections of otoliths for Lake Whitefish and Cisco, and from whole cleithra for Northern Pike. Some of the Cisco and Lake Whitefish fish in this study, however, had ages read from the disks (thick sections) that were prepared for otolith microchemistry. Ages of a subset of Cisco and Lake Whitefish were determined at the same laboratory using either cracked and burned or polished thin section methods as well as the thick section method. Estimates of fish age from cracked and burned or polished thin sections of otoliths yielded similar results to those generated using thick sections of otoliths in leucite rings. The mean difference between thin and thick section methods \pm standard error was 0.347 ± 0.0901 years (n = 49), and the mean difference between crack and burn and thick section methods \pm standard error was 0.692 ± 0.161 years (n = 39).

Annuli of otoliths prepared for analysis with the thin section method were counted under a microscope with transmitted light; the opaque zone appeared dark, and the translucent zone appeared bright under this lighting (see Panfili et al., 2002); one year of growth was counted as a translucent zone followed by an opaque zone. Annuli of otoliths prepared for otolith microchemistry (thick sections) or with the crack and burn method were counted under a microscope with reflected light, where the opaque zone appeared bright, and the translucent zone appeared dark (see Panfili et al., 2002); one year of growth was counted as an opaque zone followed by a translucent zone. Each fish was assumed to be born January first of each year.

2.4 Stable Isotope Analysis

Analyses of stable carbon, nitrogen, and sulphur isotope ratios in fish tissue were conducted to examine the importance of marine and freshwater nutrients/prey resources to the diets of each fish included in this study.

2.4.1 Sample Preparation and Analysis

Snails (Lymnaeidae, Planoribae, and Physidae), clams (Sphaeriidae and Unionidae), and marine mussels (Mytilidae) were removed from their shells. Foot muscle was dissected from the main body of both clams and marine mussels for analysis whereas whole bodies were analyzed for fingernail clams and snails. All fish muscle tissue, invertebrate foot muscle tissue, and invertebrate whole viscera were stored in Whirl-Pak bags and frozen at -20°C, until samples were freeze-dried for 48 hours on a Labconco Freezone 2.5 Liter Freeze Dry System at -54 °C and 10 mTorr (Labconco, Kansas City, Missouri, USA). Freeze-dried tissue was homogenized using a mortar and pestle or a ball mill. These samples were stored in new, clean, 20 mL borosilicate scintillation vials. Samples were weighed into tin cups on a Mettler-Toledo Analytical Microbalance (model XP05DR) (Mettler-Toledo, Greifensee, Switzerland) for

analyses of stable isotope ratios of carbon (C), nitrogen (N), and sulphur (S) (e.g., Swanson et al. (2010)). Target sample weights were 0.3-0.32 mg for C and N, and 1.9-2.1 mg for S.

Stable carbon (¹³C/¹²C) and nitrogen (¹⁵N/¹⁴N) isotope analyses for fish caught in 2011 and 2013 were completed at the Stable Isotopes in Nature Lab at the University of New Brunswick, Fredericton, New Brunswick using a Finnigan Mat Delta Plus continuous flow isotope ratio mass spectrometer (CF-IR-MS) coupled to a Thermoquest NC2500 elemental analyzer. Samples from fish captured in 2014 and 2015 were analyzed for stable C and N isotopes by the Environmental Isotope Laboratory at the University of Waterloo with an 1108 Elemental Analyzer (Fisons Instruments, Ipswich, United Kingdom) coupled to a Delta XL (Thermo Fisher Scientific, Waltham, Massachusetts, USA) continuous flow isotope ratio mass spectrometer. All sulphur isotope ratio (³⁴S/³²S) analyses were completed at the University of Waterloo Environmental Isotope Laboratory using an elemental analyzer, Costech CNSO 4010 (Costech Analytical Technologies, Valencia, California, USA) coupled with an Isochrom continuous flow isotope ratio mass spectrometer (CFIRMS) (GV Instruments Ltd. (Micromass Ltd.), Wythenshave, Manchester, UK). A subset of samples (n = 16) were analyzed for C and N stable isotope ratios at both the University of Waterloo lab and the University of New Brunswick lab. The mean percent (%) difference in δ^{15} N between instruments \pm standard error (SE) was 6.58 ± 2.37 % (mean absolute difference \pm SE = 0.747 \pm 0.282 %), and the mean percent difference in δ^{13} C between instruments \pm SE was 3.76 \pm 1.73 % (mean absolute difference \pm SE = 1.02 \pm 0.0219 %). Duplicate samples were run every 10th sample from the University of Waterloo laboratory and every 20th sample from the SINLAB, and no less than 20 % of a run was made up of standard or reference materials.

The equation for calculation of stable isotope ratios (%) is as follows:

Equation 1:
$$\delta X = \left[\left(\frac{R \ sample}{R \ standard} \right) - 1 \right] \times 10^3$$

X = element of interest

 $R = \text{ratio of heavy to light isotopes of element } X\left(\frac{j_X}{i_X}\right)$; where j is the heavy isotope, and i is the light isotope of element X.

Reference materials were Vienna Pee Dee Belemnite for C, Atmospheric Air for N, and Vienna Canyon Diablo Triolite meteorite (VCDT) for S (Gonfiantini, Stichler, & Rozanski, 1995). Standard delta (δ) notation was used to express stable isotope ratios in per mil (‰) relative to a standard (Equation 1). International reference materials (i.e. IAEA-N1 + N2, IAEA-CH3 + CH6, USGS-40 + 41, IAEA-SO-5, IAEA-SO-6, NBS-127, NBS-123, IAEA-S1 to-S3 (only IAEA reference materials at the SINLab)) and in-house standards (e.g. NIST 1577b (Bovine liver)) calibrated with these reference materials were used to ensure that analytical error for stable isotopes of carbon, nitrogen, and sulphur (δ^{13} C, δ^{15} N, and δ^{34} S, respectively) did not exceed 0.2 ‰, 0.3 ‰, and 0.3 ‰. Duplicate samples were within 0.3 ‰, 0.5 ‰, and 0.8 ‰ (2 %, 7 %, and 8 % difference) for C, N and S, respectively.

2.5 Data Analysis

2.5.1 Visual Classification of Fish as Migratory or Non-Migratory

To differentiate between migratory and non-migratory fish, I visually assessed [Sr] profiles of each fish for evidence of increased [Sr] that may be reflective of time spent in marine waters. Fish classified as non-migratory (thought to remain in freshwater) were characterized by low [Sr] and flat profiles. In contrast, fish that were characterized as migratory showed distinct oscillations between higher and lower [Sr], and the higher [Sr] was well above and clearly

differentiable from the observed baseline (e.g., Swanson et al., 2010; Kissinger et al., 2016). Although fish may not all be easily classified into categories of either migratory or nonmigratory and often there is a gradient of anadromy within a system (McDowall, 1987; see Quinn and Meyers, 2004), I used categories to classify fish as this is commonly done in the literature (e.g., Howland et al. 2001; Brown et al. 2007; Swanson et al. 2011; Harris et al. 2012), and because categories can be especially useful when there are groupings of fish with distinct behaviour. To visualize how [Sr] corresponded to annuli, and to quantify age of first migration, profiles of [Sr] were overlain onto post-ablation photographs for each otolith. For each migratory fish, the number of migrations to seawater was then assessed visually. If an oscillation in [Sr] was detected near the edge of the otolith, it was counted as a migration only if the [Sr] began to decrease, indicating that a fish was returning from the seaward migration. The number of migrations recorded for each fish was set to be less than or equal to the maximum age of the fish; fish that had one more migration than year of age likely migrated in their most recent year of life, but were captured before an annulus was laid down. Age of first migration was also quantified for each fish using [Sr] profile overlays. Migration year was recorded as the age of the fish in the year in which it first migrated. Correlation of fish age and number of migrations were determined with Pearson product moment correlation coefficients in Microsoft Excel 2013.

Deviations in [Sr] from the early freshwater life phase were relatively easy to discern in [Sr] profiles of migratory Cisco and Lake Whitefish. However, visual interpretation of Northern Pike profiles was more ambiguous, with apparent, but less differentiable elevated [Sr] relative to concentrations in the freshwater life phase. Therefore, in addition to visual assessment, comparisons were made between the Sr:Ca profile of a Northern Pike classified as migratory from this study and marine migrant Northern Pike from other published studies; Sr:Ca was

compared as this was the variable reported in the Baltic Sea Northern Pike literature. Sr:Ca profiles were selected from the literature (data from: Westin & Limburg, 2002; Engstedt et al., 2010; Rohtla et al., 2012; Engstedt et al., 2014) and were plotted with a sample migratory Northern Pike Sr:Ca profile from this study. The distance from the otolith core was scaled to the maximum distance of each individual otolith transect to standardize the profiles. Since precision, accuracy, and sensitivity differs among instrumentation types, and studies used different instrumentation (Campana et al., 1997), absolute Sr:Ca ratios were not directly compared. For each otolith profile, an average Sr:Ca was calculated for a region of the profile assumed to indicate freshwater residency. This average was used to calculate relative Sr:Ca ratios for the assumed migratory phase of each Northern Pike otolith included in the comparison plot. A 10-point moving average was calculated for the Sr:Ca values of a Northern Pike profile from this study, and plotted with scaled Sr:Ca from profiles selected from the literature. Deviations from the Sr:Ca freshwater baseline were then visually compared among studies.

2.5.2 Strontium Range and Maximum Plots

In addition to classifying fish as migratory or non-migratory based on visual analysis of overlays, I plotted [Sr] range (ppm) (Sr maximum – Sr minimum) against [Sr] maximum (ppm) for each otolith. These plots have been shown by other researchers to be helpful in differentiating among groups of fish with distinct migratory patterns; fish with higher Sr concentration range and maximum have a higher reliance on marine environments than fish that plot with low Sr concentration range and maximum (e.g., Loewen, Gillis, & Tallman, 2009, Harris et al., 2012). Strontium concentration range and maximum were calculated from the dataset of 10-point moving averages (smoothed data) that was generated for each fish. Plots were generated in Microsoft Excel 2013 for each species and each study river.

2.5.3 Stable Sulphur Isotope Ratios

Arithmetic means of $\delta^{34}S$ ratios were calculated for each invertebrate taxa, and each visually-determined (using otolith microchemistry) migratory group of fish species (if present) in each river. To determine if mean species-specific $\delta^{34}S$ were significantly different between migratory and non-migratory fish within a river, t-tests were performed when adequate sample sizes were available. To determine if mean $\delta^{34}S$ were significantly different among species within migratory groups and rivers, one-way analysis of variance (ANOVA) were performed when adequate groups and sample sizes were available. Alpha was set at 0.05, and statistics were performed in IBM SPSS Statistics v. 24. Plots of mean $\delta^{34}S$ ratios were created in Microsoft Excel 2013 for each species, migratory group, and river, with average freshwater and marine baseline values included for comparisons between rivers and species.

2.5.4 Mixing Model to Determine Proportion of Marine-Derived Nutrients

To estimate the proportion of freshwater and marine-derived nutrients in the diets of captured fish, I applied mixing models to $\delta^{34}S$ and $\delta^{13}C$ data for each river, species, and migratory group (visually classified) of fish. However, the $\delta^{13}C$ baseline was not fully characterized in this study, and the $\delta^{13}C$ ratios of consumers were not within the range of captured baseline organisms; as a result, only $\delta^{34}S$ was used in the model. Since I was only interested in differentiating between two defined sources in the diet (freshwater and marine sources), only one stable isotope tracer was necessary. I used MixSIAR, a Bayesian mixing model (Stock & Semmens, 2013) with one stable isotope tracer ($\delta^{34}S$) to estimate median (and 95 % credible intervals) proportional marine and freshwater-derived nutrient contributions for each migratory group (migratory or non-migratory), species, and river. Proportional contributions of freshwater- and marine-derived prey to fish diets were then compared among

species, migratory groups, and rivers. Bayesian mixing models allow incorporation of uncertainty measurements for food sources, isotopic signatures, and contributions of each source to the mixture (Phillips et al., 2014).

To estimate trophic fractionation for each species, I assumed that Cisco and Lake Whitefish were feeding one trophic level above the baseline organisms, and that Northern Pike were feeding at two trophic levels above the baseline organisms. Fractionation (discrimination) values for δ^{34} S were assumed to be 0.5 ± 0.56 % per trophic transfer (McCutchan et al., 2003). To generate the discrimination values included in the model, I multiplied the assumed trophic fractionation and associated error by the assigned trophic position of each species.

Each model was run with three MCMC (Markov chain Monte Carlo) chains with a length of 100 000 runs, a burn-in length of 50 000 runs, and thinning so that every 50th run was retained; these settings were the default settings using the very long model run length in MixSIAR. Chain convergence was determined through the Gelman-Rubin Diagnostic and the Geweke Diagnostic. The error term in the model was set to residual*process, as this type of error was found to be more accurate than previous methods of error estimation and is more ecologically realistic (Stock & Semmens, 2016). Priors were set to uninformative.

CHAPTER THREE - RESULTS

3.1 Water Chemistry and Baseline Analysis

There were substantial differences in molar ratios of strontium to calcium (Sr:Ca) between water sampled in the freshwater and marine environments for each river (Table 3). I was thus confident that if fish were migrating to marine waters for summer feeding, otolith microchemistry would be an effective technique for detecting migrations.

The mean marine $\delta^{34}S$ ratio in marine invertebrates from near the mouth of the Severn River was 17.8 ± 0.5 % standard deviation (Table 4); this value is within the range of other marine $\delta^{34}S$ ratios reported in other studies (~15 to 21 %) (e.g., Peterson & Fry, 1987; Fry, 1988; Mizota, Shimoyama, & Yamanaka, 1999; MacAvoy et al. 2000; Swanson et al., 2011). Although there are likely slight differences in baseline marine $\delta^{34}S$ ratios isotope ratios along the coast of James/Hudson bays, the marine isotope values from mussels collected beyond the mouth of the Severn River were assumed to be reflective of the Hudson and James Bay environment along the western coast. The freshwater invertebrate baseline $\delta^{34}S$ ratios in each river ranged between 9.9 and 14.6 % lower than the marine invertebrate baseline ($\delta^{34}S$ ratios ranging from 3.24 to 7.90 %), indicating good isotopic separation of marine and freshwater environments.

After examination of stable sulphur ($\delta^{34}S$), nitrogen ($\delta^{15}N$), and carbon ($\delta^{13}C$) ratios for freshwater and marine endmembers (Table 4), sulphur and carbon were determined to provide the most isotopic distinction between freshwater and marine baseline organisms. There was not enough isotope distinction in $\delta^{15}N$ between freshwater and marine endmembers to be useful in differentiating marine vs freshwater feeding habits.

Table 3. Strontium to calcium ratios in water from freshwater and marine locations. There were differences in Sr:Ca between freshwater and marine water collection sites in each river, indicating that otolith microchemistry would likely be an effective method for differentiating marine- vs. freshwater habitat use. Site numbers correspond to numbers on map (Figure 2).

Site #	River	Latitude and Longitude	Freshwater (FW) or Marine (M) Collection	Sr:Ca ratio (mmol)
1	Severn	55° 57′00.2″ N 087° 46′62.1″ W	FW	0.636
2	Severn	56° 00′67.6″ N 087° 34′14.5″ W	FW	0.568
3	Severn	56° 08′89.3″ N 087° 40′31.9″ W	M	8.132
4	Severn	56° 06′69.4″ N 087° 38′21.1″ W	M	6.699
5	Winisk	54° 57′46.9″ N 85° 28′52.4″ W	FW	0.057
6	Winisk	55° 10′29.4″ N 85° 15′25.7″ W	FW	0.789
7	Winisk	55° 17′54.5″ N 084° 54′20.9″ W	M	7.575
8	Winisk	55° 17′69.6″ N 084° 56′53.2″ W	M	5.785
9	Attawapiskat	52° 55′13.6″ N 82° 25′27.7″ W	FW	0.073
10	Attawapiskat	52° 59′42.4″ N 82° 11′58.0″ W	M	6.787
11	Attawapiskat	52° 59′42.4″ N 82° 11′58.0″ W	M	6.839

Table 4. Summary of mean \pm standard deviation $\delta^{34}S$, $\delta^{15}N$, and $\delta^{13}C$ ratios freshwater and marine baseline for each of the Attawapiskat, Severn, and Winisk rivers of the Hudson Bay Lowlands. The organisms included in this baseline are identified. The mean marine isotope baseline value was higher than the freshwater baseline isotope value from all rivers, however, was most different for $\delta^{34}S$, indicating good isotopic separation between freshwater and marine endmembers.

Site	Organisms	Number of Individuals	δ^{34} S (‰)	δ^{15} N (‰)	δ ¹³ C (‰)
Attawapiskat	Unionidae	4	7.90 ± 2.0	4.10 ± 0.71	-29.3 ± 3.9
	Snail*	3	7.90 ± 2.0	4.10 ± 0.71	-29.3 ± 3.9
Severn	Unionidae	3	3.24 ± 0.59	4.74 ± 0.87	-33.6 ± 2.1
	Sphaeriidae	2**	3.24 ± 0.39	4.74 ± 0.67	-33.0 ± 2.1
Winisk	Snail*	3	6.35 ± 0.51	2.76 ± 0.26	-32.7 ± 0.32
Hudson Bay near the Severn River	Mytilidae	7	17.8 ± 0.52	8.74 ± 0.14	-23.8 ± 0.27

^{*}Snails include individuals from the families: Lymnaeidae, Planoribae, and Physidae.

3.2 Otolith Microchemistry

3.2.1 Cisco

All but one Cisco (126 of 127 fish) had otolith [Sr] profiles consistent with that of a migratory fish (see Figure 3 and Table 5). All migratory Cisco grouped together on Sr range and maximum plots, and had maximum [Sr] of >3500 ppm (Figure 4). In contrast, the one Cisco that was classified as non-migratory (from the Winisk River) had a maximum Sr concentration of ~500 ppm, and plotted in the bottom left quadrant of the Sr range and maximum plot (Figure 4).

^{**}Each of these samples is a composite of 35 individuals.

One group of migratory Cisco from the Attawapiskat River had smaller Sr ranges than the rest of the migratory Cisco from this river (Figure 4). All of these Cisco had high Sr concentrations at the core of the otolith that resulted in a smaller Sr range.

The mean number of migrations for migratory Cisco was 5 from the Attawapiskat River (range: 3-7 migrations), 5 for the Severn River (range: 1-10 migrations), and 8 for the Winisk River (range: 2-14) (Table 6). Differences among rivers in number of migrations in general reflected differences in mean ages: migratory Cisco were on average 5.8 years of age in the Attawapiskat River (range: 3-10 years), 5.0 years of age in the Severn River (range: 3-10), and 10.6 years in the Winisk River (range: 5-30 years) (Table 6). There was a significant positive correlation between fish age and number of migrations for migratory Cisco of each of the study rivers (Pearson product moment correlation, r = 0.50, p = 0.003, df = 31; r = 0.79, p < 0.001, df = 46; and r = 0.70, p < 0.001, df = 45 from the Attawapiskat, Severn, and Winisk rivers, respectively). The one non-migratory Cisco from the Winisk River was 11 years old. The mean age of first migration for migratory Cisco was 0.0 years, indicating that the one non-migratory Cisco from the Winisk River was old enough to have migrated.

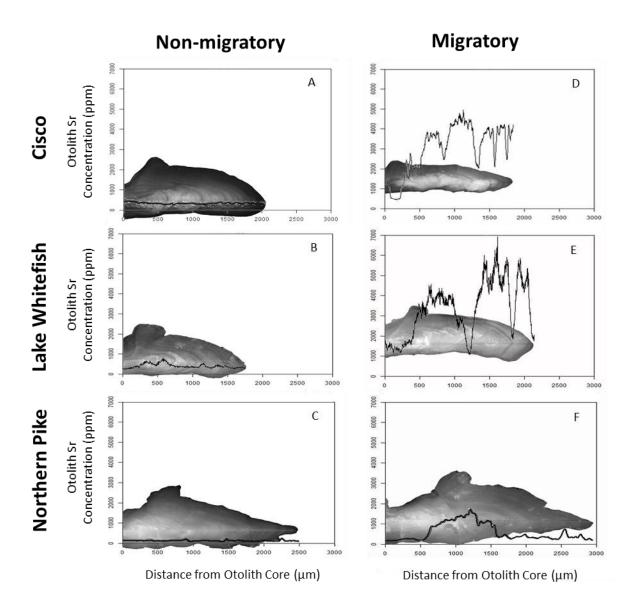


Figure 3. Example strontium (Sr) concentration profiles overlain onto otolith images. These otolith microchemical profiles are representative of non-migratory and migratory categories of each species of fish. Data have been smoothed with a 10 point moving average (see methods). Fish classified as non-migratory using visual methods had Sr profiles that were flat and low throughout the whole otolith (A,B,C) whereas fish that were classified as migratory had [Sr] profiles that oscillated between higher and lower [Sr] (D,E,F). The range of [Sr] was much larger for migratory Cisco and Lake Whitefish than for migratory Northern Pike.

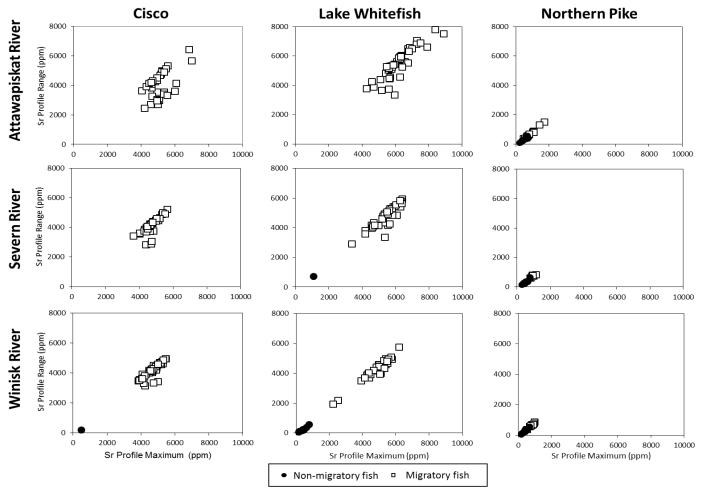


Figure 4. Plots of strontium (Sr) concentration maximum (ppm) and range (ppm) based on otolith microchemistry profiles from individual fish otoliths for all study species. Fish classifies as migratory from otolith microchemistry profiles were characterized by higher [Sr] range and [Sr] maximum than fish classified as non-migratory. Northern Pike were difficult to classify visually, and migratory categories were as not well separated on [Sr] range and maximum plots; see Figure 5 for a [Sr] range and maximum plot for Northern Pike at an expanded scale.

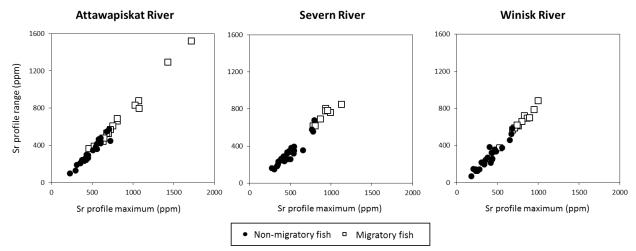


Figure 5. Plots of [Sr] maximum (ppm) and [Sr] range (ppm) based on [Sr] profiles from otolith microchemistry of individual Northern Pike otoliths. Scale is expanded from Figure 4. Fish classified as migratory were characterized by higher [Sr] range and [Sr] maximum than fish classified as non-migratory, but overlap between the two visually-classified categories was observed.

Table 5. Proportion of individuals visually classified as non-migratory and migratory from each river. The majority of Cisco and Lake Whitefish were classified as migratory, and the majority of Northern Pike were classified as non-migratory.

Species	River	Total # of Fish	Proportion Non- migratory	Proportion Migratory
Cisco	Attawapiskat	33	0	1
	Severn	46	0	1
	Winisk	48	0.02	0.98
Lake	Attawapiskat	47	0	1
Whitefish	Severn	42	0.02	0.98
	Winisk	43	0.23	0.77
Northern	Attawapiskat	41	0.61	0.39
Pike	Severn	38	0.79	0.21
	Winisk	40	0.70	0.30

3.2.2 Lake Whitefish

The majority of Lake Whitefish in this study were visually classified as migratory (100%) from the Attawapiskat River, 98 % from the Severn River, and 77 % from the Winisk River) (see Figure 3 and Table 5). The proportion of non-migratory fish identified in this study was higher in the Winisk River than in the other two rivers (Table 5). All Lake Whitefish that were classified as migratory using the visual technique grouped together on [Sr] range and maximum plots; migratory fish had high [Sr] range and maximum values (>2000 ppm maximum Sr; Figure 4), whereas non-migratory fish had relatively lower Sr range and maximum values (<900 ppm maximum Sr; Figure 4). The number of migrations for migratory individuals, on average, was highest for Lake Whitefish from the Winisk River, followed by the Severn and then Attawapiskat rivers (Table 6). Similar to the results for Cisco, this appeared to be explained by mean age of fish. Lake Whitefish from the Winisk River were older, on average, than Lake Whitefish from the Severn and Attawapiskat rivers (see Table 6), and older fish made more migrations to sea (mean age of first migration was similar; Table 6). There was a significant positive correlation between fish age and number of migrations for migratory Lake Whitefish from each of the study rivers (Pearson product moment correlation, r = 0.89, p < 0.001, df = 45; r= 0.68, p < 0.001, df = 39; and r = 0.50, p = 0.003, df = 31, from the Attawapiskat, Severn, and Winisk rivers, respectively). The range of ages of non-migratory and migratory Lake Whitefish from the Winisk River did not overlap, which could indicate that non-migratory fish were too young to have migrated, although some differences could be a result of error associated with fish age estimation. The mean age of first migration of Lake Whitefish from the Winisk River was 1.6 years, however, which is younger than the mean age of non-migratory fish from this river

(6.5 years). It thus appears that non-migratory Lake Whitefish from the Winisk River were old enough to have migrated.

Table 6. Mean age (range) for visually classified non-migratory and migratory Cisco, Lake Whitefish, and Northern Pike from the Attawapiskat, Severn, and Winisk rivers. Also included is the number of migrations for migratory fish. See text for definitions of migratory groups, as well as assignment methods.

		Non-migratory Fish			Mig		
Species	Location	#	Mean	# of	Mean age,	Mean #	Mean Age
		of	age,	fish	range	migrations,	of First
		fish	range			range	Migration*
Cisco	Attawapiskat	0	N/A	33	5.8 (3-10)	5.0 (3-7)	0.0 (0-1)
	Severn	0	N/A	46	5.0 (3-10)	4.7 (1-10)	0.0(0-1)
	Winisk	1	11 (N/A)	47	10.6 (5-30)	8.1 (2-14)	0.0 (0-1)
Lake	Attawapiskat	0	N/A	47	4.1 (1-11)	3.8 (1-10)	0.1 (0-1)
Whitefish	Severn	1	9 (N/A)	41	7.4 (4-22)	6.1 (4-13)	0.2(0-7)
	Winisk	10	6.5 (3-8)	33	14.8 (8-35)	8.8 (1-16)	0.6(0-6)
Northern	Attawapiskat	25	5.0 (1-11)	16	7.6 (3-13)	1.7 (1-3)	2.8 (0-8)
Pike	Severn	30	4.6 (2-10)	8	4.6 (2-6)	1.5 (1-4)	1.3 (0-4)
	Winisk	28	5.8 (2-9)	12	5.8 (4-10)	1.8 (1-5)	2.0 (0-4)

^{*} Missing from the calculation of age of first migration due to unavailability of otolith post-ablation photos are: six, two, and three Lake Whitefish from the Attawapiskat, Severn, and Winisk rivers, respectively, and two Northern Pike from the Attawapiskat River.

3.2.3 Northern Pike

The majority of Northern Pike in this study were classified visually as non-migratory (61 % from the Attawapiskat River, 79 % from the Severn River, and 70 % from the Winisk River), although Northern Pike were difficult to classify visually compared to Cisco and Lake Whitefish (Figure 3 and Table 5). Most otoliths from Northern Pike were characterized by low, flat [Sr] profiles indicative of fish that remained in freshwaters. However, I also observed fish with oscillating [Sr], possibly indicating some use of marine or brackish waters. I found that

oscillations in otolith [Sr] were much less distinct for Northern Pike than for either Cisco or Lake Whitefish, and that Northern Pike classified visually as migratory had lower [Sr] range and [Sr] maximum than migratory Cisco and Lake Whitefish.

Unlike Cisco and Lake Whitefish, there was no clear distinction in [Sr] range and maximum between fish classified visually as migratory and those classified visually as non-migratory; the two categories overlapped, especially in the Attawapiskat River (Figures 4 and 5). Strontium concentration range and maximum of Northern Pike were in general similar among study rivers; however, two fish from the Attawapiskat River had higher [Sr] maximum and [Sr] range than the other fish, leading to a wider spread of these values in the Attawapiskat River compared to the other study rivers (Figure 5). The mean number of migrations was similar among rivers (Table 6). The mean ages of non-migratory and migratory Northern Pike were also similar, and the range in ages overlapped between the two migratory categories (Table 6). Compared to both migratory Cisco and Lake Whitefish, migratory Northern Pike made fewer migrations, and had older mean ages of first migration (Table 6).

Despite the much smaller range in otolith [Sr] in Northern Pike than in the other two species, Northern Pike from the current study had normalized Sr:Ca similar to those from Northern Pike considered to be anadromous from the Baltic Sea (Figure 6). Variability exists among the patterns in scaled Sr:Ca profiles from Northern Pike captured in the Baltic Sea, as well as in maximum scaled Sr:Ca values. This could perhaps indicate individual and/or geographic differences in migrations in Northern Pike from the Baltic Sea. Although Northern Pike were difficult to classify, the similarity of these normalized Sr:Ca plots, and the higher normalized Sr:Ca of the Northern Pike from the HBL compared to that of a brackish water resident

individual in the Baltic Sea provides evidence that at least some Northern Pike were making use of brackish waters in this study.

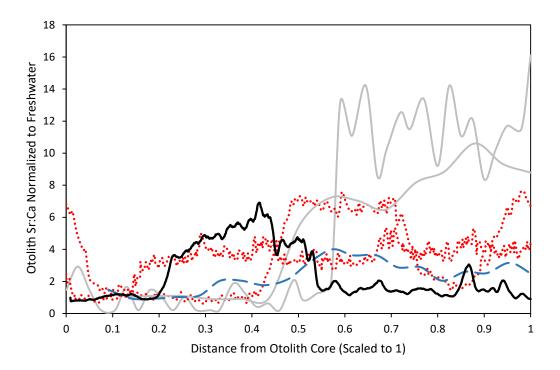


Figure 6. Comparison of Northern Pike otolith microchemistry results with results from literature. The distance from otolith core was scaled to the maximum length of each otolith. Strontium to calcium ratios were scaled to the mean of the freshwater Sr:Ca value within each otolith. The solid black line (—) represents one otolith from a Northern Pike classified as migratory from this study, the long dashed blue line (—) represents a brackish water resident individual (Rohtla et al. 2012), short dashed red lines (——) represent anadromous individuals moving to salinities of ~6-7 ppt in the Baltic Sea (Engstedt et al. 2010, 2014) and the solid grey lines (—) represent additional example otoliths classified as making use of marine waters from other studies (Westin & Limburg, 2002; Rohtla et al., 2012). While some profiles showed distinct differences between high and low [Sr] (profiles with grey lines), the profiles with red lines were similar to that of the Northern Pike plotted from the current study and were classified

as anadromous in the Baltic Sea. The profile with the blue line was classified as a brackish water resident individual in the Baltic Sea and had a lower normalized Sr:Ca than the Northern Pike included from the current study, indicating that the Northern Pike from the current study was likely making use of estuarine or marine habitats.

3.3 Stable Isotopes

Mean δ^{34} S ratios were observed to be higher in migratory (based on otolith microchemistry) than in non-migratory fish for each species in each river, with the exception of Northern Pike from the Attawapiskat River (Figure 7, 8, 9, Table 7). Consistent with the otolith microchemistry results, the magnitude of difference in mean $\delta^{34}S$ between non-migratory and migratory fish was greater for Cisco and Lake Whitefish than for Northern Pike. Unfortunately, only one nonmigratory Cisco was captured, and thus statistical analyses were not possible for this species, but a >10 % difference in δ^{34} S was observed between the one non-migratory Cisco and the mean of the migratory Cisco from the Winisk River (Table 7). No non-migratory Lake Whitefish were captured in the Attawapiskat River, and only one non-migratory Lake Whitefish was captured from the Severn River, again precluding statistical analysis. There was a difference of >8 % in δ^{34} S between the one non-migratory Lake Whitefish and the mean of 41 migratory Lake Whitefish from the Severn River (Table 7). In the Winisk River, migratory Lake Whitefish had significantly higher δ^{34} S (independent samples t test, t=-9.049, df=41, p<0.0001) than nonmigratory Lake Whitefish (Figure 8, Table 7). In each river, mean δ^{34} S ratios were highest in Cisco, followed by Lake Whitefish, and Northern Pike (Table 7).

Of all species, non-migratory and migratory (visually classified from otolith microchemistry profiles) Northern Pike had the most similar mean $\delta^{34}S$ ratios. Despite some visual differences in $\delta^{34}S$ between the two groups, there were no significant differences in $\delta^{34}S$ between non-

migratory and migratory Northern Pike in either the Attawapiskat (independent samples t test, t=-0.457, df=39, p=0.65) or the Severn (independent samples t test, t=-0.454, df=36, p=0.653) rivers. There was, however, a significant difference in $\delta^{34}S$ between non-migratory and migratory Northern Pike in the Winisk River (independent samples t test, t= -3.11, df=37, p=0.004). The $\delta^{34}S$ of non-migratory Cisco and Lake Whitefish were much more similar to the $\delta^{34}S$ of the freshwater baseline than was the $\delta^{34}S$ of non-migratory Northern Pike. The relatively high $\delta^{34}S$ in non-migratory Northern Pike, and the similarity in $\delta^{34}S$ between migratory and non-migratory groups is consistent with the lack of observed difference between groups in [Sr] range and maximum plots.

Within each river, δ^{34} S of migratory fishes differed significantly among species (Attawapiskat River: One Way ANOVA, F=85.595, df=2, 94, p<0.0001; Severn River: One Way ANOVA, F=78.475, df=2,93, p<0.0001; Winisk River: One Way ANOVA, F=56.158, df=2,88, p<0.0001). Migratory Cisco had significantly higher δ^{34} S than either migratory Lake Whitefish or Northern Pike, and migratory Lake Whitefish had significantly higher δ^{34} S than Northern Pike (Tukey's HSD, p<0.05).

Table 7. Summary of mean δ^{34} S ratios for migratory and non-migratory Cisco, Lake Whitefish, and Northern Pike from the Attawapiskat, Severn, and Winisk rivers. Mean values are presented \pm standard error (minimum value, maximum value). A single value indicates that there was only one fish for the category, and standard error could not be calculated. In general, migratory fish were more enriched in the heavier isotope than non-migratory fish. Values presented are not corrected for baseline or trophic fractionation.

		δ^{34} S		
Species	River	Non-migratory	Migratory	
Cisco	Attawapiskat		16.6 ±0.1	
			(14.2, 18.0)	
	Severn		15.7 ±0.1	
			(13.8, 17.5)	
	Winisk	5.9	16.5 ±0.1	
		3.9	(14.4, 17.9)	
Lake	Attawapiskat		15.2 ±0.1	
Whitefish			(12.5, 16.7)	
	Severn	6.0	14.6 ± 0.1	
		0.0	(13.0, 16.5)	
	Winisk	5.94 ± 0.4	13.6 ± 0.4	
		(4.44, 8.86)	(5.1, 19.6)	
Northern	Attawapiskat	12.1 ±0.4	12.0 ±0.4	
Pike		(8.8, 14.8)	(9.6, 14.7)	
	Severn	8.81 ± 0.5	9.69 ± 1.5	
		(4.6, 16.8)	(1.9, 16.9)	
	Winisk	8.63 ± 0.4	10.8 ±0.6	
		(5.4, 13.4)	(7.3, 12.9)	

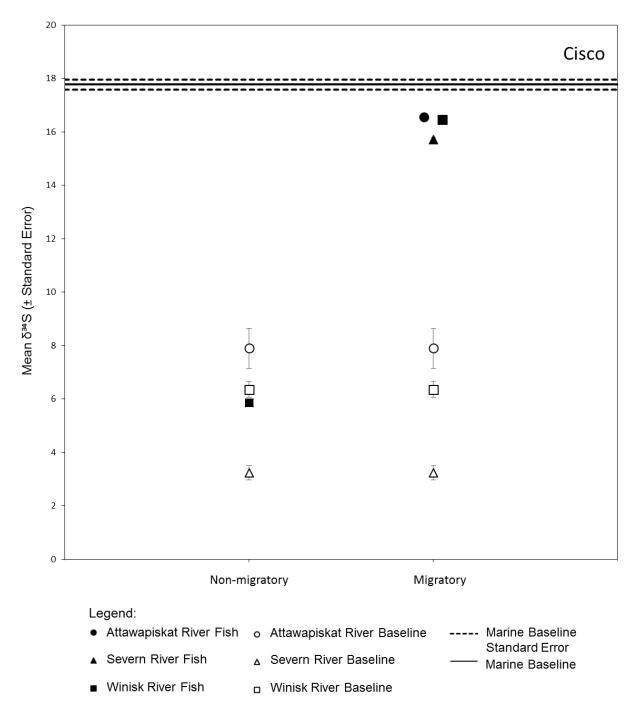


Figure 7. Mean $\delta^{34}S$ (±standard error) of non-migratory and migratory Cisco from the Attawapiskat, Severn, and Winisk rivers. The marine baseline ±standard error is also shown for each river. Mean $\delta^{34}S$ values were higher in migratory than in non-migratory groups of Cisco.

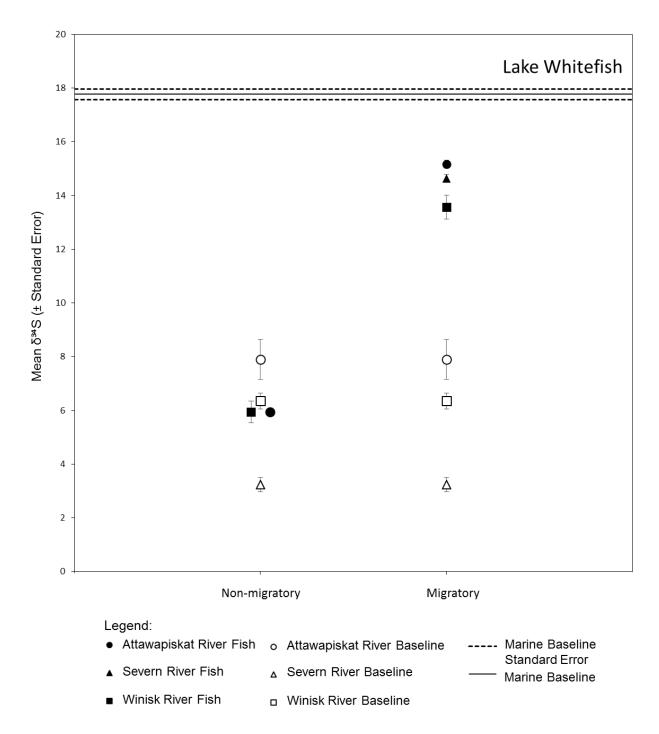


Figure 8. Mean $\delta^{34}S$ (±standard error) of non-migratory and migratory Lake Whitefish from the Attawapiskat, Severn, and Winisk rivers. The marine baseline ±standard error is also shown for each river. Mean $\delta^{34}S$ values were higher in migratory than in non-migratory groups of Lake Whitefish.

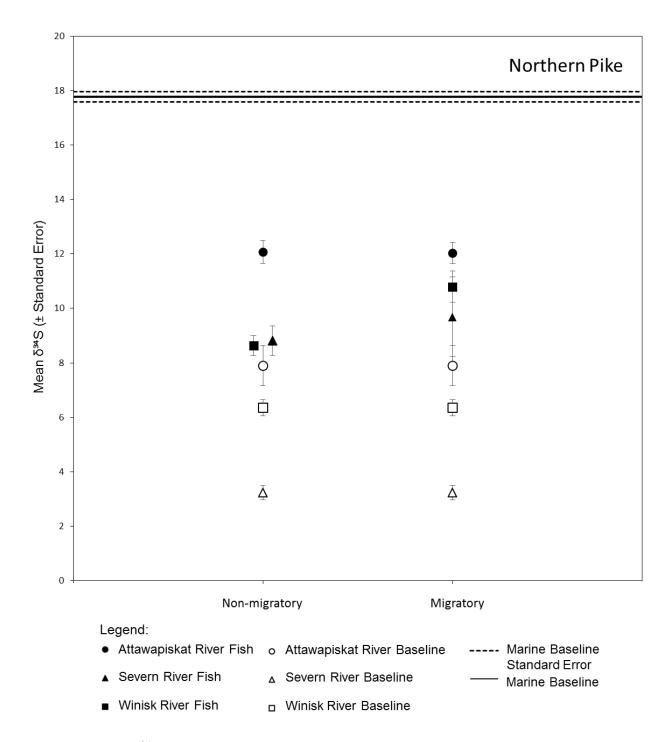


Figure 9. Mean $\delta^{34}S$ (±standard error) of non-migratory and migratory Northern Pike from the Attawapiskat, Severn, and Winisk rivers. The marine baseline ±standard error is also shown for each river. Mean $\delta^{34}S$ values were higher in migratory than in non-migratory groups from the

Severn and Winisk rivers, but the differences between these two groupings were less than what was seen in Cisco and Lake Whitefish (Figures 7 and 8).

3.4 Proportion of Marine – Derived Nutrients in Fish Diets

MixSIAR, a Bayesian mixing model, was used to estimate proportions of freshwater and marine-derived nutrients in the diets of migratory and non-migratory Cisco, Lake Whitefish, and Northern Pike from each river (Table 8). Two Lake Whitefish from the Winisk River were classified as migratory, but did not migrate in the most recent year of life, and as a result had low δ^{34} S ratios that were reflective of feeding in freshwater. These two fish were removed from mixing model analyses.

Results of the MixSIAR mixing model indicated that migratory Cisco and Lake Whitefish had higher proportions of marine-derived nutrients/prey in their diet than non-migratory individuals, and that migratory Cisco were more reliant on marine-derived nutrients/prey than Lake Whitefish. For migratory Cisco, the estimated proportion of marine-derived nutrients/prey to fish diet was consistent among rivers, and ranged from a median of 0.76 in the Severn River to 0.85 in the Attawapiskat River (Table 8). Marine-derived nutrients were found to contribute little to the diet of the one non-migratory Cisco captured in the Winisk River; the proportional contribution of marine-derived nutrients/prey was estimated to be 0.12 (Table 8).

The proportion of marine-derived nutrients/prey in diets of migratory Lake Whitefish was highest in the Severn River (0.75), followed by the Attawapiskat River (0.73) and Winisk River (0.59) (Table 8). The one Lake Whitefish from the Severn River that was classified as non-migratory had a smaller fraction (0.19, Table 8) of the diet originating from marine resources. This fish may have made short marine migrations that were not long enough for incorporation of

a marine [Sr] signature in the otoliths, or may have eaten food of marine origin in the freshwater environment. Alternatively, it is possible that the freshwater $\delta^{34}S$ baseline was not fully characterized. Similar to the result for the one non-migratory Cisco from the Winisk River, marine-derived nutrients/prey contributed little to none of the diet of visually-classified non-migratory Lake Whitefish (n=10) from the Winisk River; the estimated proportion of marine-derived nutrients/prey was 0.08 (Table 8), and thus this group of fish appeared to be feeding primarily on freshwater-derived prey sources. There were no non-migratory Lake Whitefish captured from the Attawapiskat River.

Marine-derived prey/nutrients appeared to contribute to the diets of both migratory and non-migratory Northern Pike. Median proportions of between 0.15 and 0.40 (depending on river) of the diets of non-migratory Northern Pike were estimated to be of marine origin, and median proportions of between 0.28 and 0.49 (depending on river) of the diets of migratory Northern Pike were estimated to be of marine origin. There was a greater difference in the proportion of marine-derived nutrients/prey between non-migratory and migratory Northern Pike in the Winisk River than in the other rivers (Table 8). The relatively high proportion of marine-derived nutrients/prey in the diets of non-migratory Northern Pike indicates that although these individuals were likely not migrating to marine waters, they were still reliant on marine-derived nutrients/prey.

Table 8. Median proportional contribution of marine and freshwater –derived nutrients (lower 95 % credible interval (CI), upper 95 % CI) based on a MixSIAR isotope mixing model using δ^{34} S. Individuals were classified visually based on otolith microchemical profiles. Migratory individuals were more reliant on marine-derived nutrients/prey than non-migratory individuals.

		Non-migratory		Migrat	tory
Species	River	Marine	Freshwater	Marine	Freshwater
		Fraction	Fraction	Fraction	Fraction
Cisco	Attawapiskat			0.85	0.15
				(0.80, 0.89)	(0.11, 0.20)
	Severn			0.76	0.25
				(0.73, 0.78)	(0.22, 0.27)
	Winisk	0.12	0.88	0.84	0.16
		(0.04, 0.32)	(0.68, 0.96)	(0.80, 0.88)	(0.12, 0.20)
Lake	Attawapiskat			0.73	0.27
Whitefish				(0.67, 0.78)	(0.22, 0.34)
	Severn	0.19	0.81	0.75	0.25
		(0.08, 0.32)	(0.69, 0.92)	(0.72, 0.78)	(0.22, 0.28)
	Winisk	0.08	0.92	0.59	0.41
		(0.02, 0.18)	(0.82, 0.98)	(0.51, 0.67)	(0.33, 0.48)
Northern	Attawapiskat	0.40	0.60	0.49	0.51
Pike		(0.28, 0.50)	(0.50, 0.72)	(0.25, 0.64)	(0.36, 0.75)
	Severn	0.32	0.68	0.34	0.66
		(0.24, 0.41)	(0.59, 0.76)	(0.13, 0.34)	(0.48, 0.87)
	Winisk	0.15	0.85	0.28	0.72
		(0.07, 0.23)	(0.77, 0.93)	(0.08, 0.44)	(0.56, 0.92)

CHAPTER FOUR - DISCUSSION

4.1 Life History of Cisco and Lake Whitefish

Previous authors have reported that migrations are obligatory for Cisco and Lake Whitefish from coastal rivers of James Bay (Lambert & Dodson, 1990), and that Cisco and Lake Whitefish in the Hudson and James Bay area are anadromous (Morin et al., 1981; Kemp, Bernatchez, & Dodson, 1989). My findings indicate that the majority of Cisco and Lake Whitefish from the three study rivers were migratory. There is unpublished evidence that rivers on the eastern coast of Hudson Bay support sympatric migratory and non-migratory (i.e., partially migratory populations) Lake Whitefish (Michael Power, University of Waterloo, unpublished data). My results also indicate that there are sympatric migratory and non-migratory Lake Whitefish and Cisco in some rivers on the western coast of Hudson Bay, and that these populations can be described as partially anadromous. Large oscillations in otolith [Sr] found in most Cisco and Lake Whitefish indicate that most fish were migrating to seawater, although there were a few fish with low and flat otolith [Sr] that were freshwater residents. I found that there were more non-migratory Lake Whitefish than Cisco, and more non-migratory Lake Whitefish were observed in the Winisk River than from either the Severn or Attawapiskat rivers.

The group of non-migratory Lake Whitefish (n=10) in the Winisk River appears to represent a freshwater riverine life history type. Often, fish migrate to marine waters to access areas with more productive prey resources (Gross, 1987). Based on the circulation pattern and salinity gradient within Hudson and James bays, I expected there to be a greater incentive for fish to migrate at higher latitudes. The Winisk River is less productive than the Severn River, based on total phosphorus and total nitrogen data (personal communication, Bill Keller, Laurentian University, Sudbury, ON), and both rivers enter Hudson Bay along the same coast in areas with similar salinities, indicating that fish should have a relatively greater incentive to migrate to

Hudson Bay from the Winisk River than from the Severn River. Since I did not observe a higher proportion of migratory Lake Whitefish in the Winisk River (as expected based on productivity alone), it is possible that there was a nearby lacustrine population of Lake Whitefish that migrated into the Winisk River. Lake Whitefish spawn in the fall (e.g., Dymond, 1943; Ryder et al., 1973), and some lacustrine populations of Lake Whitefish migrate to rivers to spawn (e.g., Roseman et al., 2007). The group of non-migratory Lake Whitefish from the Winisk River was captured in June, however, and therefore were likely not accessing the river to spawn. It is possible that these Lake Whitefish moved from a lacustrine environment to the river for greater access to food or more favourable habitat conditions, although this needs further study.

The average age of first migration was 0.0 for Cisco in all rivers and 0.1, 0.2, and 0.6 for Lake Whitefish in the Attawapiskat, Severn, and Winisk rivers, respectively, indicating that most fish migrated within the first year of life. Migratory Cisco and Lake Whitefish appeared to migrate annually once migrations began. The one non-migratory Cisco captured from the Winisk River was 11 years of age, the one non-migratory Lake Whitefish from the Severn River was 9 years of age, and the non-migratory group of Lake Whitefish from the Winisk River had a mean age of 6.5 years. Non-migratory Cisco and Lake Whitefish were older than mean age of first migration for each river-species combination, and were thus likely true freshwater-resident individuals.

Previous authors have reported that in eastern James Bay, larval Cisco are transported to marine waters in spring, after hatch, while Lake Whitefish larvae move to the river mouth in spring, and to marine waters as juveniles (Morin et al., 1981). My results support the life history pattern observed for Cisco by Morin et al. (1981), and indicate that Cisco migrate to marine water within their first year.

Cisco classified as migratory had relatively high mean δ^{34} S ratios that were 1.2 to 2.1 % below the mean of the marine endmember, and 8.7 to 12.5 % above the mean of freshwater endmember, depending on the river, indicating large reliance of these fish on marine dietary sources. The one Cisco classified as non-migratory had a relatively low δ^{34} S ratio that was 11.9 % below the mean of the marine endmember and within 0.49 % of the freshwater endmembers, indicating large reliance of this fish on freshwater dietary sources. All but two Lake Whitefish classified as migratory had relatively high δ^{34} S ratios, and the two Lake Whitefish that had relatively lower δ^{34} S (i.e., closer to the freshwater δ^{34} S ratio) had not migrated (and therefore not eaten marine-derived prey) in their most recent year of life. All non-migratory Lake Whitefish had δ^{34} S ratios near that of the freshwater baseline, reflective of freshwater feeding. In the Severn, Winisk, and Attawapiskat rivers, my data indicate that migratory classifications of Cisco and Lake Whitefish can be effectively accomplished with either otolith microchemistry or $\delta^{34}S$ analyses. However, due to the rate of isotopic turnover (approximately four months up to a year), (e.g., Hesslein, Hallard, & Ramlal, 1993; Buchheister and Latour, 2010; Franssen et al. 2017), δ^{34} S analysis can only indicate relatively recent life history.

A group of Cisco from the Attawapiskat River that migrated within their first year had a relatively small [Sr] range; this was the result of high [Sr] throughout the otolith core. Progeny of anadromous females can have high Sr concentrations in the core of their otoliths (Kalish, 1990). Typically, this otolith [Sr] decreases to reflect a freshwater larval period after hatch (as seen in otolith microchemical profiles of Zimmerman & Reeves, 2000; Engstedt et al., 2010; Courter et al., 2013; Hart et al., 2015). Maternal influence could explain the high [Sr] in the core of some Cisco and Lake Whitefish otoliths in this study. The amount of time required for saturation of elements from surrounding water into otoliths differs among species, but was 20 days in Black

Bream (*Acanthopagrus butcheri*) (Elsdon & Gillanders, 2005), and ~80 to 100 days in Northern Pike (Engstedt et al., 2012). The group of Cisco with a smaller [Sr] range may have been progeny of anadromous females, and these progeny may not have remained in freshwater as larvae for an adequate period of time to incorporate the freshwater elemental signature into their otoliths. Literature from rivers in Eastern James Bay indicates that larval Cisco can be passively transported after hatch (~ 2 weeks) into the waters of the Bay, and that it may even be possible for larval fish to migrate up to 80 km within a day (Lindroth, 1957; Ochman & Dodson, 1982).

Migrations and reproduction are both energetically expensive (see Roff, 1988). Anadromous fishes may skip spawning migrations in some years to increase energy stores to maximize fitness in future years (Jørgensen et al., 2006), and some anadromous fishes do not migrate in the year that they spawn (Jonsson & Jonsson, 1993). Two Lake Whitefish from the Winisk River that were classified as migratory had lower δ^{34} S ratios than would be expected if the fish were largely feeding in marine waters. These fish did not migrate in their most recent year of life, and appear to have skipped other migrations in recent years. Skipped migrations could reflect allocation of energy to reproduction rather than migrations, but further research is required. Skipped migrations were not observed in Cisco from any of the study rivers, or in Lake Whitefish from the Attawapiskat or Severn rivers.

4.2 Reliance of Cisco and Lake Whitefish on Marine-Derived Nutrients

Marine resources can subsidize fisheries productivity in freshwater environments, especially at northern latitudes where productivity of marine waters is in general higher than that of freshwaters. Species that migrate between freshwater and marine waters serve as a biotransport vector for nutrients between these two habitats. Catadromous fishes are a mechanism of transport of freshwater nutrients to marine waters, whereas anadromous fishes are a mechanism of

transporting marine-derived nutrients into freshwaters (Flecker et al., 2010). Both migration distance and the number of migratory individuals within a population can affect the extent of nutrient transport by anadromous fishes. Spawning iteroparous fishes (e.g., Alewife (*Alosa pseudoharengus*, Wilson, 1811), Atlantic Salmon (*Salmo salar*, Linnaeus 1758), American Shad (*A. sapidissima*, Wilson, 1811), and Blueback Herring (*A. aestivalis*, Mitchill, 1814)), may provide an important source of marine-derived nutrients to freshwaters through direct consumption of migrants by organisms of higher trophic positions, nutrient excretion, and spawning mortality (see Flecker et al., 2010). Anadromous Cisco and Lake Whitefish were identified in each study river; these species therefore transport marine-derived nutrients from the marine system of Hudson and James Bay into the Severn, Winisk, and Attawapiskat rivers, and likely subsidize productivity of higher trophic-level fishes, such as Northern Pike.

To my knowledge, this study provides the first quantitative estimates of marine- and freshwater-derived nutrients/prey to diets of migratory Cisco and Lake Whitefish. The higher contribution of marine-derived nutrients/prey to migratory Cisco could reflect the observed younger age of first migration to sea, relative to Lake Whitefish. Differences among rivers in marine-derived contributions to diets of migratory Lake Whitefish deserve further investigation, but could reflect variation in prey availability, early growth rates, different migration distances, or a baseline that was not completely characterized. Non-migratory Cisco and Lake Whitefish had a median of 8 % to 19 % marine-derived nutrients/prey in their diet. Non-migratory Cisco and Lake Whitefish thus still appeared to access marine nutrients, but to a lesser extent than the migratory individuals. It does not appear that the non-migratory fish accessed the marine food sources by feeding in marine waters (based on otolith microchemistry results), and thus this study provides the first observation, to the best of my knowledge, that fish may have fed on

marine food sources brought in with the tide, or migrated to sea for very short periods of time, not reflected in otolith microchemistry. Further research that more fully characterizes freshwater baseline $\delta^{34}S$ is also needed to rule out the possibility that apparent reliance on marine-derived nutrients by non-migratory Cisco and Lake Whitefish is due to incomplete characterization of the freshwater baseline.

4.3 Northern Pike Life History and Reliance on Marine Nutrients

In contrast to the large amount of research conducted on Northern Pike in the Baltic Sea, (e.g., Laikre et al., 2005; Engstedt et al., 2010; Rohtla et al., 2012; Engstedt et al., 2014; Rohtla et al., 2014; Larsson et al., 2015; Jacobsen et al., 2017), movements to marine waters and reliance of Northern Pike on marine-derived nutrients/prey have not yet been studied in North America. Northern Pike in North America are thought to live in freshwaters (Scott & Crossman, 1973), although anecdotal evidence from local fishers in the Hudson Bay Lowlands region suggests that Northern Pike have been captured at the mouths of the study rivers; this has also been observed by researchers at the mouths of the Yukon and Kuskokwim rivers (personal communication, Christian Zimmerman, United States Geological Survey, Anchorage, Alaska). Anadromous Northern Pike in the Baltic Sea migrate to salinities of ~6 to 7 parts per thousand after approximately 2.8 months of rearing in freshwater (Rohtla et al., 2012; Westin & Limburg, 2002), and are known to feed on brackish and marine prey fishes (see Engstedt et al., 2014). Since these Baltic Sea Northern Pike are only migrating to salinities of ~6 to 7 parts per thousand, they can be considered semi-anadromous.

Northern Pike in this study were more challenging to classify with otolith microchemistry than Cisco and Lake Whitefish. Otolith microchemistry has, however, been successfully used to

differentiate between freshwater resident, anadromous, and brackish-water resident Northern Pike in the Baltic Sea (e.g., Engstedt et al., 2010; Rohtla et al., 2012; Engstedt, Engkvist, & Larsson, 2014). When I standardized otolith microchemistry results such that comparisons could be made between my study and studies conducted in the Baltic Sea, it appears that Northern Pike classified as migratory in my study made use of marine/brackish waters. The low otolith [Sr] in Northern Pike classified visually as migratory could indicate semi-anadromous migrations to brackish rather than full-strength seawater. Migrations may also be relatively shorter than those of Cisco and Lake Whitefish, possibly shorter than the 80 to 100 days required for otolith Sr to reach equilibrium with Sr in the surrounding water (Engstedt et al., 2012).

Based on [Sr] range and [Sr] maximum plots, it was apparent that rather than distinct groupings of migratory and non-migratory Northern Pike, there was a continuum of reliance on marine/brackish waters. In the Baltic Sea, there are three known life history types of Northern Pike, a brackish water resident type, a freshwater resident type, and a semi-anadromous type (Rohtla et al., 2012). The latter two life history types comprise a partially, semi-anadromous population. Brackish water resident Northern Pike can reproduce in salinities of ~6 to 11 parts per thousand (Westin & Limburg, 2002; Jacobsen et al., 2017) whereas semi-anadromous individuals require freshwater to spawn (Westin & Limburg, 2002). In each of the Severn, Winisk, and Attawapiskat rivers in this study, the relatively small oscillations in otolith [Sr] indicate that migratory Northern Pike, if they are in fact migratory, are likely partially semi-anadromous, as the individuals are likely only moving to brackish waters. Very few freshwater resident individuals seem to be reported in the Baltic Sea area (e.g., Rohtla et al., 2012), however, the majority of the Northern Pike in this study were identified as non-migratory, or freshwater resident individuals. These differences in observed migratory behaviour between the

Hudson and James Bay and Baltic Sea system may be explained by differences in salinities between the two systems.

Within the Baltic Sea, there appeared to be a wide range of maximum [scaled] otolith Sr:Ca values. Although the salinity was similar among sampling regions in the Baltic Sea, it is possible there were differences in salinity of waters in which fish hatched, with some hatching in less saline water than others. This would result in relatively higher peaks once migrations to regions of similar (and higher) salinity began. The Northern Pike from the current study had a similar maximum scaled Sr:Ca ratio to that of sample otoliths from three separate studies; two of these studies reported the fish to be anadromous, although the reported salinity in these regions is only ~5-7 parts per thousand, while the third study reports the fish to be brackish water resident. It thus appears that at least some Northern Pike from the present study are making use of brackish waters.

Because Hudson and James Bay have higher salinities than the Baltic Sea, and Sr:Ca ratios were higher in marine waters than in freshwaters of the Hudson and James Bay system, I expected otolith microchemistry to be an effective technique for differentiating between migratory and non-migratory Northern Pike. Otolith microchemistry is most effective for reconstructing migrations that occurred between habitats with relatively large differences in salinity (i.e., it can be used to differentiate between freshwater, brackish, and marine waters (Zimmerman, 2005)), and is much less effective when fish migrate between habitats with similar salinities. Relatively higher salinity of Hudson and James bays (~10 and 33 parts per thousand (Prinsenberg, 1978; Ingram & Prinseberg, 1998; Granskog et al., 2011)) compared to the Baltic Sea (~6-12 parts per thousand (Jacobsen et al., 2017)), however, likely restricts marine habitat use by Northern Pike. In many parts of Hudson and James bays, salinity exceeds the known

salinity tolerances of Northern Pike, which is estimated to be between 11 and 13 parts per thousand for juveniles (Jacobsen et al., 2007; Jørgensen et al., 2010), and up to 18 parts per thousand for adults (Dahl, 1961 (in Danish) referenced in Jacobsen et al., 2007). As a result of these salinity limitations, Northern Pike may restrict migrations to brackish waters at river mouths, or reside in relatively fresher layers of the vertical water column. Mixing of fresh and marine waters in the HBL is complex. There is a gradient of salinity from the freshwater rivers into Hudson Bay and James Bay, and there is also a vertical salinity gradient within each of the bays; water of higher salinity remains near the bottom with fresher waters from river discharge on top (Freeman, 1982). In addition, tidewaters can extend from Hudson and James bays upstream into the rivers. In the Attawapiskat River, tidewater extends approximately 7.5 km upstream, forming a layer below the less dense freshwater (Glooschenko & Martini, 1983). While I am confident that Northern Pike are not using the marine environment to the same extent as Cisco and Lake Whitefish, otolith microchemistry results did not allow full determination of Northern Pike habitat use in this study, and further research, preferably using tagging and telemetry approaches (e.g., as has been done by Jepsen et al., 2001 and Jacobsen et al., 2017), is necessary. Otolith microchemistry and comparison of results with that of other studies indicates that some Northern Pike were making use of brackish waters, however, contribution of Sr to otoliths occurs not only through water, but also through sources of food (Engstedt et al., 2012).

Elemental concentrations in otoliths can be influenced by many factors, including diet.

Engstedt, Koch-Schmidt, & Larsson (2012) have shown that otoliths of Northern Pike held at constant salinity (7 parts per thousand) have higher concentrations of Sr when fish are fed diets that are consistently high in Sr than when fish are fed diets consistently low in Sr. Northern Pike are known to prey on Cisco and Lake Whitefish (Scott & Crossman, 1973), and some Northern

Pike in this study had Cisco or Lake Whitefish in their stomachs upon dissection (data not presented). In one study, Lake Whitefish were found to make up 9.8 % of the diet of Northern Pike in the Winisk River (Henschel, 1989). Most Cisco and Lake Whitefish in this study were anadromous and had elevated δ^{34} S ratios reflective of marine feeding; feeding of Northern Pike on these anadromous fishes could have resulted in elevated otolith [Sr] and elevated tissue δ^{34} S ratios in Northern Pike (above values expected for fish feeding solely on freshwater-derived nutrients, even after accounting for trophic fractionation), even if Northern Pike themselves were not migrating to brackish or marine waters. In addition to migratory Cisco and Lake Whitefish, Brook Trout and Longnose Sucker also migrate between marine and freshwaters in this area (Stewart & Lockhart, 2004), and could provide Northern Pike with additional sources of marinederived nutrients. Mean δ^{34} S ratios did not differ between migratory and non-migratory groups of Northern Pike in the Attawapiskat and Severn rivers; this may indicate migratory and nonmigratory Northern Pike alike were feeding on marine or anadromous prey, or that Northern Pike migrated to sea for periods of time that were not reflected in otolith microchemistry. Additional research is required to determine how Northern Pike are accessing marine nutrients.

Some Northern Pike in this study had oscillations in otolith [Sr] and $\delta^{34}S$ ratios higher than the freshwater baseline, and I inferred that these fish were using marine or brackish habitats and feeding on marine or anadromous prey. It could also be argued that these Northern Pike remained in freshwater, fed on marine or anadromous prey, and that marine/brackish diet could have resulted in high otolith [Sr]. In each river, however, there were also Northern Pike with low, flat otolith [Sr] (no oscillations) and $\delta^{34}S$ ratios that indicated feeding on marine or anadromous prey. If dietary Sr explained high otolith [Sr], all Northern Pike with marine-influenced $\delta^{34}S$ ratios would be expected to have had elevated otolith [Sr]; this was not the case, as some fish had

low [Sr] but high δ^{34} S ratios. This indicated that at least some fish appeared to be migrating to brackish waters.

Assuming that the elevated otolith [Sr] in some Northern Pike otoliths of this study reflected migration to brackish waters, the fish began to migrate later than what has been observed in the Baltic Sea. In the Baltic Sea, individuals born in freshwater that later migrated to sea began migrating in their first year, at an average of 2.8 ± 1.0 months old (Rohtla et al., 2012). In contrast, the mean age of first migration for Northern Pike in the current study ranged between 1.3 to 2.8 years, much older than what has been observed in the Baltic Sea. Since the salinity of the Baltic Sea is much less than what is observed in Hudson and James Bay, and some fish need to reach a certain size before migrating in order to increase salinity tolerance (e.g., Conte & Wagner, 1965; McCormick & Naiman, Robert, 1984), Northern Pike may have needed to increase size before migrating to increase probability of survival. However, within the Baltic Sea, Northern Pike that migrate to sea at a comparable time to that of fish from the present study (in their third or fourth year of life) have been reported, although one study showed that these late migrants were less prevalent than early migrants (Rohtla et al., 2012).

4.4 Comparisons of Cisco, Lake Whitefish and Northern Pike

In all species, results of otolith microchemistry indicated that there was variation within the migratory classification category of fish with some individuals having higher [Sr] range and [Sr] maximum than others within the same category. Cisco and Lake Whitefish separated distinctly into two migratory groupings based on [Sr] range and [Sr] max plots, similar to classifications made for Broad Whitefish in the Mackenzie River (Harris et al., 2012). Northern Pike did not show this same differentiation on [Sr] range vs [Sr] max plots. Comparisons of mean δ^{34} S values

of migratory groupings of fish within the same river indicate that Cisco had the highest mean $\delta^{34}S$ value, followed by Lake Whitefish, and then Northern Pike. Differences in $\delta^{34}S$ values among species reflect different reliance on marine environments and marine prey. Cisco in this study had the largest proportion of migratory individuals, the highest mean $\delta^{34}S$ values of migratory individuals, and therefore the greatest reliance on the marine environment. This was followed by Lake Whitefish, with a smaller proportion of migratory individuals identified in this study, lower mean $\delta^{34}S$ of migratory individuals, and lower reliance on marine-derived nutrients/prey. Northern Pike had the lowest proportion of migratory individuals identified in this study, the lowest $\delta^{34}S$ values of migratory individuals, and thus the lowest reliance on marine environments and marine prey items. In contrast to Cisco and Lake Whitefish, many non-migratory Northern Pike had marine-derived prey in their diets. Based on these results, I suggest that anadromous Cisco and Lake Whitefish may contribute substantially to the diets of non-migratory Northern Pike in coastal rivers of the Hudson Bay Lowlands.

4.5 Summary and Conclusions

Information on fish life history is necessary for conservation managers and policy makers to ensure protection of all environments used by a species throughout its life. In this study, for the first time in North America, I showed that Northern Pike relied on marine-derived food sources, and that some Northern Pike may make migrations to brackish waters. Regardless of whether otolith microchemistry appeared to indicate movement to brackish waters or not, the majority of Northern Pike appeared to access marine-derived nutrients. Otolith microchemistry results of Northern Pike in the HBL system were more challenging to interpret than otolith microchemistry results from Northern Pike from the Baltic Sea. However, comparisons of scaled Sr:Ca ratios for

migratory individuals did seem comparable between these two systems. Otolith microchemistry was, however, effective at differentiating between migratory and non-migratory Cisco and Lake Whitefish in this study.

In order to improve comparability among studies, it is important to have knowledge of the water chemistry and salinity to which fish are exposed; it would be useful for this information to be consistently presented in published studies. Although I reported Sr:Ca ratios in water, I relied on salinity data from published literature; local mixing of fresh and marine waters made it difficult to infer the extent of use of marine waters being used by Northern Pike, and determination of the actual salinity of the water which fish were using was beyond the scope of this study. Future research in the HBL should involve telemetry studies of Northern Pike movement and habitat use (e.g., as has been done by Jepsen et al., 2001 and Jacobsen et al., 2017) so that more specific descriptions of habitat use by Northern Pike can be made. Using otolith stable Sr isotope ratios to determine Northern Pike life history (e.g., as done by Rohtla et al., 2014) may also be useful in gaining a better understanding of fish movement, as the oceanic Sr isotopic ratio is globally known and consistent, the isotopic ratios in otoliths are not affected by environmental physiological factors, and otolith isotopic ratios differ based on geology and can therefore provide information on finer scale movements than can be obtained through otolith microchemistry concentration analysis alone (Kennedy et al., 2000). Stable Sr isotope ratios in otoliths can be used to differentiate between residency in freshwater and marine environments (e.g., Outridge et al., 2002; Woodhead et al., 2005), but also different areas within a freshwater system (Kennedy et al., 2000).

In the face of a changing climate, fish migrations are susceptible to change as diadromous species of fish rely on two distinct but connected habitats (Gross, 1987; Reist et al., 2006). The

temperature of the Hudson Bay Lowlands region was previously moderated by the ice on the bays, however, more recently, the extent of the ice coverage and therefore cooling effect on surrounding land has decreased (Hochheim & Barber, 2010; Rouse, 1991). The HBL region is expected to experience many impacts of climate change, including decreased sea ice extent, increased precipitation, decreased permafrost, and increased surface warming (Gagnon & Gough, 2005a). Climate change has the potential to influence anadromous behaviour in fish (Reist et al., 2006), and since fish life history can influence fish contaminant concentrations, it also has the potential to affect concentrations of contaminants, such as mercury, in fish tissue (e.g., Swanson et al., 2010; Stern et al., 2012). Contaminants in fish are of concern to many stakeholders, including many Aboriginal communities, and by understanding the life history types of fish that are present in the rivers of this study, we can better predict how tissue mercury concentrations may be affected by a changing climate.

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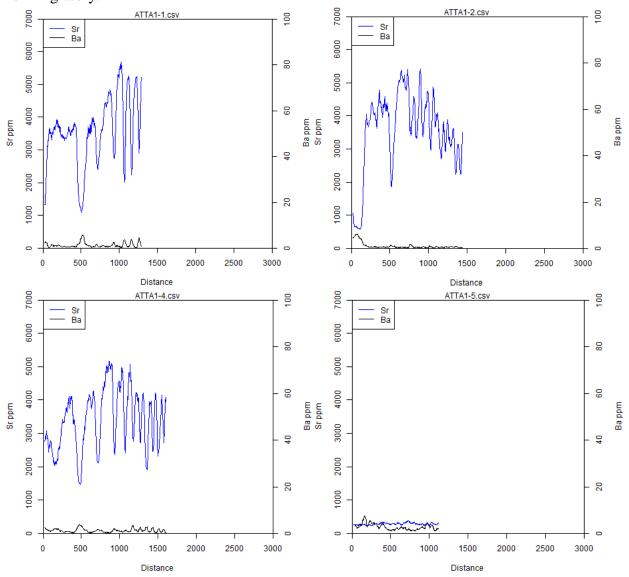
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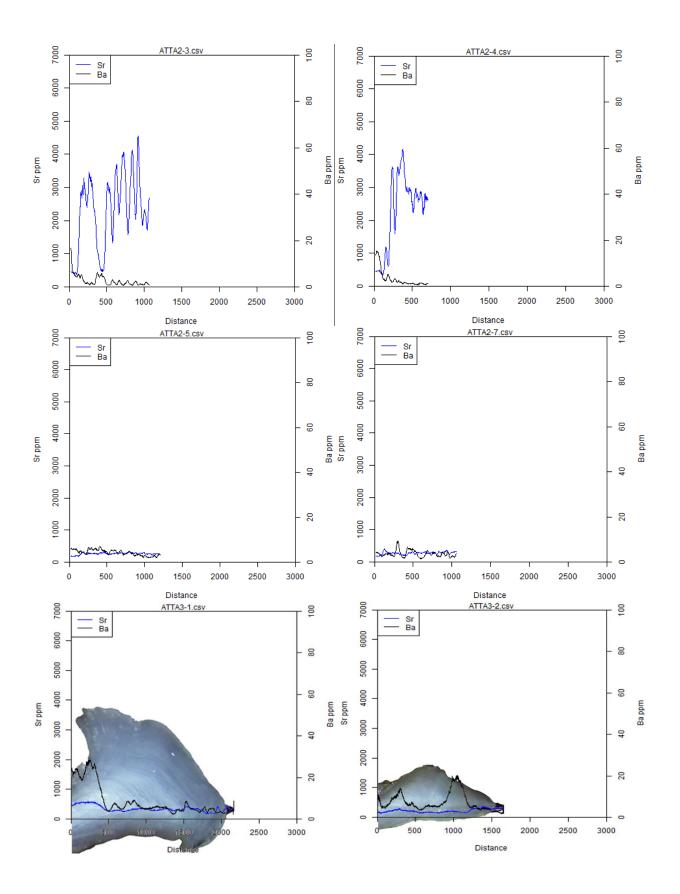
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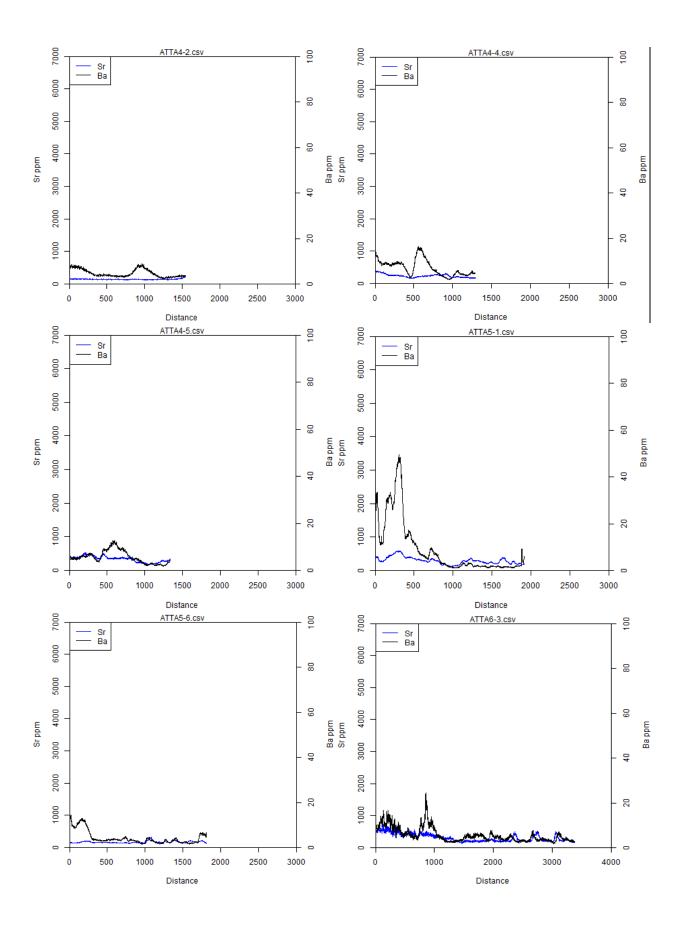
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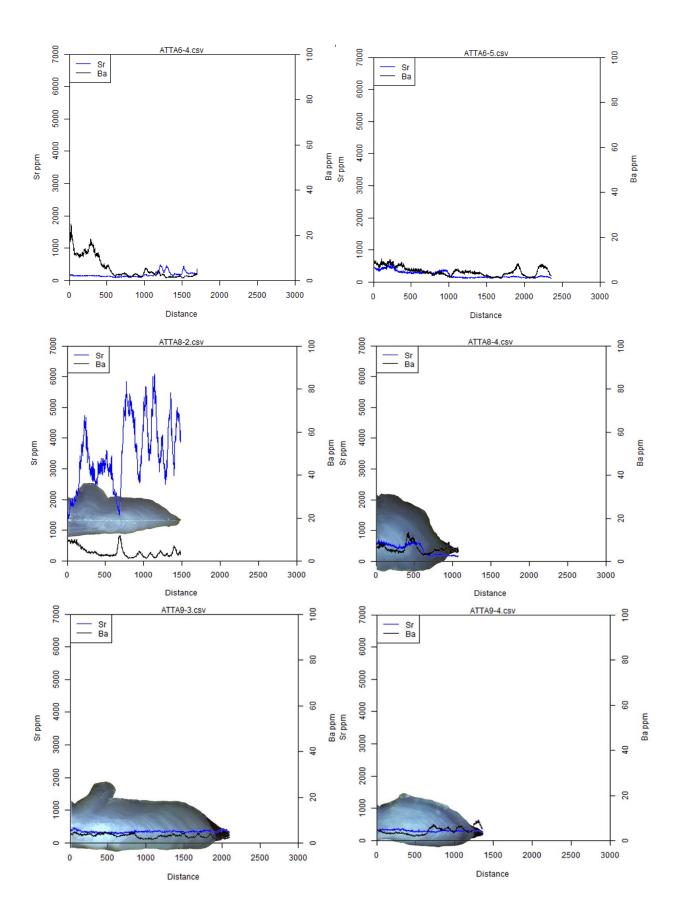
Appendix A - Otolith Microchemical Profiles

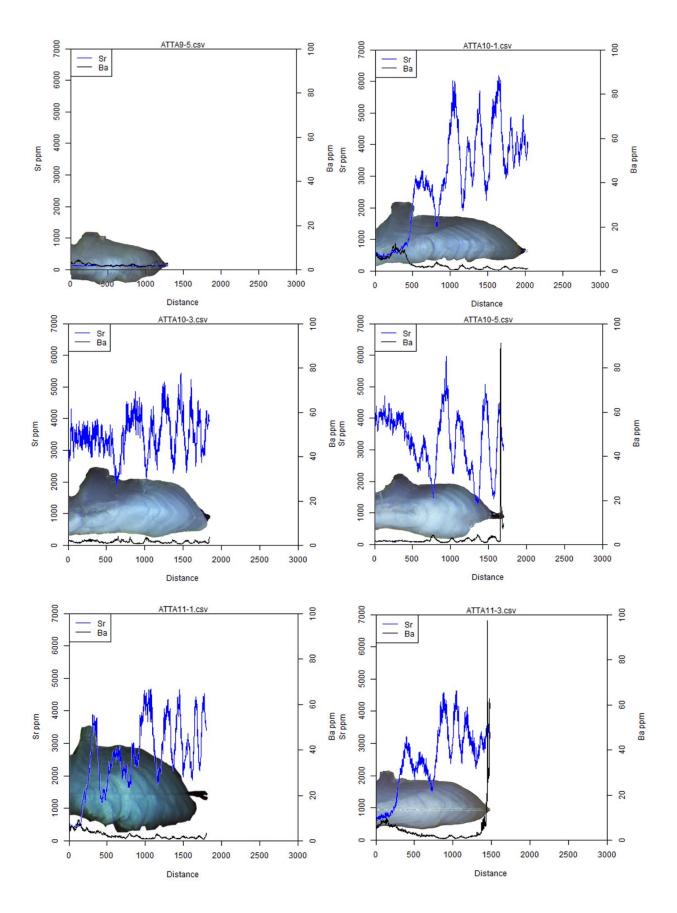
Note: plots shown are of both strontium (Sr) and barium (Ba), however, Ba was not used to classify fish. Strontium and zinc (Zn) plots are shown when Ba data were unavailable. In cases where no postablation photos were available, Sr plots are shown. Table A in this appendix outlines the included fish codes, river of collection, and classification of fish as migratory or non-migratory.

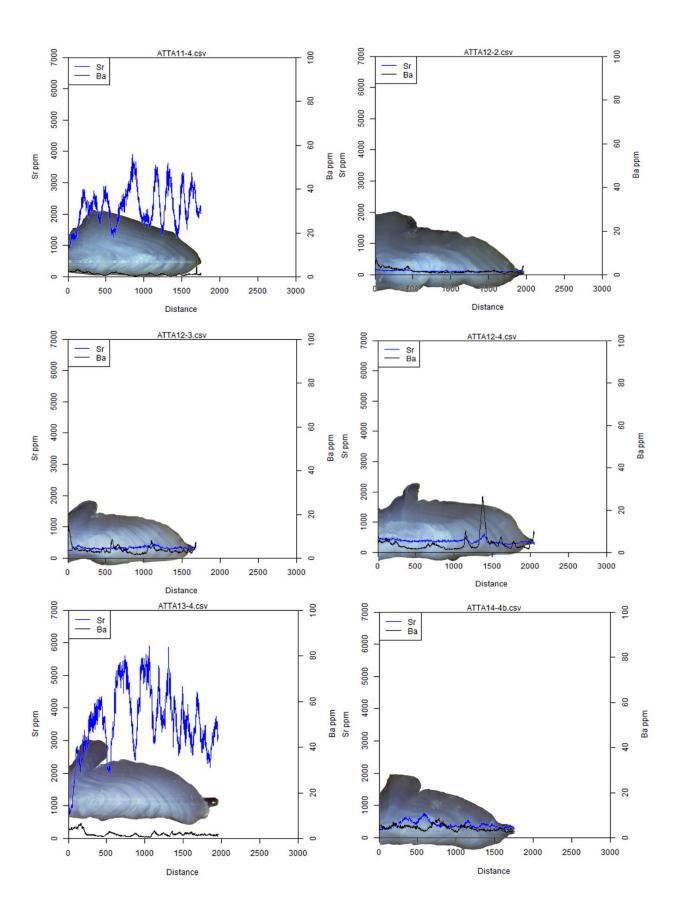


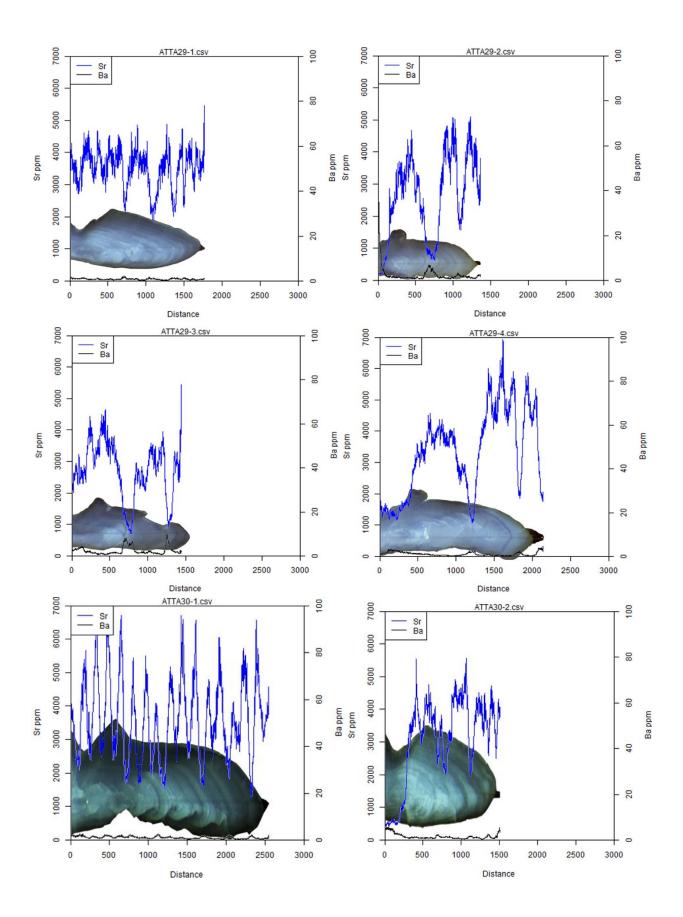


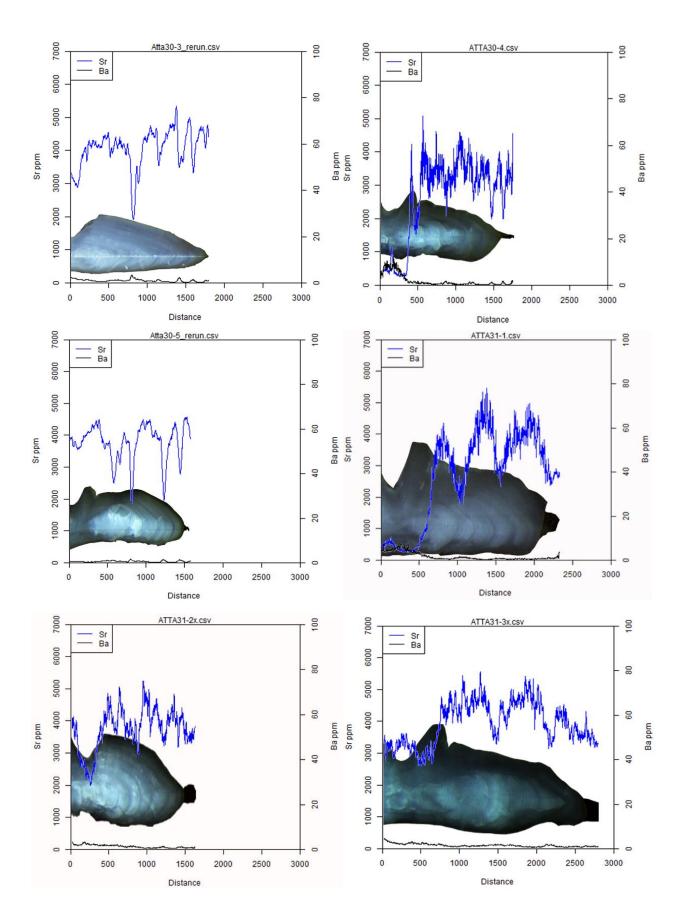


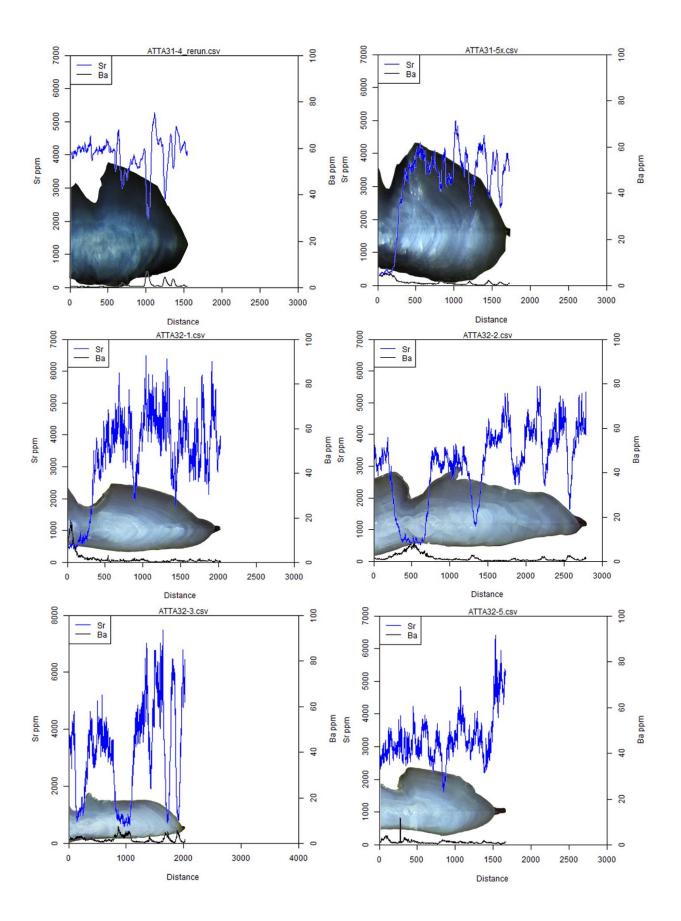


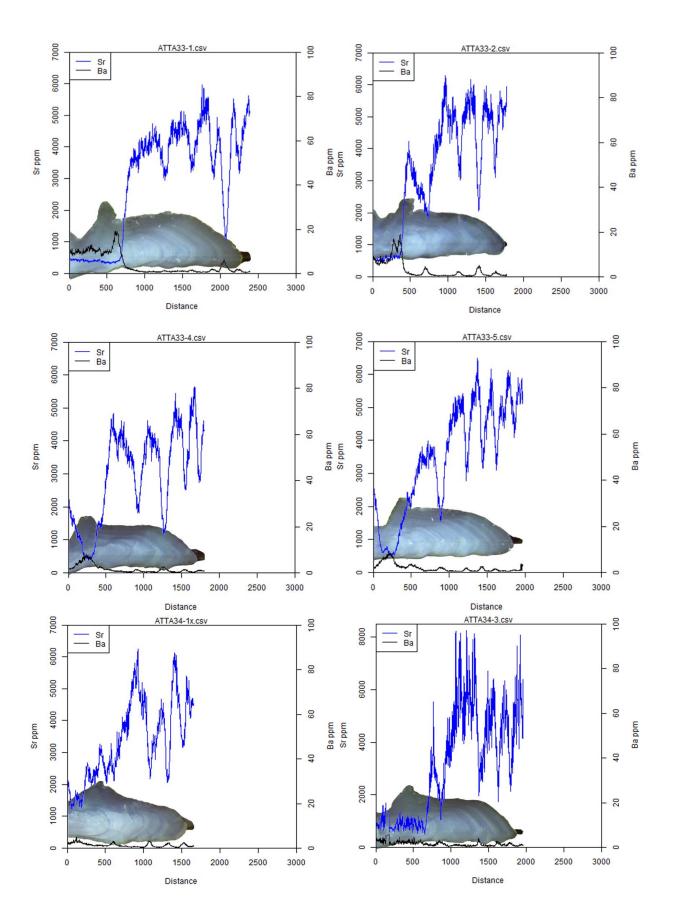


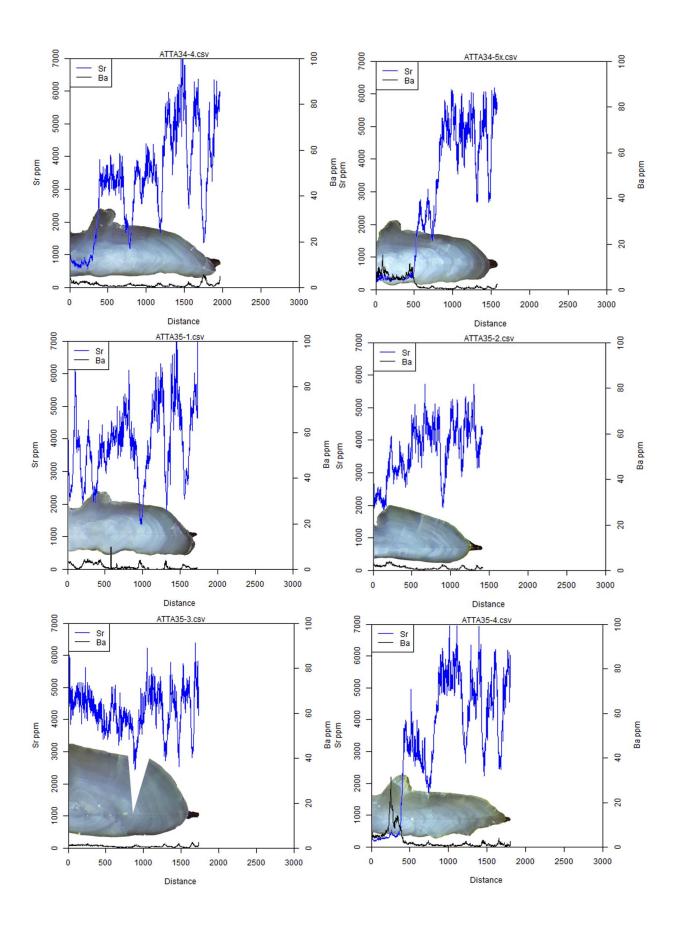


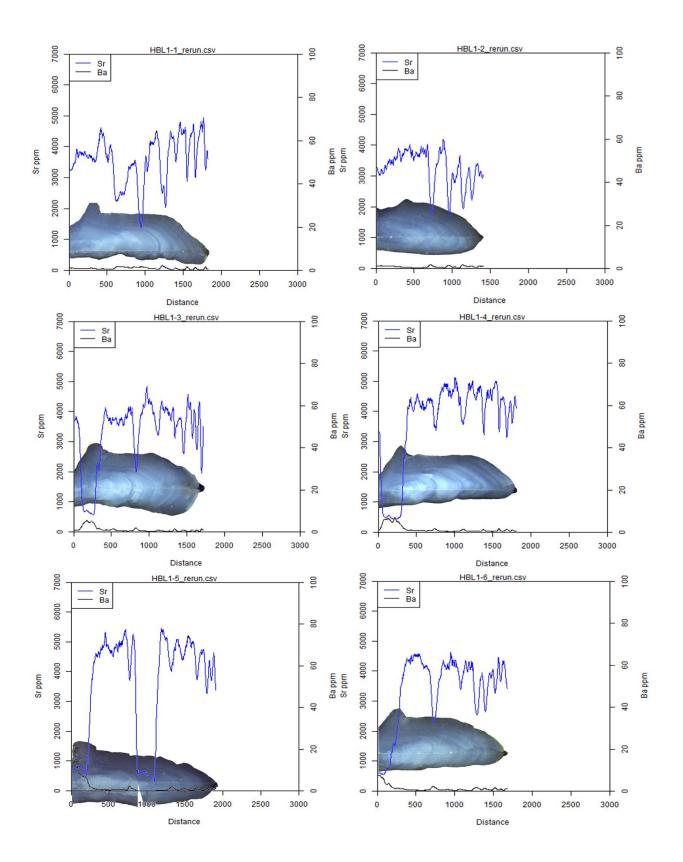


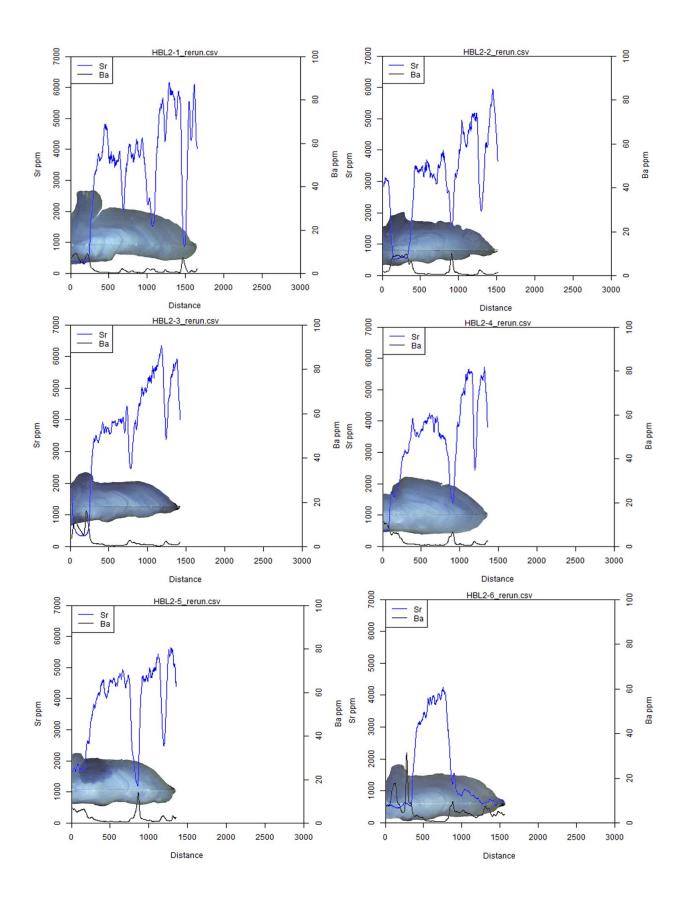


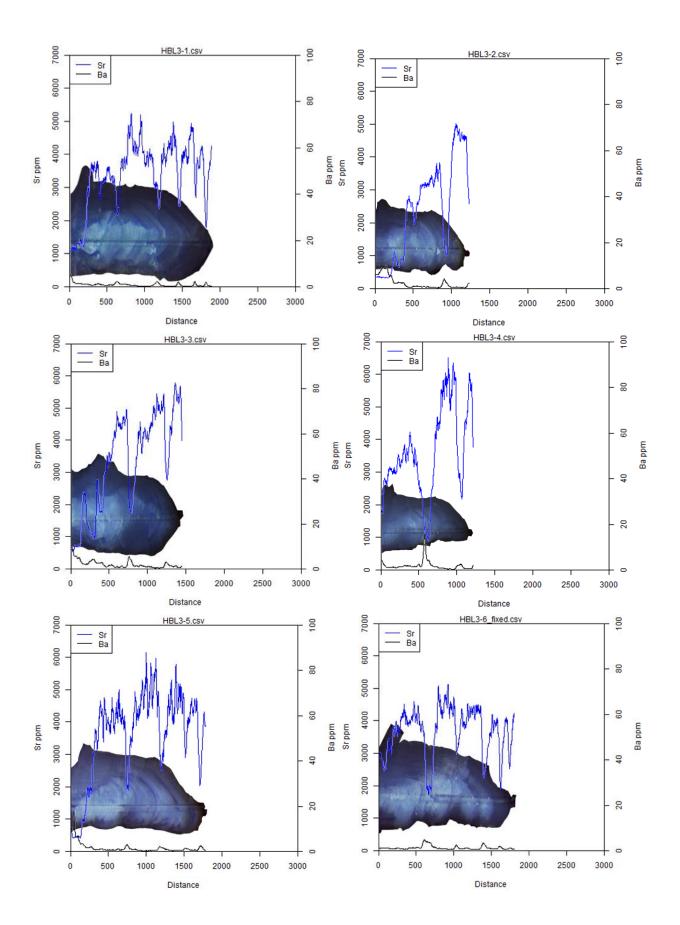


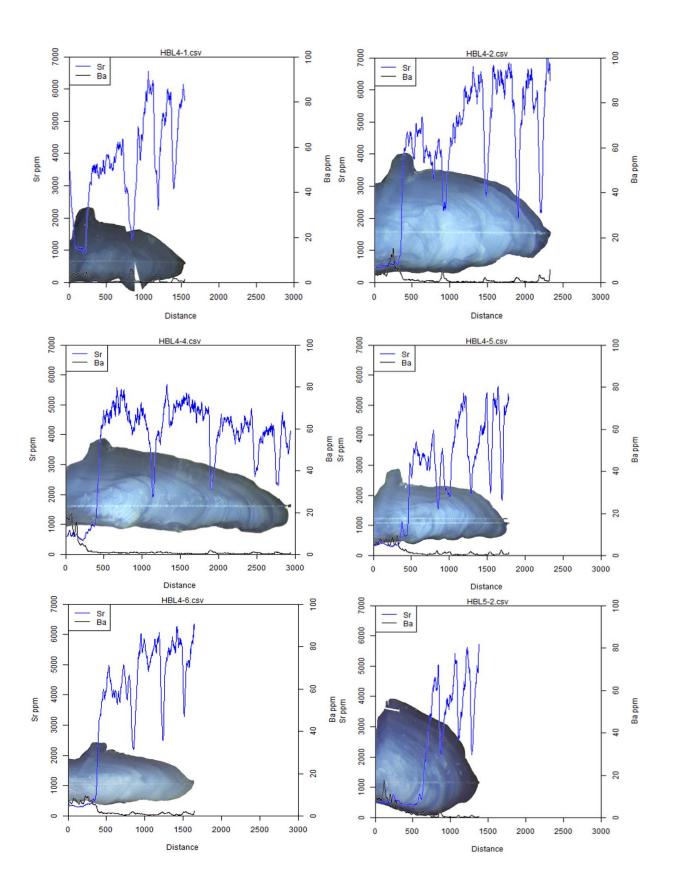


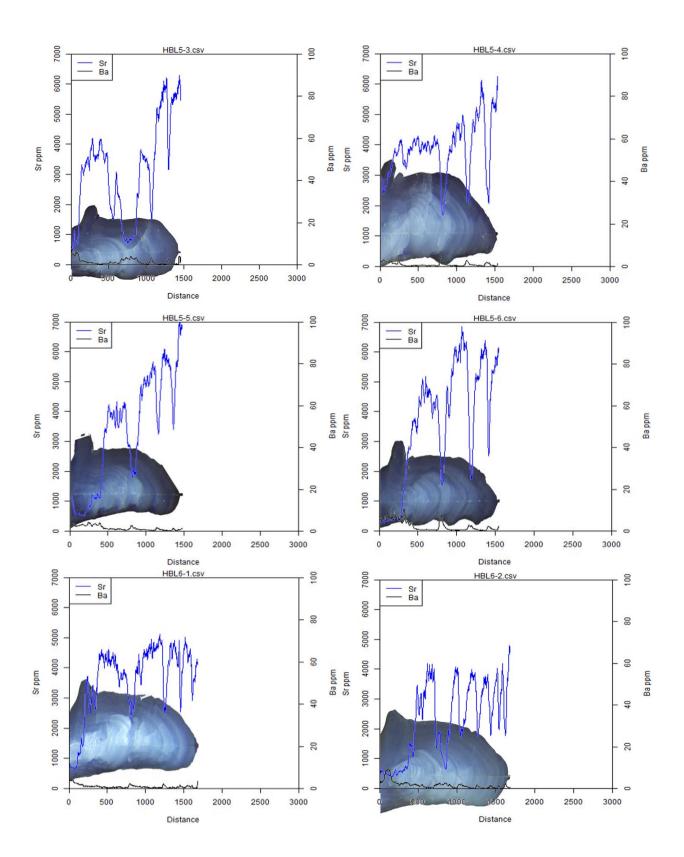


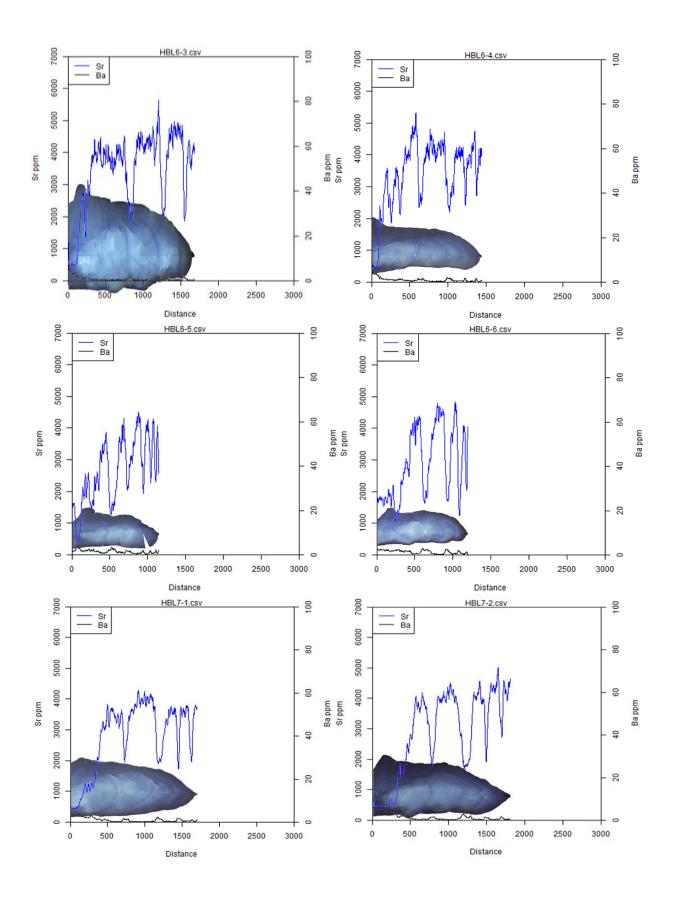


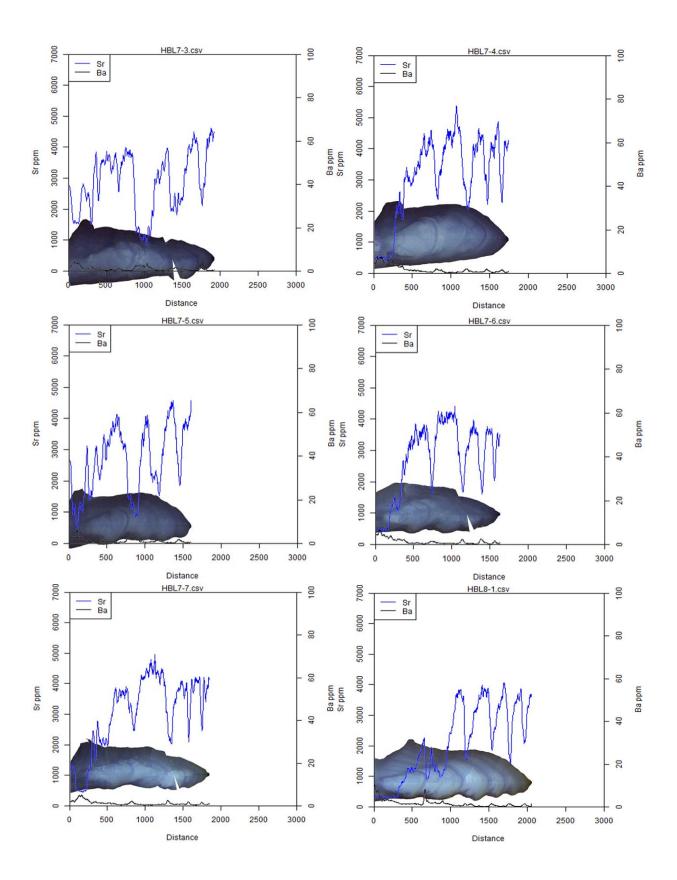


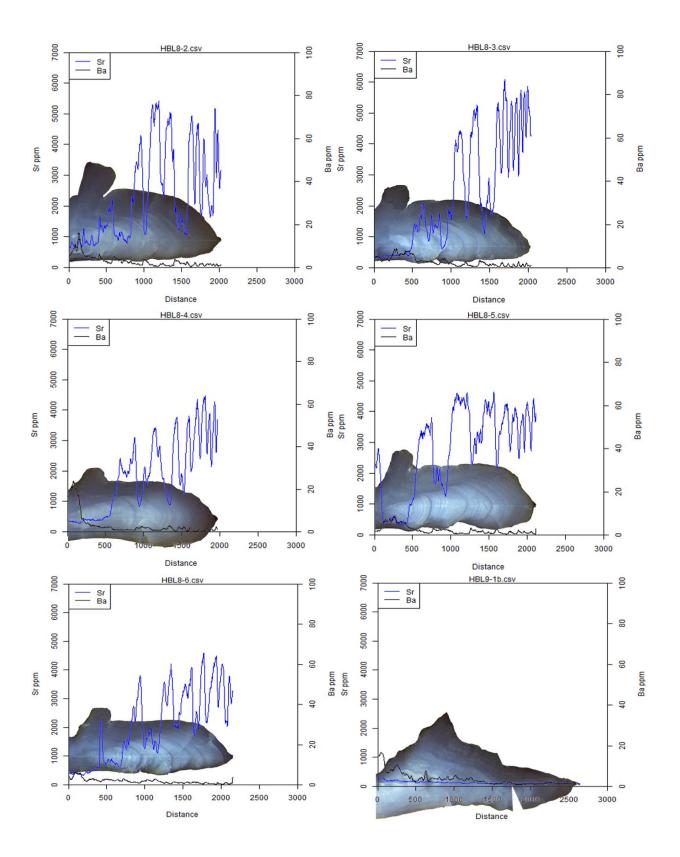


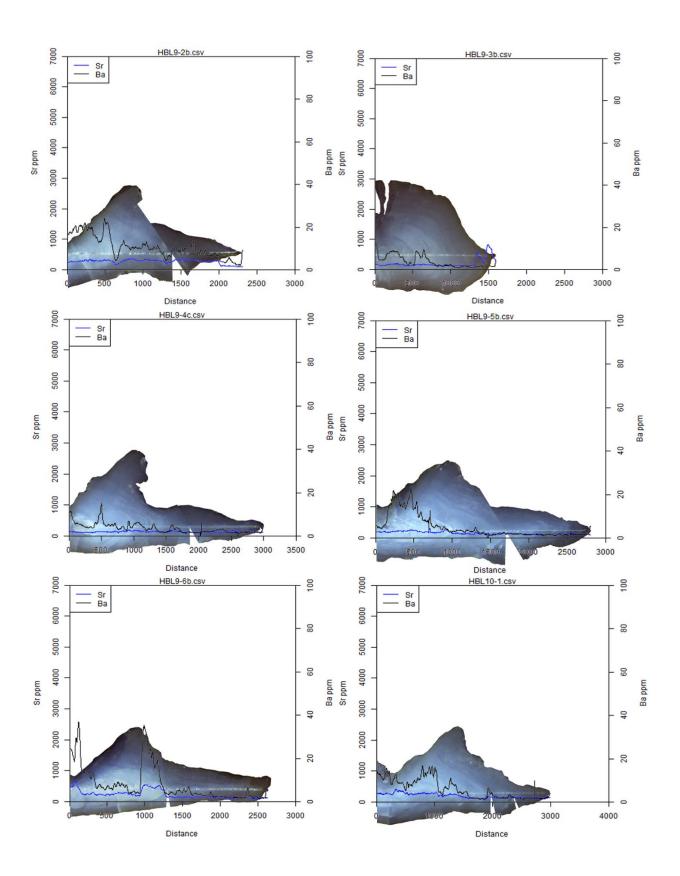


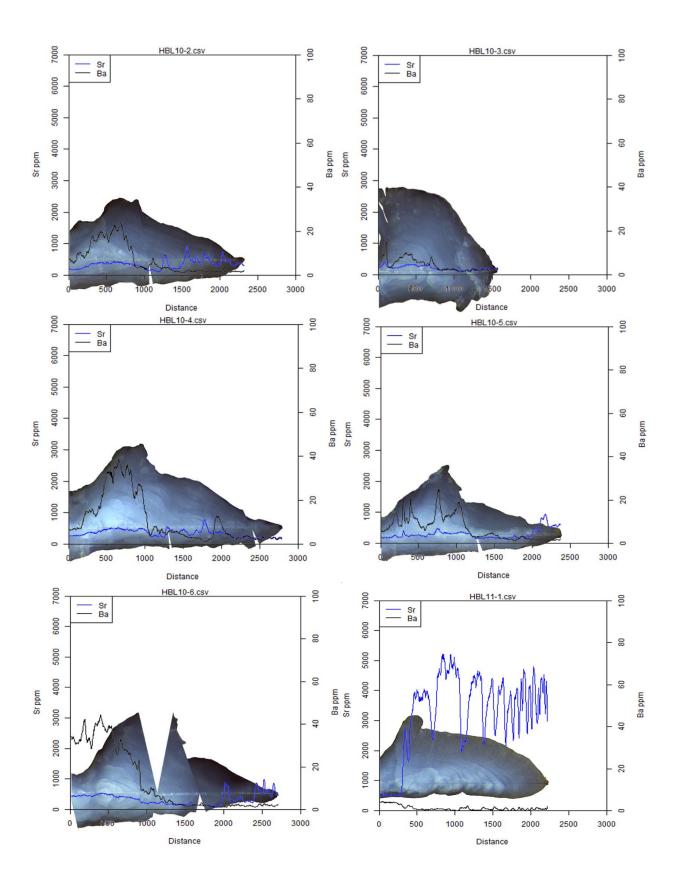


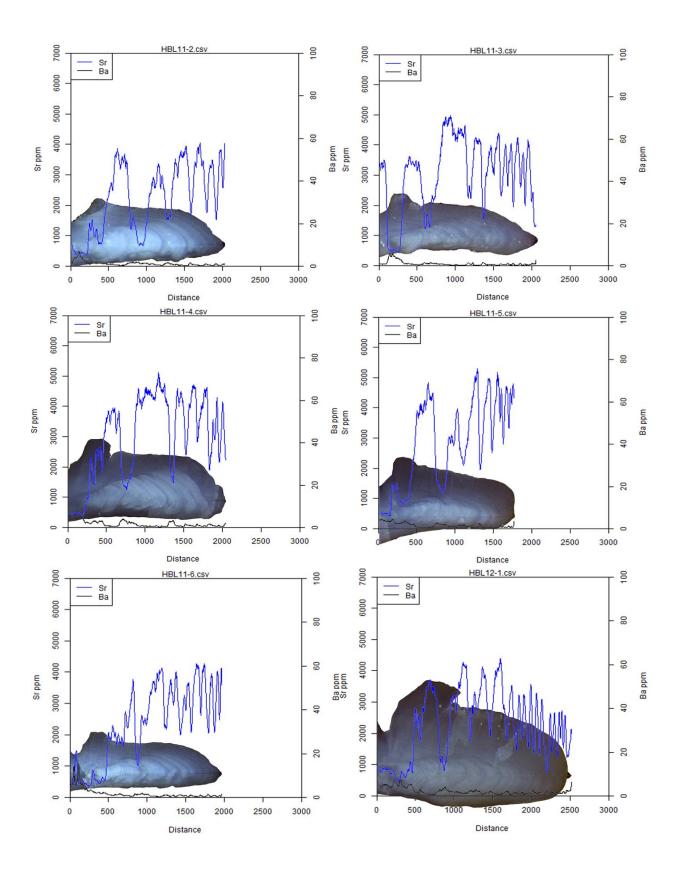


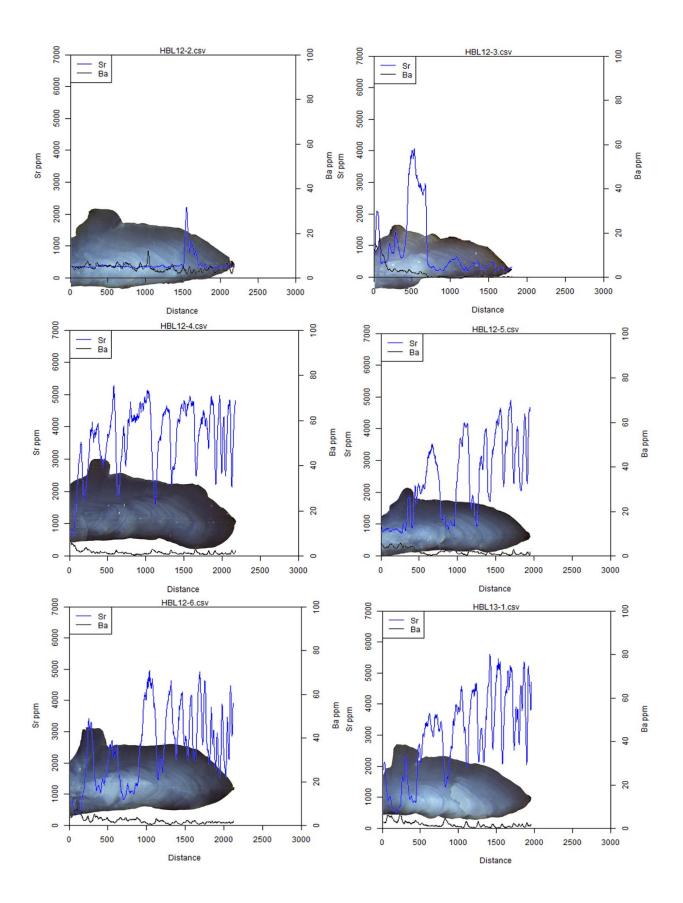


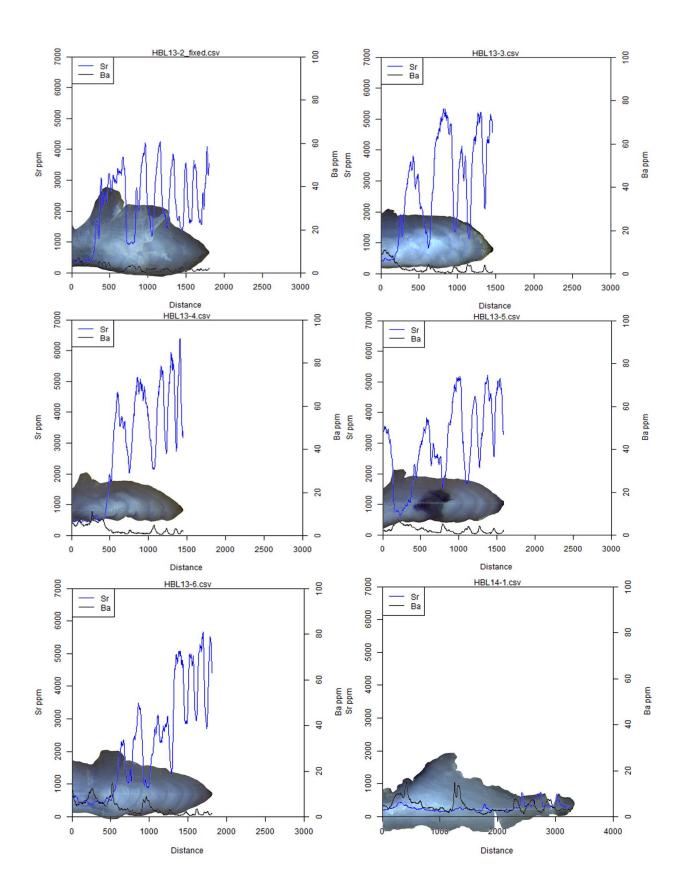


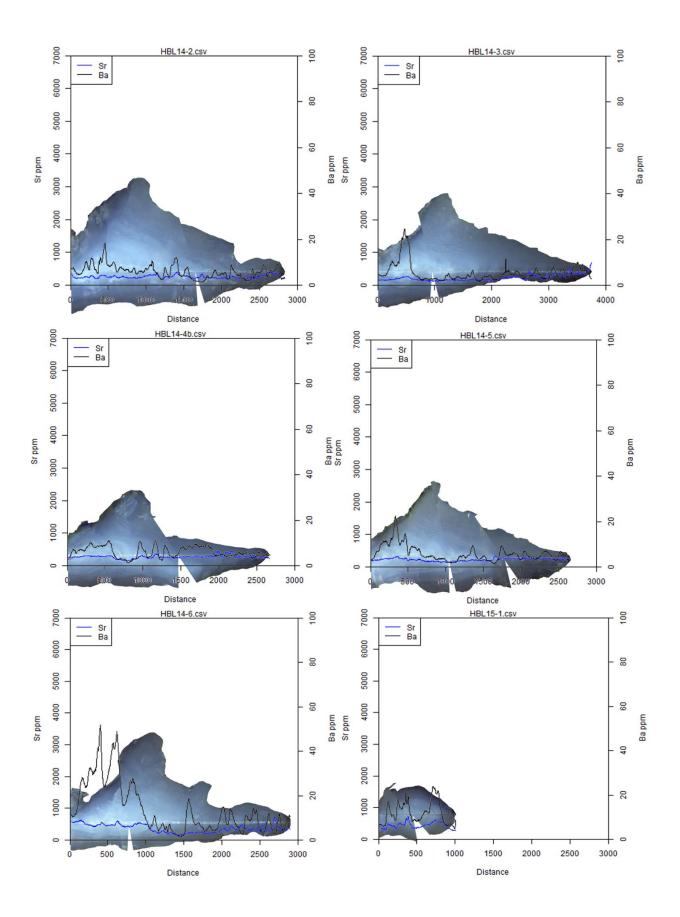


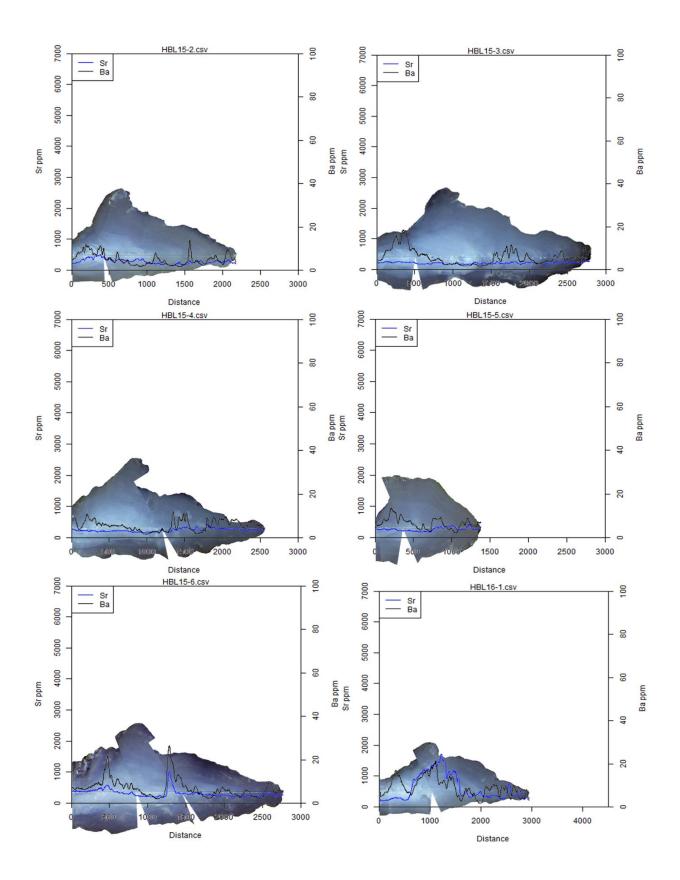


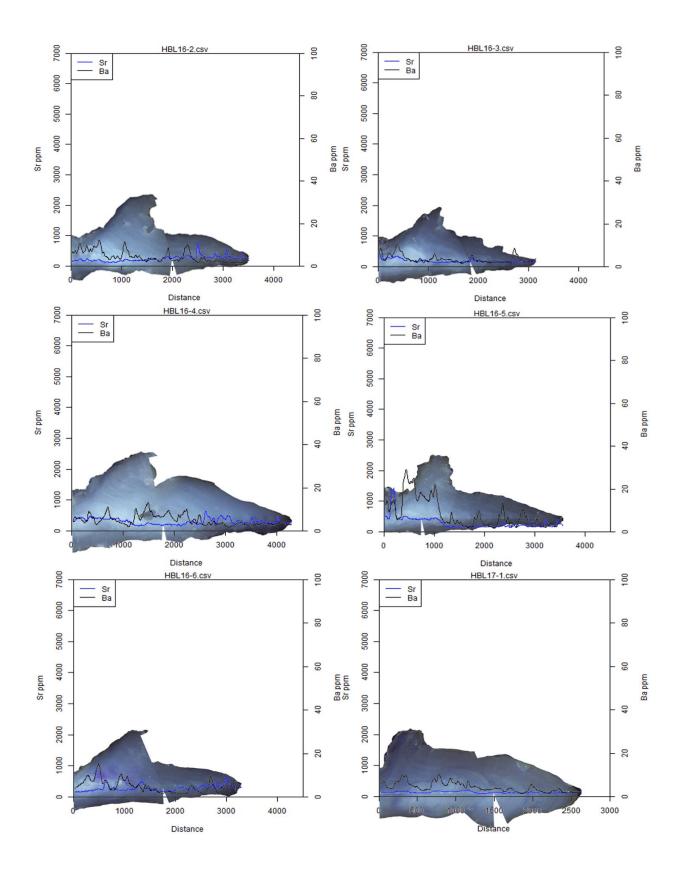


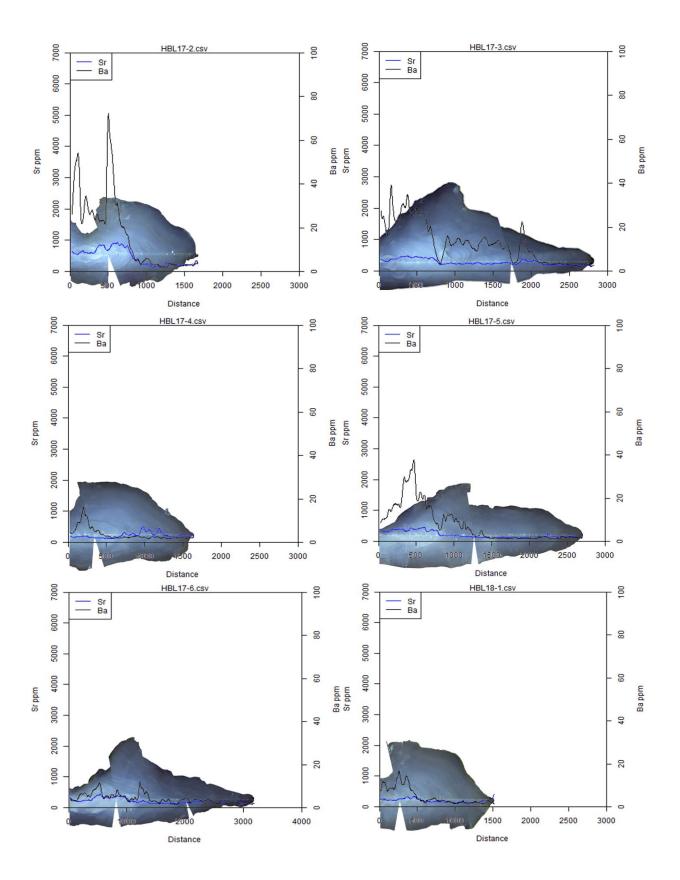


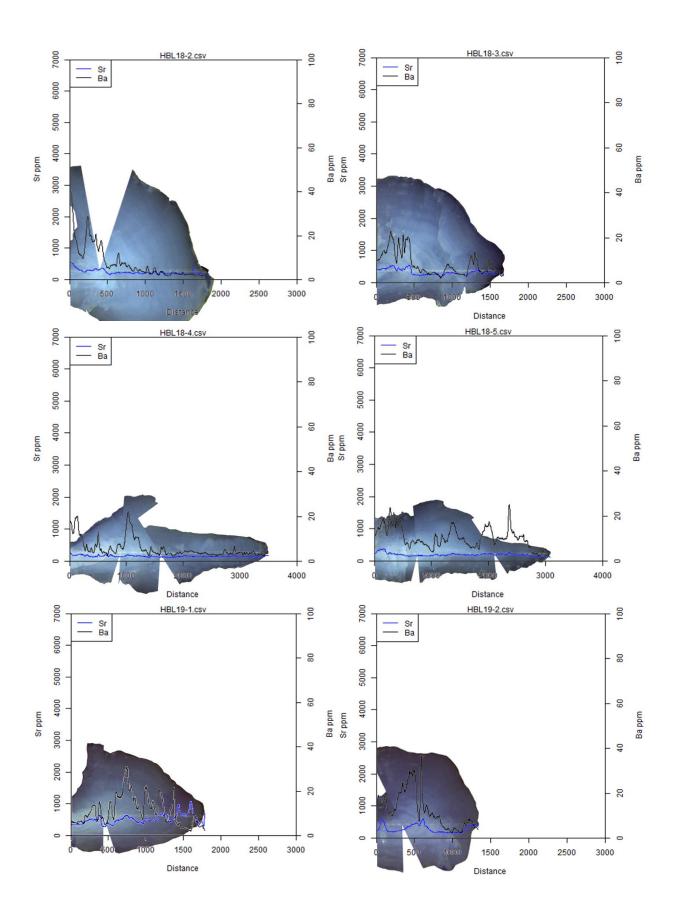


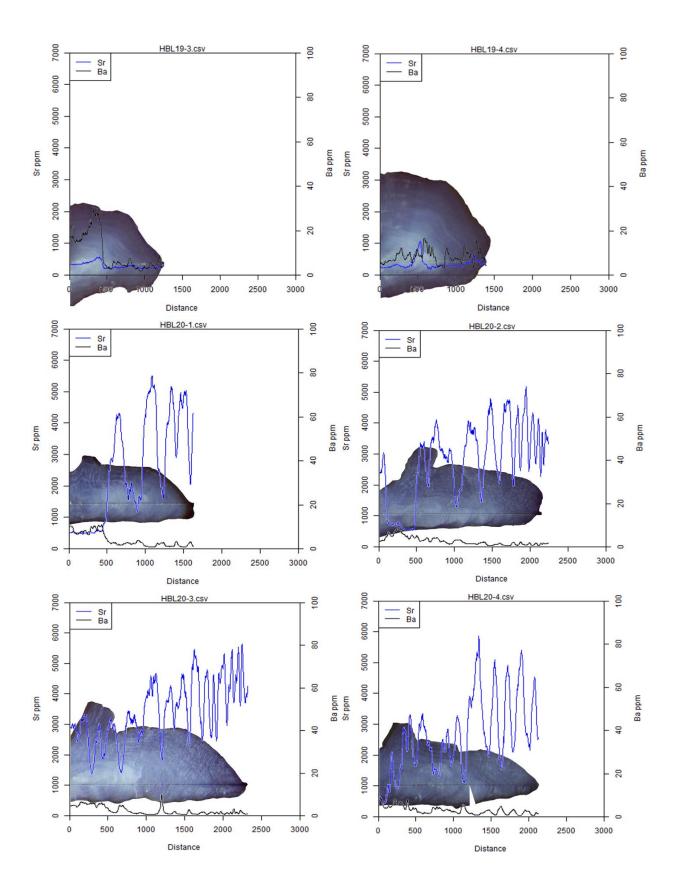


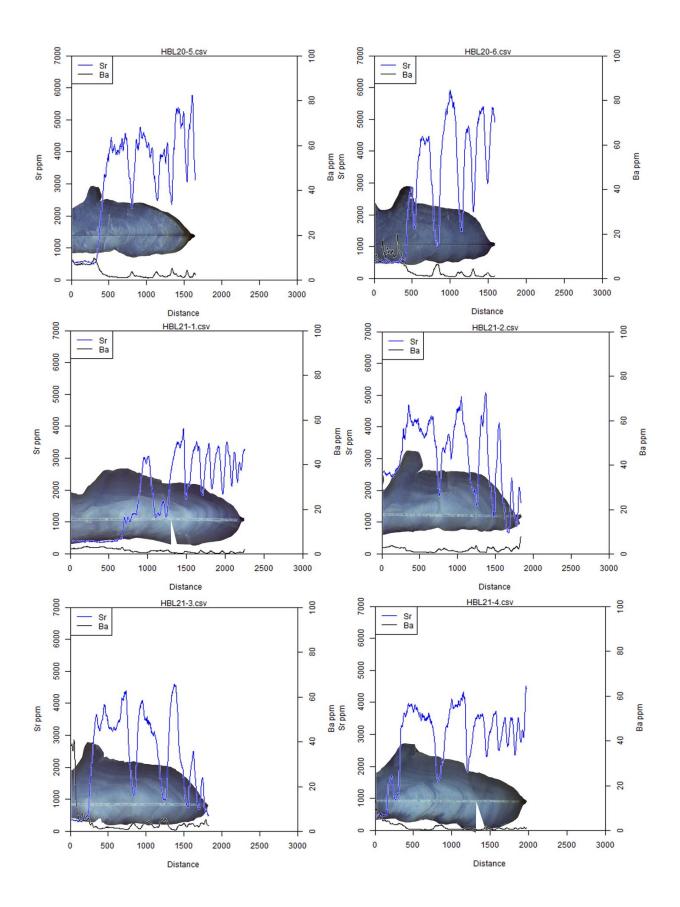


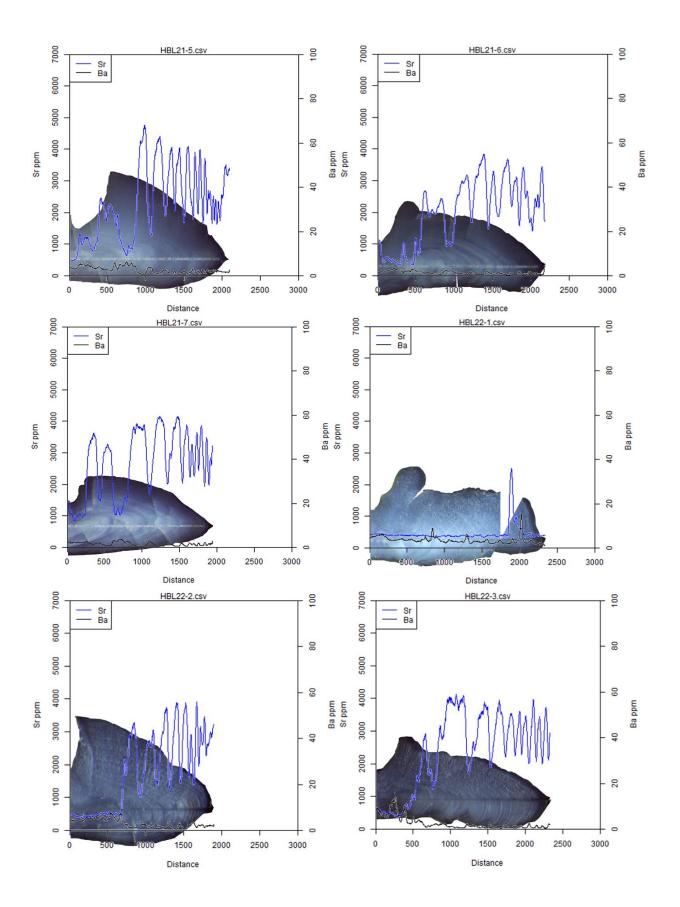


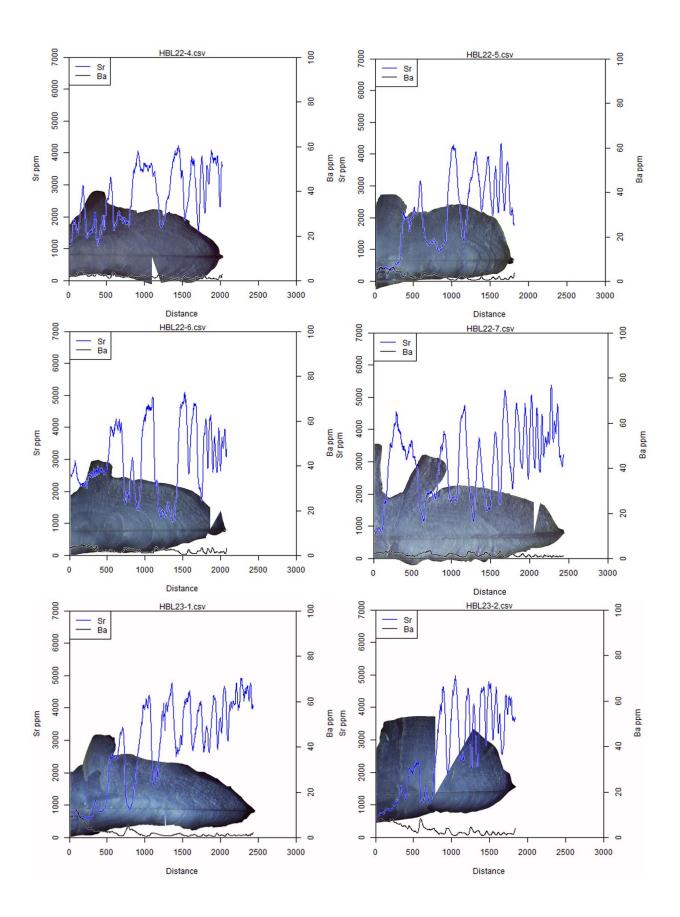


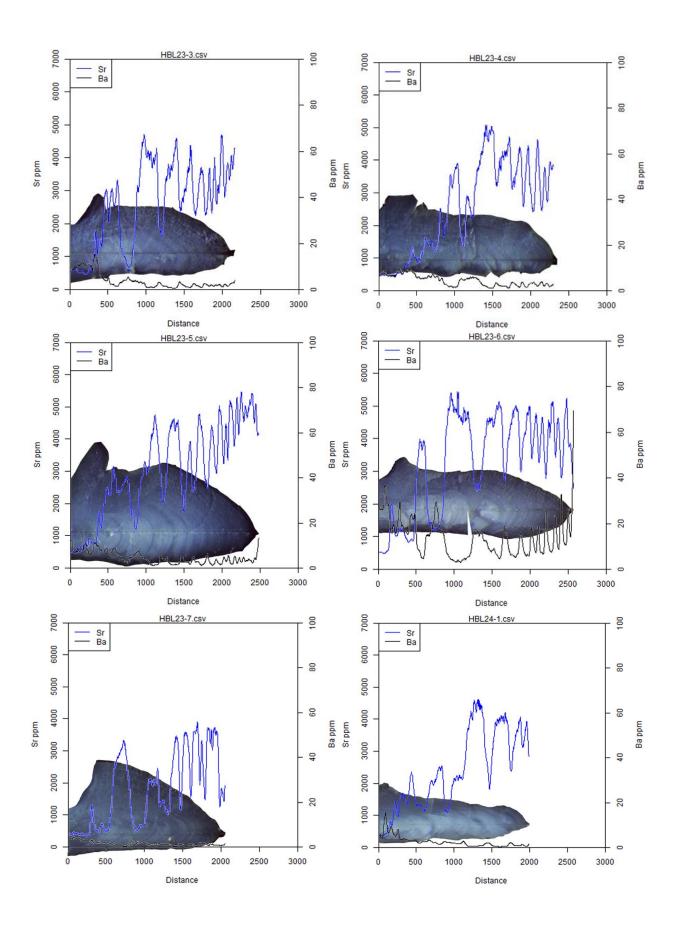


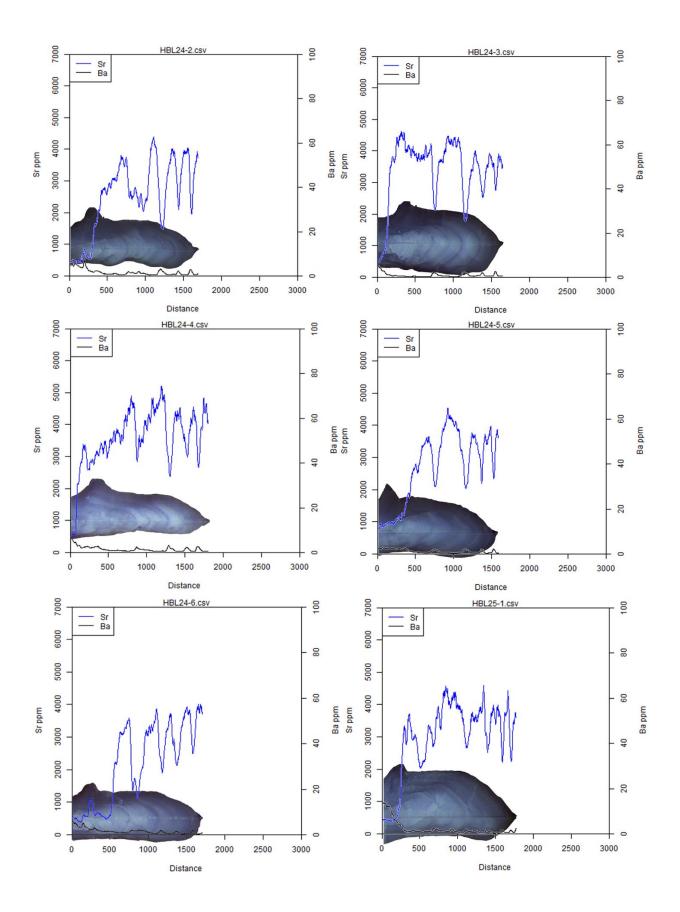


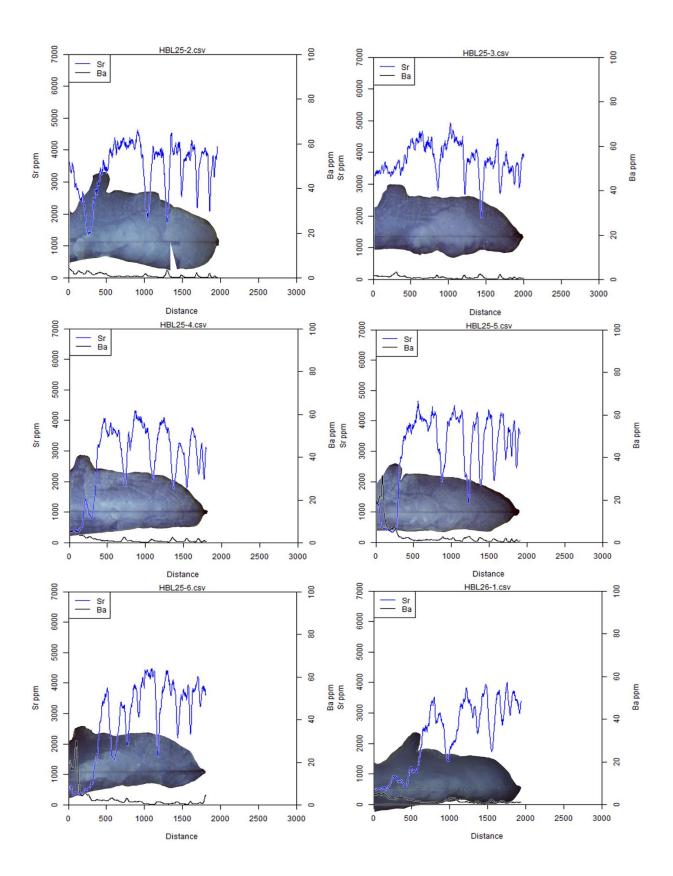


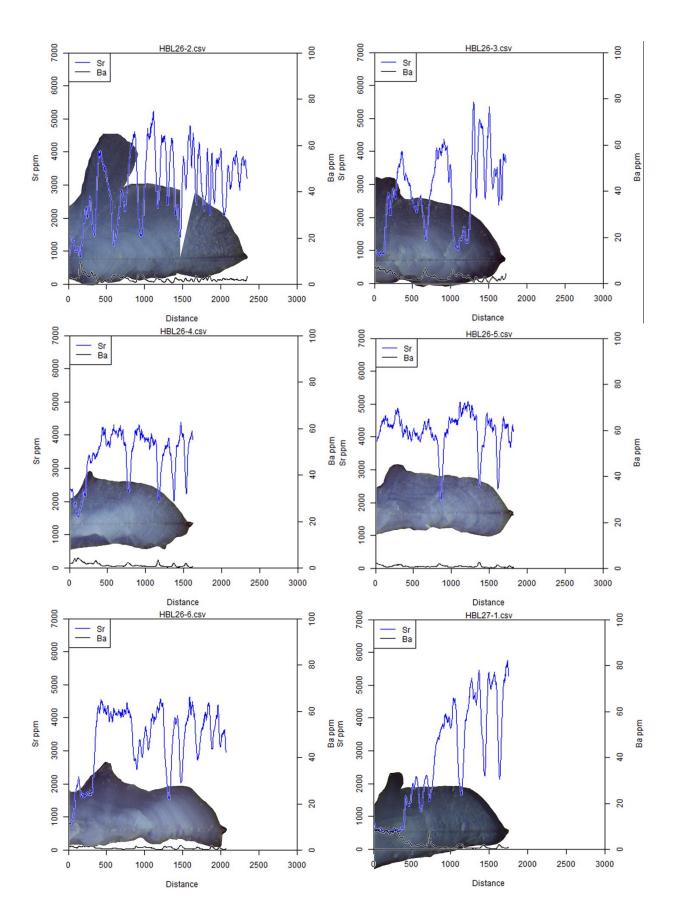


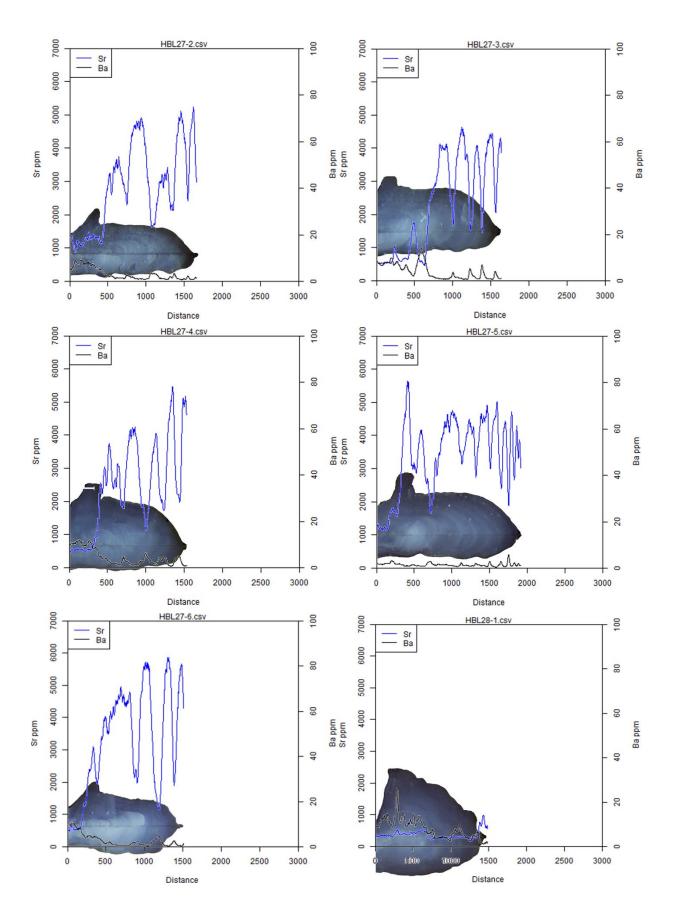


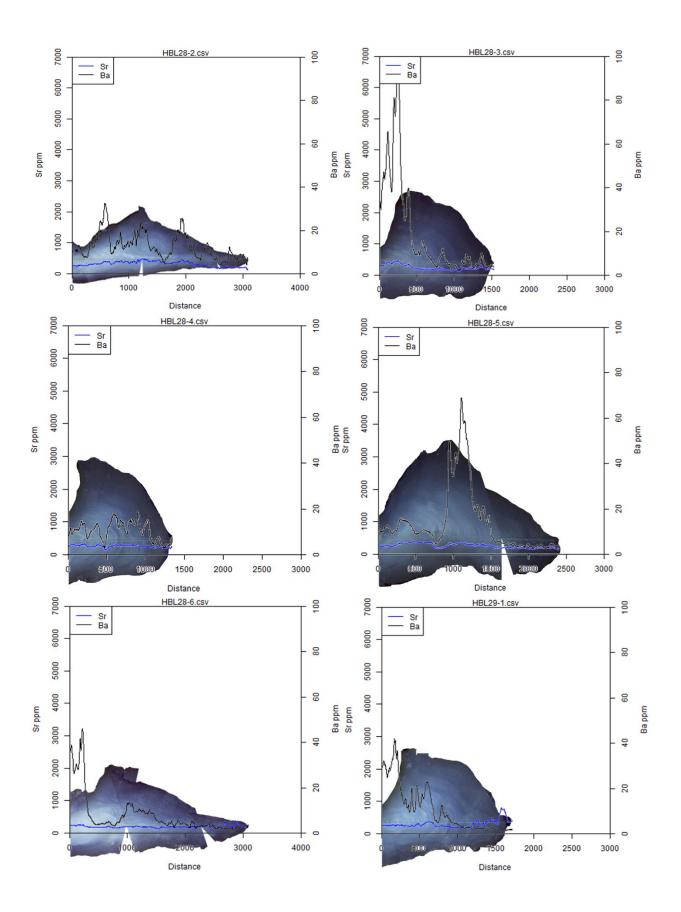


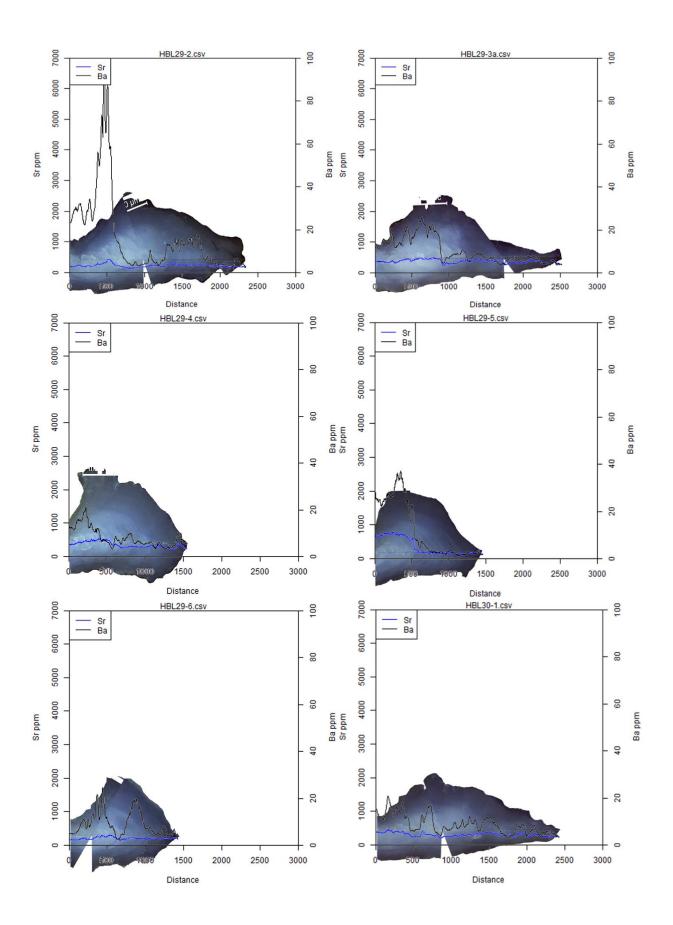


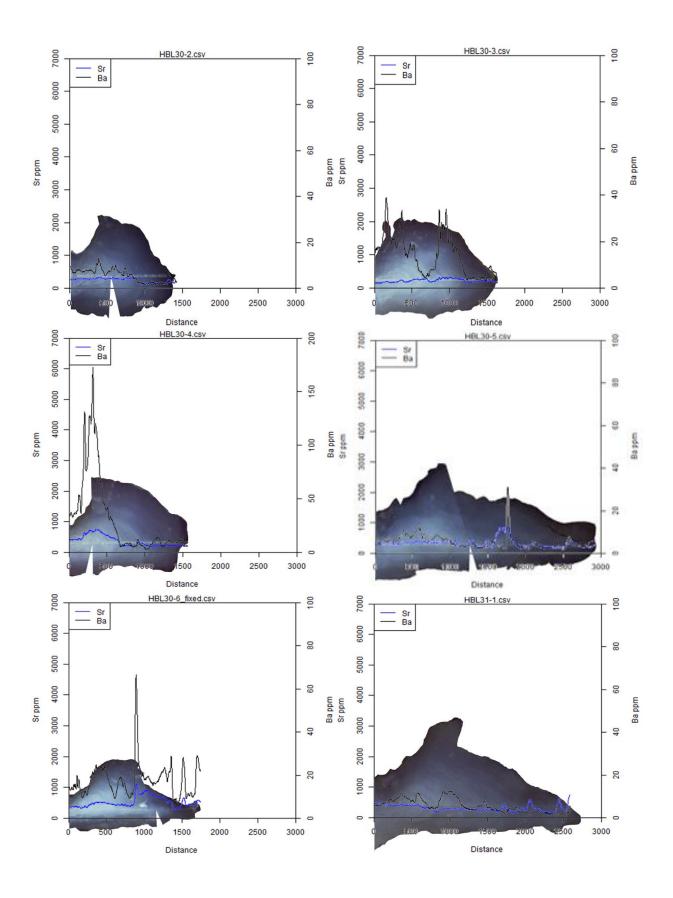


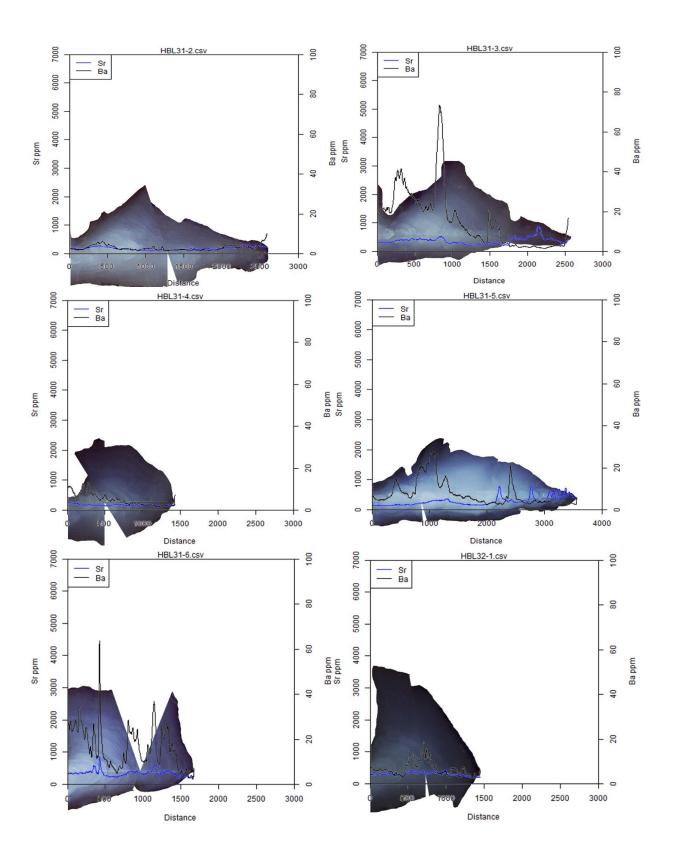


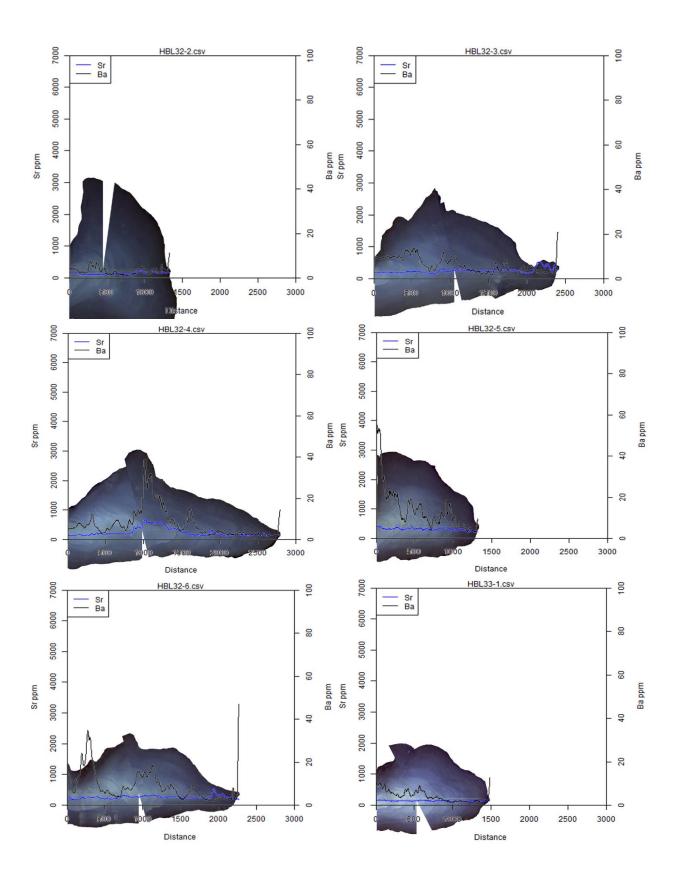


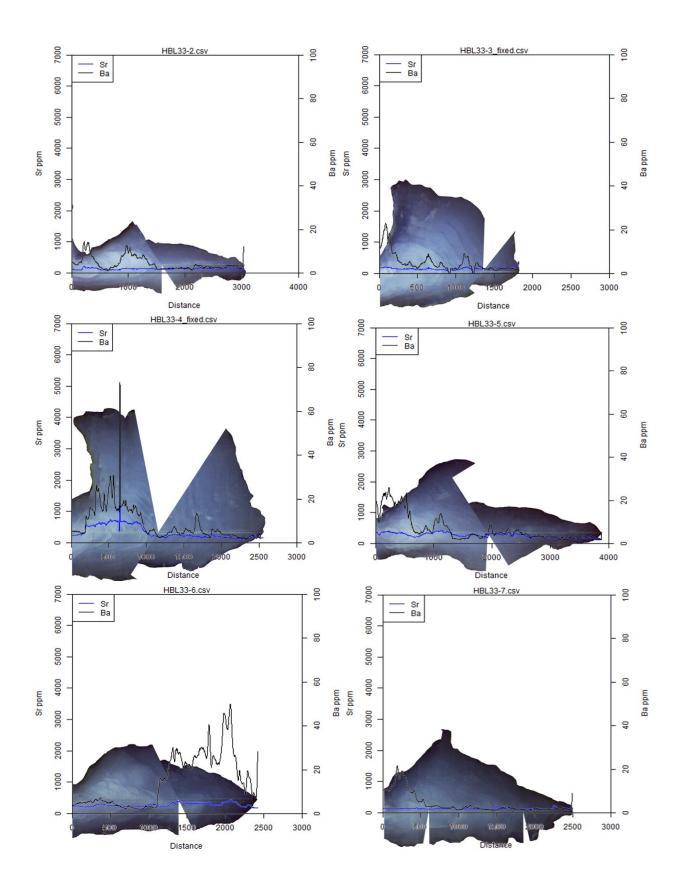


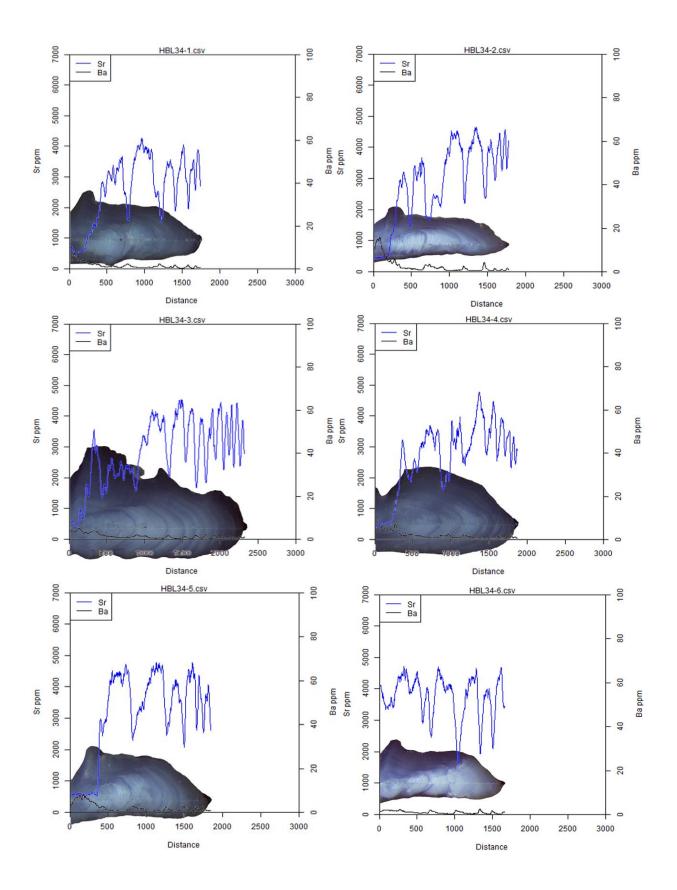


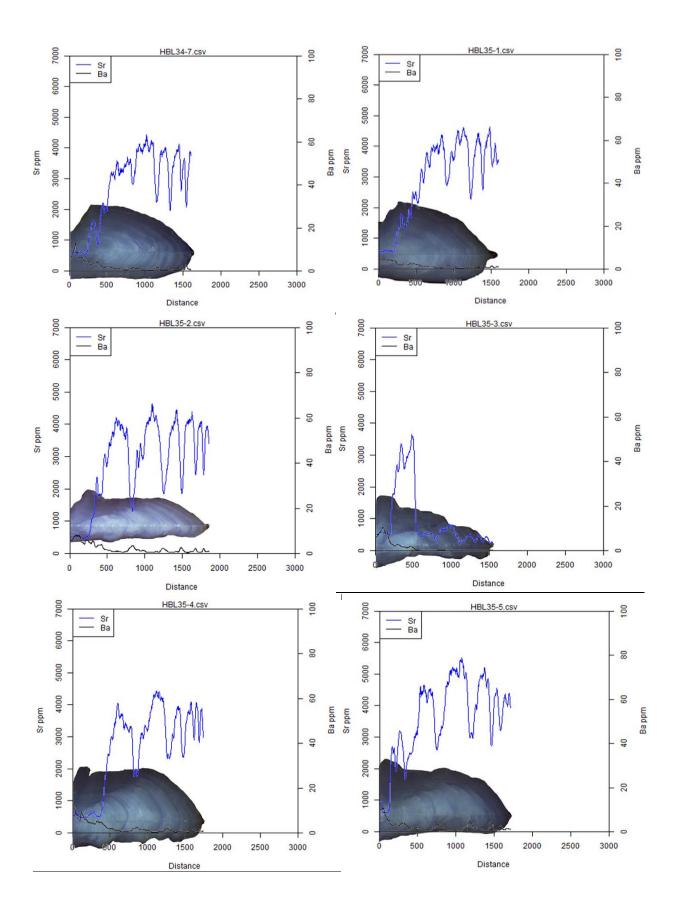


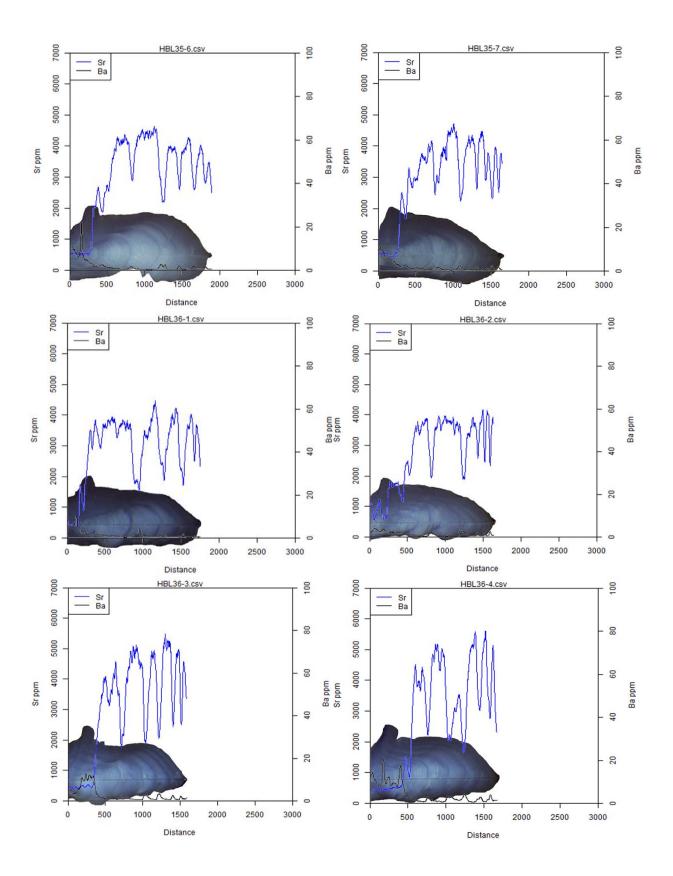


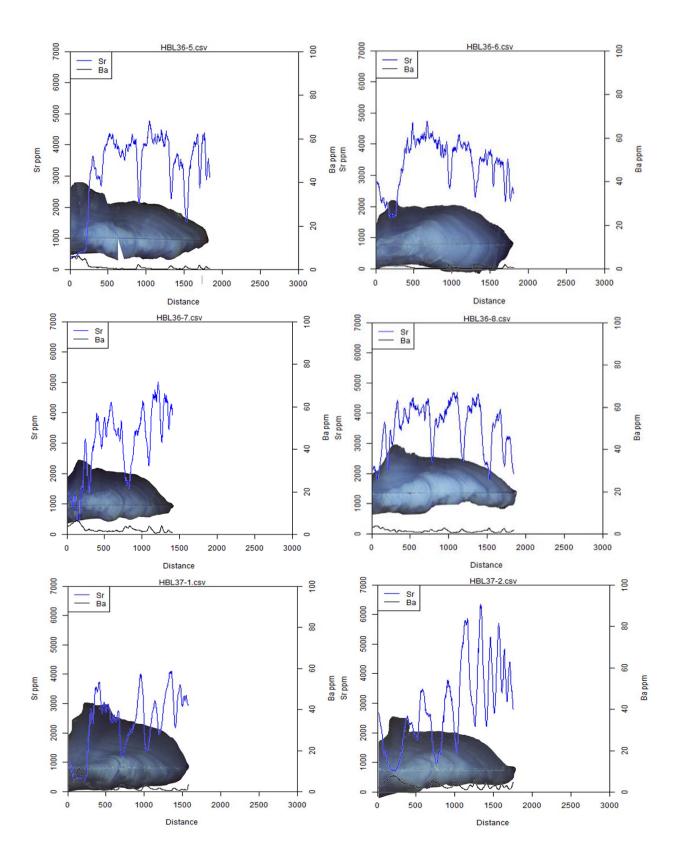


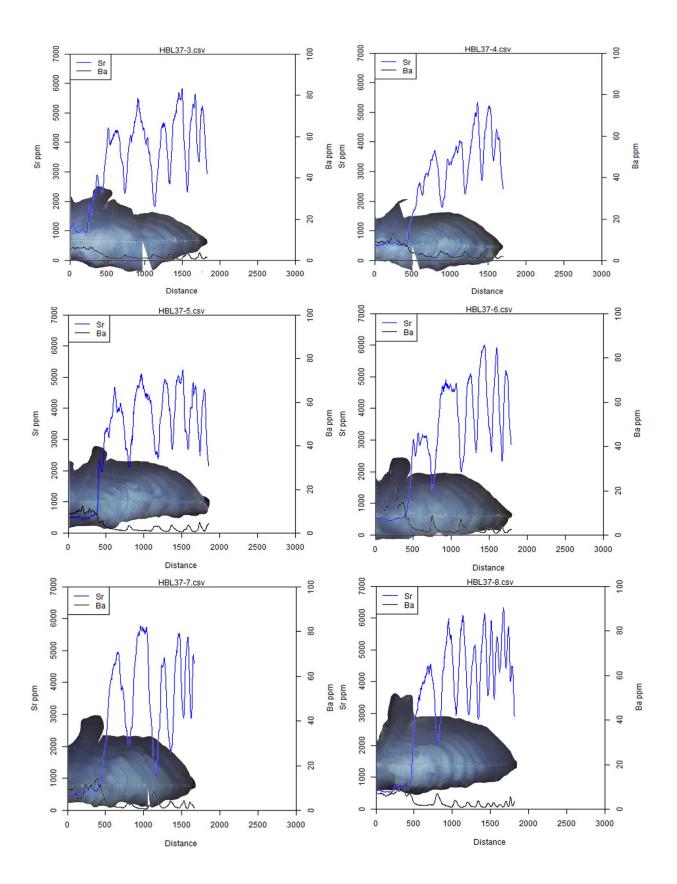


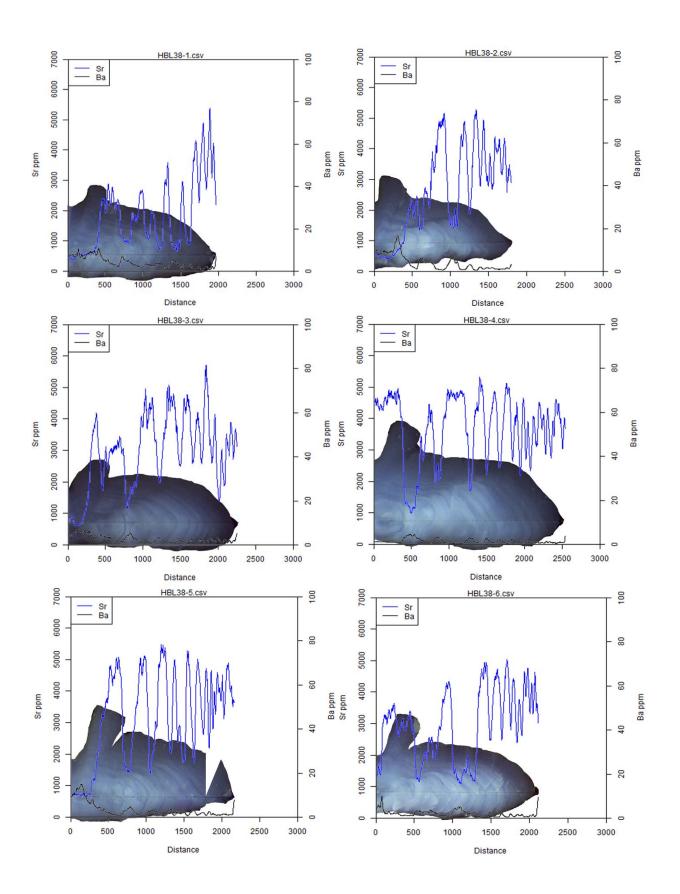


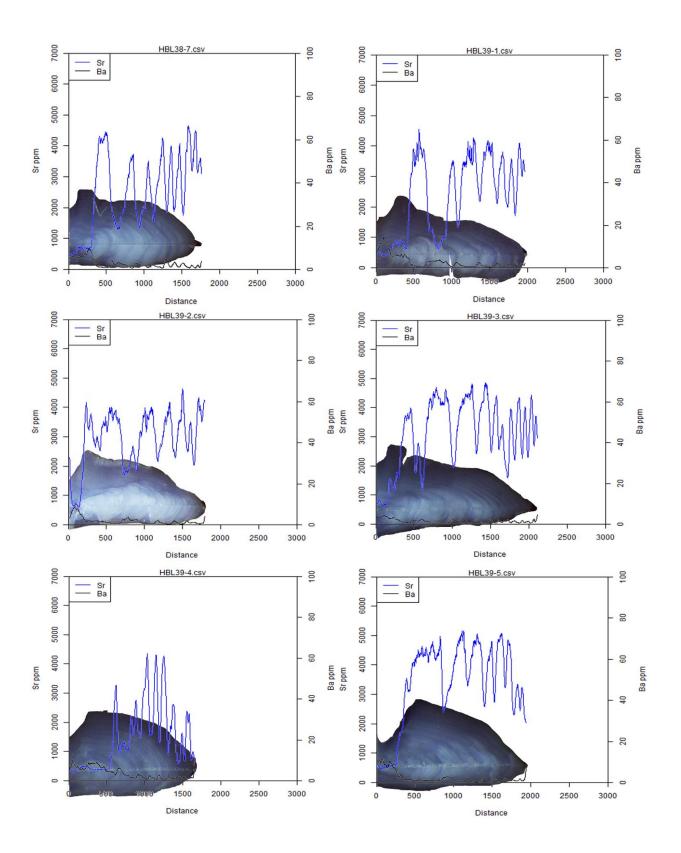


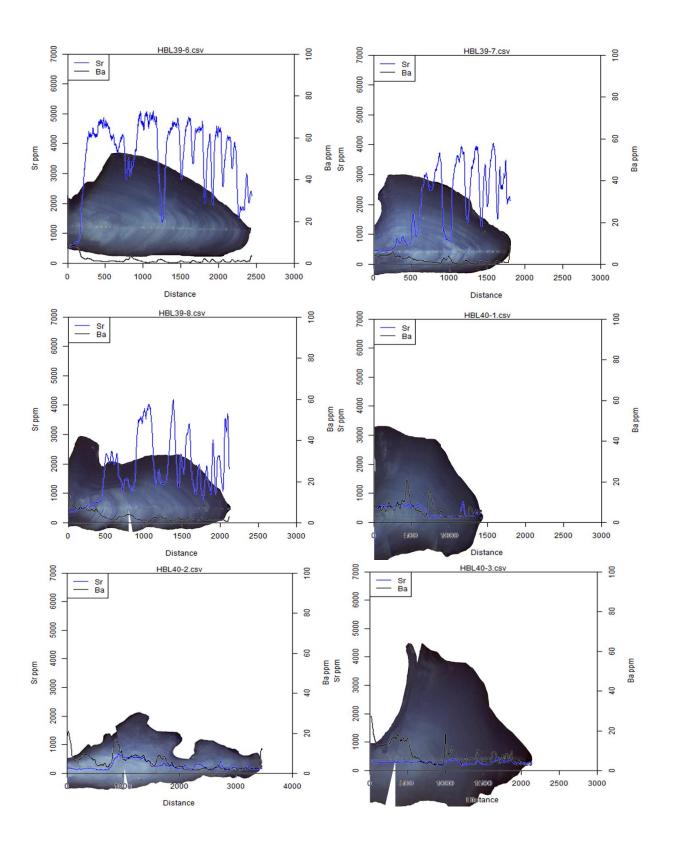


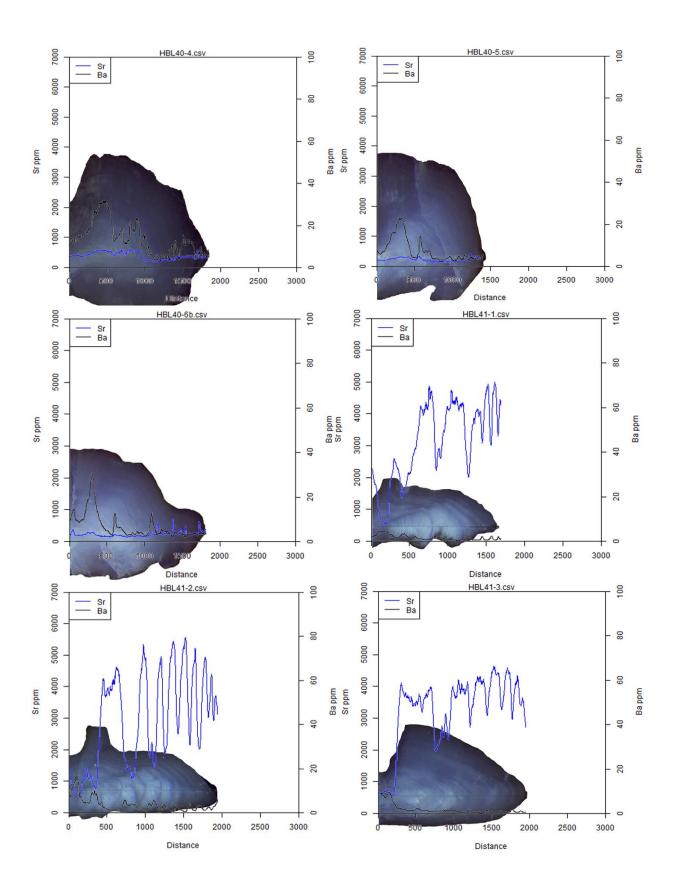


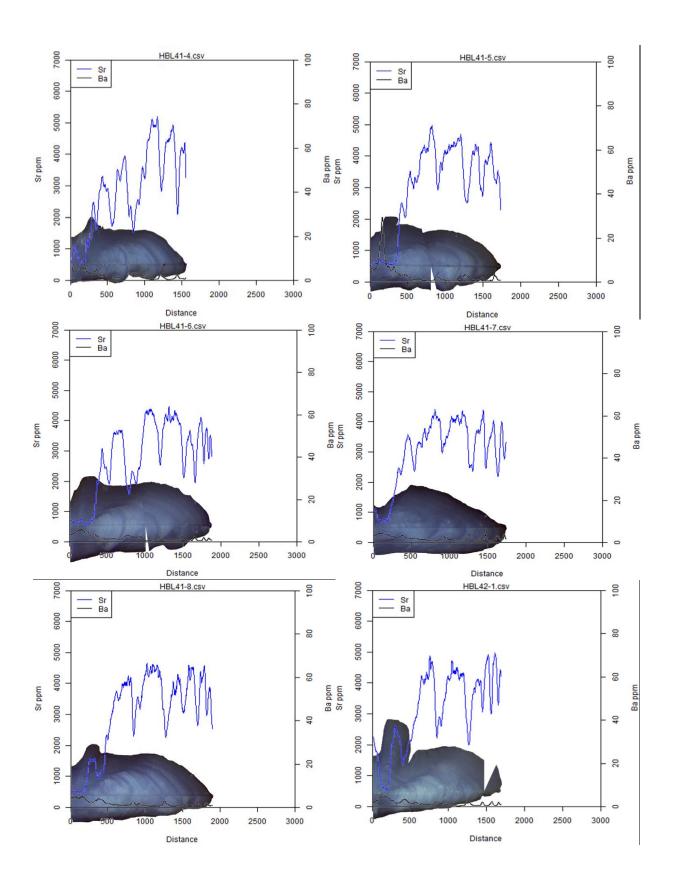


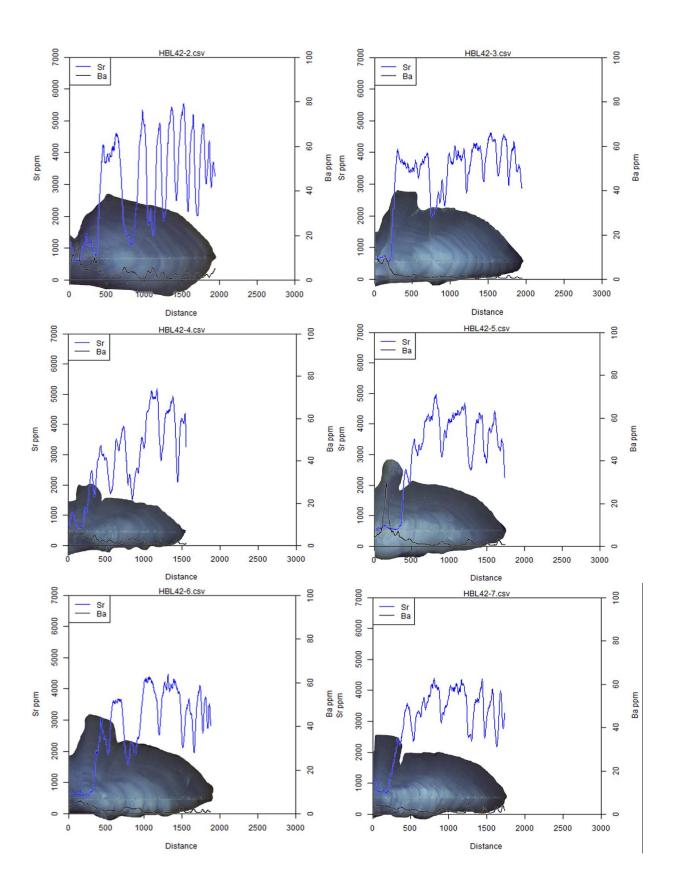


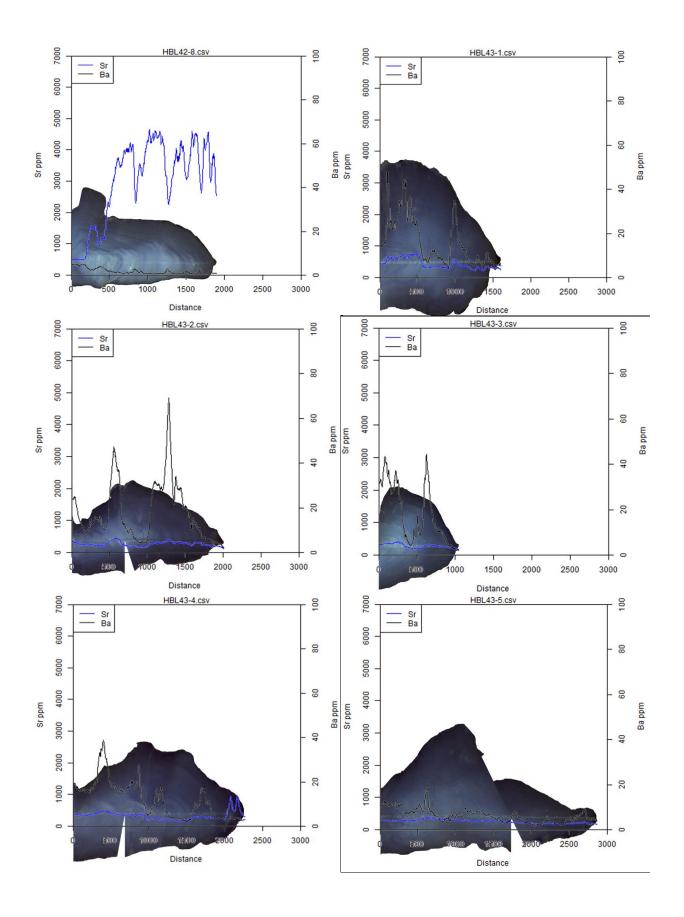


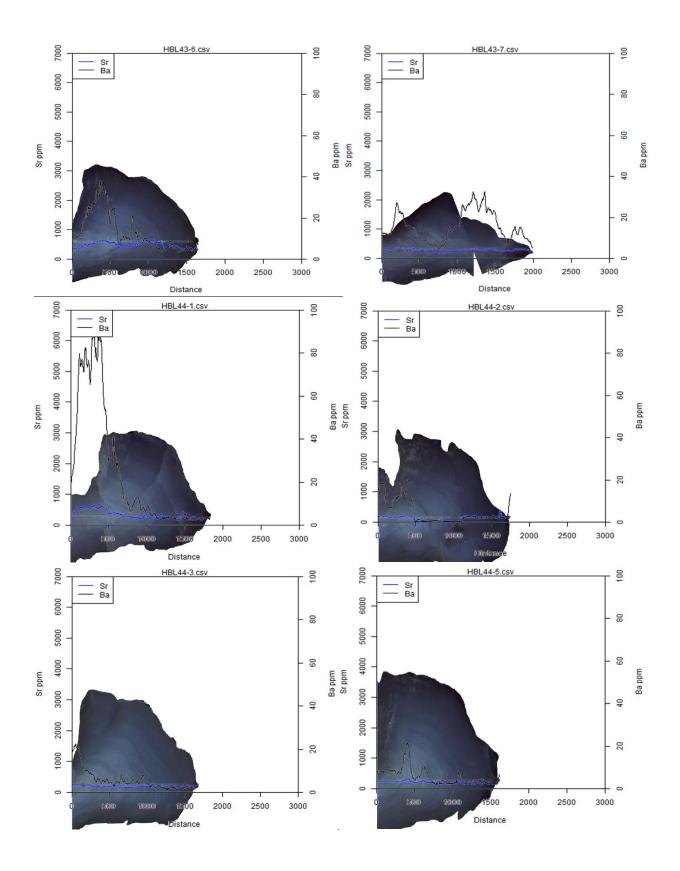


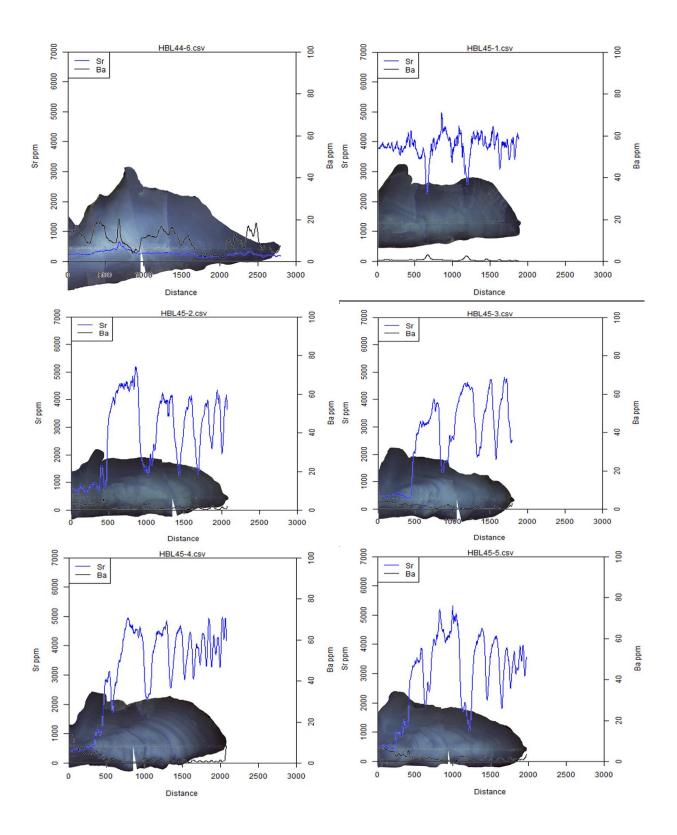


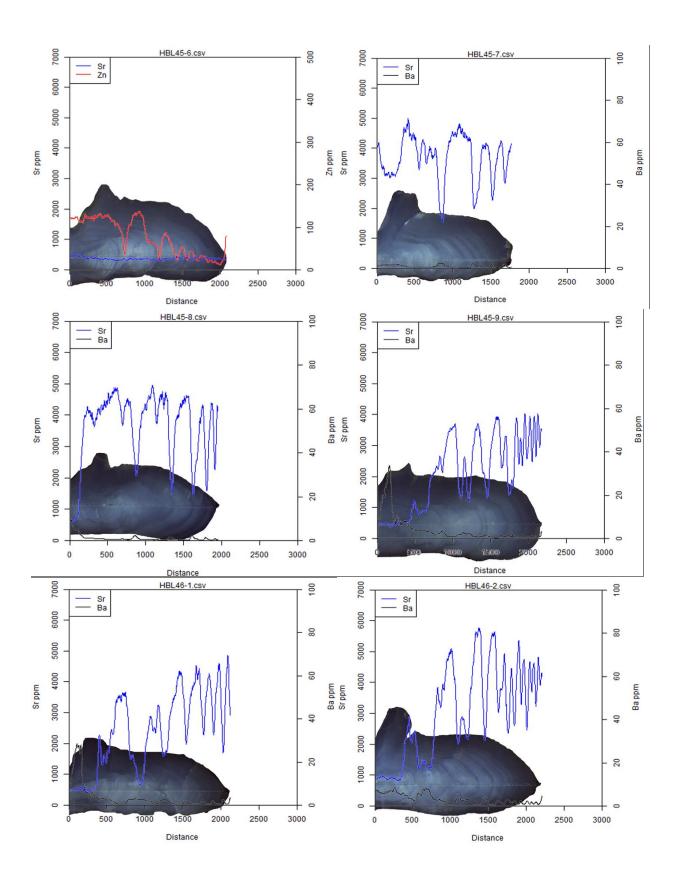


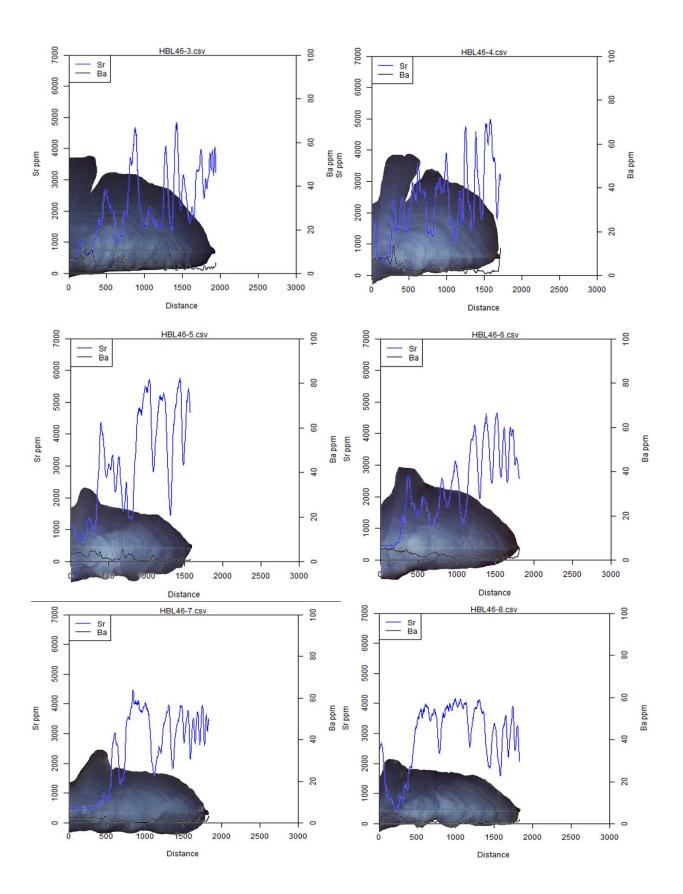


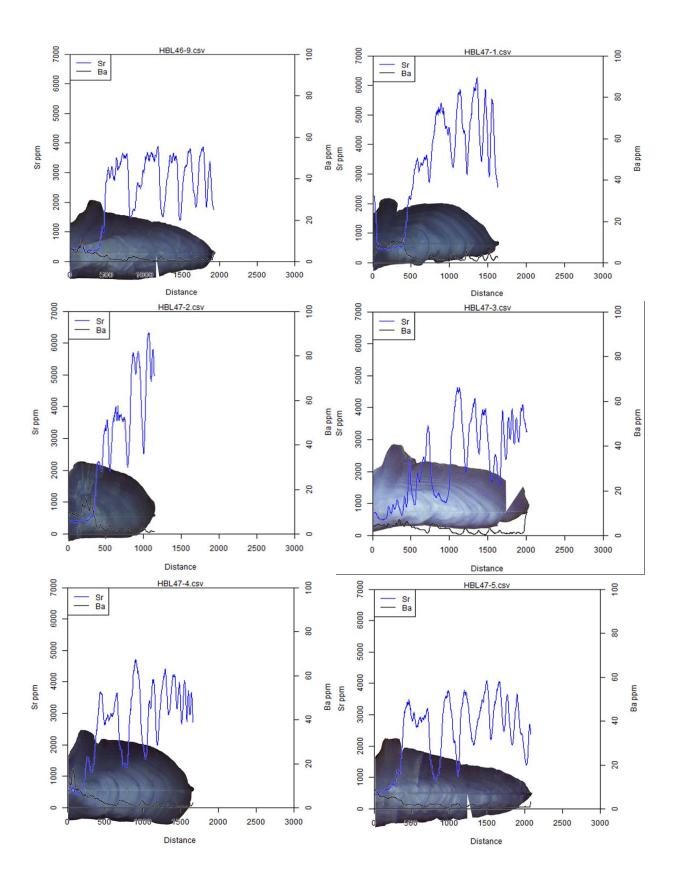


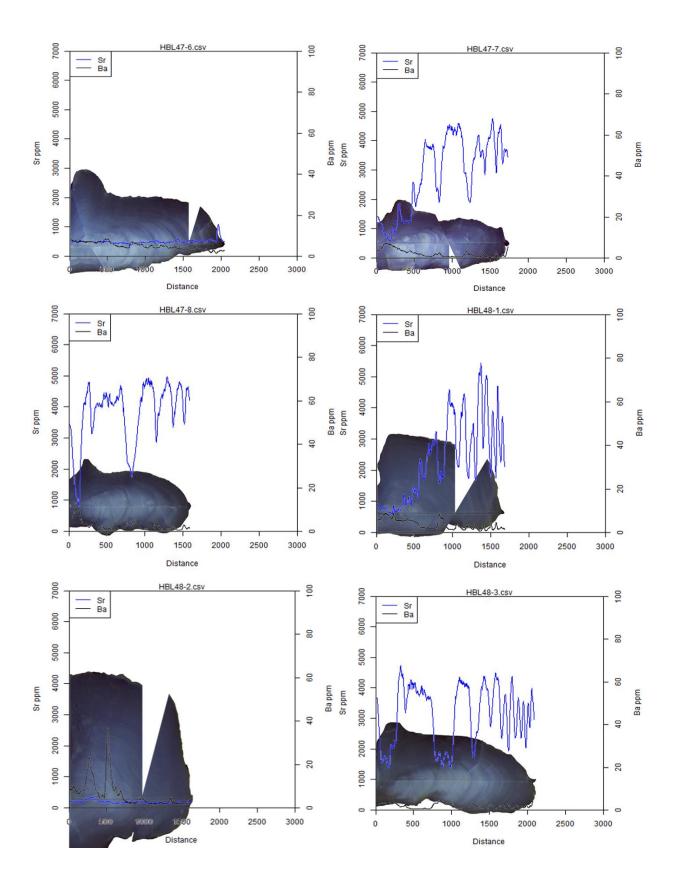


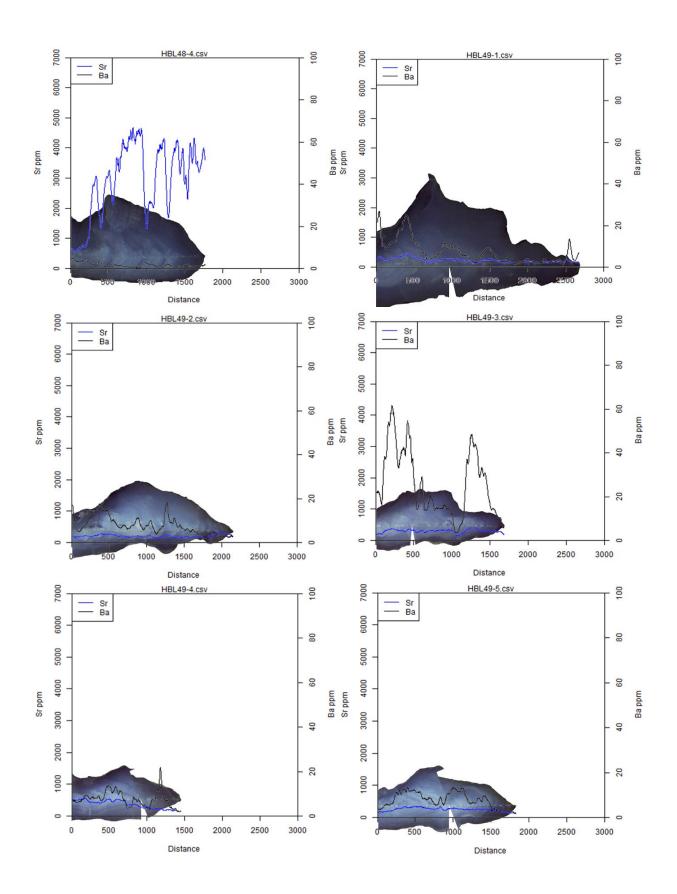


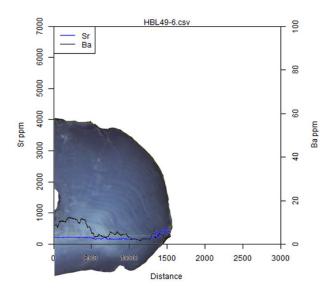












Appendix B - Raw Data

Table A. Summary of fish included in this study, including river of collection, fish age, and migratory classification of fish.

Ring Position	Fish #	River	Species	Migratory group	Age	δ ³⁴ S (‰)
ATTA1-1	12054	Attawapiskat	LKWH	migratory	6	14.69045
ATTA1-2	12024	Attawapiskat	LKWH	migratory	11	15.601
ATTA1-4	12055	Attawapiskat	LKWH	migratory	10	13.35932
ATTA1-5	12200	Winisk	LKWH	non-migratory	7	8.861511
ATTA2-3	12117	Severn	LKWH	migratory	13	15.65289
ATTA2-4	12131	Severn	LKWH	migratory	22	16.32
ATTA2-5	12202	Winisk	LKWH	non-migratory	8	5.754779
ATTA2-7	12194	Winisk	LKWH	non-migratory	8	5.749125
ATTA3-1	12099	Attawapiskat	NRPK	migratory	11	10.9383
ATTA3-2	12084	Attawapiskat	NRPK	non-migratory	2	9.108497
ATTA4-2	12094	Attawapiskat	NRPK	non-migratory	4	8.811749
ATTA4-4	12085	Attawapiskat	NRPK	non-migratory	6	9.059428
ATTA4-5	12080	Attawapiskat	NRPK	non-migratory	6	10.48225
ATTA5-1	12093	Attawapiskat	NRPK	non-migratory	7	12.07013
ATTA5-5	12092	Attawapiskat	NRPK	non-migratory	8	9.314355
ATTA6-3	12098	Attawapiskat	NRPK	migratory	7	10.68916
ATTA6-4	12100	Attawapiskat	NRPK	migratory	9	10.80465
ATTA6-5	12096	Attawapiskat	NRPK	non-migratory	4	9.178178
ATTA8-2	12116	Severn	LKWH	migratory	6	15.08249
ATTA8-4	12081	Attawapiskat	NRPK	non-migratory	3	13.63991
ATTA9-3	12203	Winisk	LKWH	non-migratory	7	4.823993
ATTA9-4	12196	Winisk	LKWH	non-migratory	3	4.439377
ATTA9-5	12210	Winisk	LKWH	non-migratory	4	5.29463
ATTA10-1	12128	Severn	LKWH	migratory	9	15.08396
ATTA10-3	12127	Severn	LKWH	migratory	9	13.92027
ATTA10-5	12119	Severn	LKWH	migratory	6	14.27697
ATTA11-1	12122	Severn	LKWH	migratory	6	15.00254
ATTA11-3	12118	Severn	LKWH	migratory	6	13.82086
ATTA11-4	12112	Severn	LKWH	migratory	9	16.27162
ATTA12-2	12209	Winisk	LKWH	non-migratory	6	4.929621
ATTA12-3	12205	Winisk	LKWH	non-migratory	7	6.399758
ATTA12-4	12197	Winisk	LKWH	non-migratory	7	6.617788
ATTA13-4	12121	Severn	LKWH	migratory	16	14.86457
ATTA14-4	12199	Winisk	LKWH	non-migratory	8	6.534145
ATTA29-1	12019	Attawapiskat	CISC	migratory	8	17.23471
ATTA29-2	12074	Attawapiskat	LKWH	migratory	2	14.15696

Ring Position	Fish #	River	Species	Migratory group	Age	δ ³⁴ S (‰)
ATTA29-3	12075	Attawapiskat	LKWH	migratory	2	12.84396
ATTA29-4	12076	Attawapiskat	LKWH	migratory	3	15.16038
ATTA30-1	12007	Attawapiskat	CISC	migratory	4	17.63302
ATTA30-2	12002	Attawapiskat	CISC	migratory	4	16.77114
ATTA30-3	12009	Attawapiskat	CISC	migratory	5	16.69943
ATTA30-4	12011	Attawapiskat	CISC	migratory	4	14.2475
ATTA30-5	12010	Attawapiskat	CISC	migratory	3	16.26973
ATTA31-1	12003	Attawapiskat	CISC	migratory	10	17.18873
ATTA31-2	12001	Attawapiskat	CISC	migratory	4	16.79934
ATTA31-3	12006	Attawapiskat	CISC	migratory	4	15.7114
ATTA31-4	12008	Attawapiskat	CISC	migratory	7	15.90057
ATTA31-5	12005	Attawapiskat	CISC	migratory	4	16.80524
ATTA32-1	12004	Attawapiskat	CISC	migratory	10	16.78158
ATTA32-2	12047	Attawapiskat	LKWH	migratory	4	15.69437
ATTA32-3	12051	Attawapiskat	LKWH	migratory	5	13.18494
ATTA32-5	12048	Attawapiskat	LKWH	migratory	5	16.57607
ATTA33-1	12025	Attawapiskat	LKWH	migratory	5	13.62762
ATTA33-2	12020	Attawapiskat	LKWH	migratory	4	15.19344
ATTA33-4	12035	Attawapiskat	LKWH	migratory	4	14.83388
ATTA33-5	12056	Attawapiskat	LKWH	migratory	6	14.37155
ATTA34-1	12059	Attawapiskat	LKWH	migratory	4	15.51918
ATTA34-3	12037	Attawapiskat	LKWH	migratory	5	16.57583
ATTA34-4	12022	Attawapiskat	LKWH	migratory	6	14.38951
ATTA34-5	12043	Attawapiskat	LKWH	migratory	4	15.90933
ATTA35-1	12023	Attawapiskat	LKWH	migratory	3	15.02275
ATTA35-2	12061	Attawapiskat	LKWH	migratory	4	16.204
ATTA35-3	12033	Attawapiskat	LKWH	migratory	4	15.34441
ATTA35-4	12026	Attawapiskat	LKWH	migratory	5	15.78175
HBL1-1	12013	Attawapiskat	CISC	migratory	6	14.90704
HBL1-2	12015	Attawapiskat	CISC	migratory	8	16.21227
HBL1-3	12012	Attawapiskat	CISC	migratory	8	17.08081
HBL1-4	12018	Attawapiskat	CISC	migratory	5	16.81752
HBL1-5	12017	Attawapiskat	CISC	migratory	7	16.48907
HBL1-6	12016	Attawapiskat	CISC	migratory	8	17.00261
HBL2-1	12063	Attawapiskat	LKWH	migratory	6	12.51047
HBL2-2	12068	Attawapiskat	LKWH	migratory	2	16.00828
HBL2-3	12067	Attawapiskat	LKWH	migratory	2	16.61412
HBL2-4	12066	Attawapiskat	LKWH	migratory	3	13.57356
HBL2-5	12065	Attawapiskat	LKWH	migratory	2	14.47311
HBL2-6	12064	Attawapiskat	LKWH	migratory	3	15.79502
HBL3-1	12105	Attawapiskat	CISC	migratory	5	16.70124

Ring Position	Fish #	River	Species	Migratory group	Age	δ ³⁴ S (‰)
HBL3-2	12073	Attawapiskat	LKWH	migratory	1	15.63543
HBL3-3	12071	Attawapiskat	LKWH	migratory	2	16.06431
HBL3-4	12069	Attawapiskat	LKWH	migratory	2	16.73939
HBL3-5	12107	Attawapiskat	CISC	migratory	4	16.67272
HBL3-6	12106	Attawapiskat	CISC	migratory	5	16.29274
HBL4-1	12027	Attawapiskat	LKWH	migratory	3	15.10826
HBL4-2	12040	Attawapiskat	LKWH	migratory	4	16.4004
HBL4-4	12034	Attawapiskat	LKWH	migratory	4	14.64803
HBL4-5	12031	Attawapiskat	LKWH	migratory	4	15.78347
HBL4-6	12029	Attawapiskat	LKWH	migratory	3	15.82726
HBL5-2	12062	Attawapiskat	LKWH	migratory	5	15.33807
HBL5-3	12060	Attawapiskat	LKWH	migratory	3	15.49234
HBL5-4	12058	Attawapiskat	LKWH	migratory	3	15.31967
HBL5-5	12057	Attawapiskat	LKWH	migratory	3	14.97891
HBL5-6	12045	Attawapiskat	LKWH	migratory	3	14.67331
HBL6-1	12135	Severn	CISC	migratory	4	16.90657
HBL6-2	12142	Severn	CISC	migratory	6	16.93616
HBL6-3	12141	Severn	CISC	migratory	3	16.94576
HBL6-4	12140	Severn	CISC	migratory	5	16.43552
HBL6-5	12139	Severn	CISC	migratory	6	16.71262
HBL6-6	12138	Severn	CISC	migratory	5	15.93747
HBL7-1	12148	Severn	CISC	migratory	4	15.0824
HBL7-2	12159	Severn	CISC	migratory	4	15.7618
HBL7-3	12157	Severn	CISC	migratory	4	15.54632
HBL7-4	12155	Severn	CISC	migratory	4	15.60986
HBL7-5	12153	Severn	CISC	migratory	4	15.52288
HBL7-6	12151	Severn	CISC	migratory	4	16.01055
HBL7-7	12149	Severn	CISC	migratory	4	15.41344
HBL8-1	12213	Winisk	CISC	migratory	5	17.20142
HBL8-2	12250	Winisk	LKWH	migratory	14	14.74021
HBL8-3	12244	Winisk	LKWH	migratory	13	13.46048
HBL8-4	12222	Winisk	CISC	migratory	7	16.6882
HBL8-5	12215	Winisk	CISC	migratory	10	16.67927
HBL8-6	12214	Winisk	CISC	migratory	8	17.46078
HBL9-1	12270	Winisk	NRPK	non-migratory	5	6.517043
HBL9-2	12263	Winisk	NRPK	non-migratory	6	6.097459
HBL9-3	12262	Winisk	NRPK	migratory	6	10.498
HBL9-4	12261	Winisk	NRPK	non-migratory	8	6.531745
HBL9-5	12259	Winisk	NRPK	non-migratory	5	6.685555
HBL9-6	12258	Winisk	NRPK	non-migratory	4	7.386747
HBL10-1	12264	Winisk	NRPK	non-migratory	9	8.740499

Ring Position	Fish #	River	Species	Migratory group	Age	δ ³⁴ S (‰)
HBL10-2	12182	Severn	NRPK	migratory	5	11.59068
HBL10-3	12180	Severn	NRPK	non-migratory	6	6.444952
HBL10-4	12179	Severn	NRPK	migratory	6	9.555874
HBL10-5	12268	Winisk	NRPK	migratory	6	7.281568
HBL10-6	12267	Winisk	NRPK	migratory	5	12.50092
HBL11-1	12228	Winisk	CISC	migratory	18	17.34254
HBL11-2	12237	Winisk	CISC	migratory	7	15.66696
HBL11-3	12235	Winisk	CISC	migratory	11	17.56873
HBL11-4	12234	Winisk	CISC	migratory	14	17.31313
HBL11-5	12233	Winisk	CISC	migratory	14	16.93731
HBL11-6	12229	Winisk	CISC	migratory	8	15.30117
HBL12-1	12255	Winisk	LKWH	migratory	35	16.5848
HBL12-2	12251	Winisk	LKWH	migratory	8	5.405315
HBL12-3	12240	Winisk	CISC	migratory	7	16.05871
HBL12-4	12239	Winisk	CISC	migratory	12	17.20164
HBL12-5	12238	Winisk	CISC	migratory	8	16.25245
HBL12-6	12252	Winisk	LKWH	migratory	14	13.64884
HBL13-1	12165	Severn	LKWH	migratory	12	14.07069
HBL13-2	12242	Winisk	LKWH	migratory	18	15.19801
HBL13-3	12176	Severn	LKWH	migratory	4	15.01843
HBL13-4	12174	Severn	LKWH	migratory	4	14.36813
HBL13-5	12173	Severn	LKWH	migratory	4	14.92795
HBL13-6	12169	Severn	LKWH	migratory	5	14.27539
HBL14-1	12282	Attawapiskat	NRPK	migratory	4	14.71387
HBL14-2	12290	Attawapiskat	NRPK	non-migratory	7	14.46652
HBL14-3	12280	Attawapiskat	NRPK	non-migratory	9	14.81026
HBL14-4	12293	Attawapiskat	NRPK	non-migratory	4	12.80871
HBL14-5	12279	Attawapiskat	NRPK	non-migratory	3	12.28569
HBL14-6	12283	Attawapiskat	NRPK	migratory	6	13.15014
HBL15-1	12288	Attawapiskat	NRPK	non-migratory	1	12.89053
HBL15-2	12296	Attawapiskat	NRPK	non-migratory	4	13.97538
HBL15-3	12286	Attawapiskat	NRPK	non-migratory	3	14.21772
HBL15-4	12285	Attawapiskat	NRPK	non-migratory	3	12.79324
HBL15-5	12281	Attawapiskat	NRPK	non-migratory	4	14.36578
HBL15-6	12284	Attawapiskat	NRPK	migratory	3	13.79358
HBL16-1	12295	Attawapiskat	NRPK	migratory	5	14.31055
HBL16-2	12321	Attawapiskat	NRPK	migratory	9	11.9392
HBL16-3	12322	Attawapiskat	NRPK	non-migratory	5	9.504905
HBL16-4	12320	Attawapiskat	NRPK	migratory	10	10.81829
HBL16-5	12327	Attawapiskat	NRPK	migratory	7	10.93177
HBL16-6	12289	Attawapiskat	NRPK	migratory	7	12.64309

Ring Position	Fish #	River	Species	Migratory group	Age	δ ³⁴ S (‰)
HBL17-1	12269	Winisk	NRPK	non-migratory	5	11.66402
HBL17-2	12184	Severn	NRPK	migratory	5	8.476055
HBL17-3	12189	Severn	NRPK	non-migratory	5	8.396176
HBL17-4	12190	Severn	NRPK	non-migratory	5	7.106386
HBL17-5	12257	Winisk	NRPK	non-migratory	5	6.492162
HBL17-6	12256	Winisk	NRPK	non-migratory	8	7.965795
HBL18-1	12181	Severn	NRPK	non-migratory	7	7.158126
HBL18-2	12185	Severn	NRPK	non-migratory	10	7.312913
HBL18-3	12191	Severn	NRPK	non-migratory	9	13.28366
HBL18-4	12188	Severn	NRPK	non-migratory	10	7.68404
HBL18-5	12183	Severn	NRPK	non-migratory	6	6.795483
HBL19-1	12294	Attawapiskat	NRPK	migratory	6	13.25178
HBL19-2	12277	Attawapiskat	NRPK	non-migratory	11	13.74326
HBL19-3	12276	Attawapiskat	NRPK	non-migratory	4	13.72
HBL19-4	12278	Attawapiskat	NRPK	migratory	10	14.11599
HBL20-1	12172	Severn	LKWH	migratory	4	14.4111
HBL20-2	12163	Severn	LKWH	migratory	18	14.18718
HBL20-3	12164	Severn	LKWH	migratory	15	14.94265
HBL20-4	12166	Severn	LKWH	migratory	7	15.83158
HBL20-5	12168	Severn	LKWH	migratory	4	14.64974
HBL20-6	12171	Severn	LKWH	migratory	4	15.29438
HBL21-1	12236	Winisk	CISC	migratory	8	16.7467
HBL21-2	12299	Attawapiskat	LKWH	migratory	5	15.59753
HBL21-3	12297	Attawapiskat	LKWH	migratory	6	14.87878
HBL21-4	12227	Winisk	CISC	migratory	9	17.11409
HBL21-5	12230	Winisk	CISC	migratory	30	15.18079
HBL21-6	12231	Winisk	CISC	migratory	12	17.36629
HBL21-7	12232	Winisk	CISC	migratory	10	16.4242
HBL22-1	12249	Winisk	LKWH	migratory	9	5.093171
HBL22-2	12247	Winisk	LKWH	migratory	26	14.35569
HBL22-3	12224	Winisk	CISC	migratory	10	17.29384
HBL22-4	12225	Winisk	CISC	migratory	10	17.46233
HBL22-5	12243	Winisk	LKWH	migratory	14	14.7789
HBL22-6	12246	Winisk	LKWH	migratory	11	13.9582
HBL22-7	12248	Winisk	LKWH	migratory	17	15.07497
HBL23-1	12223	Winisk	CISC	migratory	19	17.51726
HBL23-2	12245	Winisk	LKWH	migratory	14	15.42599
HBL23-3	12211	Winisk	CISC	migratory	11	16.5743
HBL23-4	12212	Winisk	CISC	migratory	9	16.94202
HBL23-5	12216	Winisk	CISC	migratory	17	17.91982
HBL23-6	12217	Winisk	CISC	migratory	10	16.74658

Ring Position	Fish #	River	Species	Migratory group	Age	δ ³⁴ S (‰)
HBL23-7	12218	Winisk	CISC	migratory	14	17.48949
HBL24-1	12161	Severn	CISC	migratory	5	15.81478
HBL24-2	12150	Severn	CISC	migratory	4	15.06618
HBL24-3	12152	Severn	CISC	migratory	5	13.77427
HBL24-4	12154	Severn	CISC	migratory	4	15.71117
HBL24-5	12156	Severn	CISC	migratory	4	15.54583
HBL24-6	12158	Severn	CISC	migratory	4	16.02771
HBL25-1	12330	Attawapiskat	CISC	migratory	5	17.14145
HBL25-2	12014	Attawapiskat	CISC	migratory	7	16.93781
HBL25-3	12311	Attawapiskat	CISC	migratory	8	14.80452
HBL25-4	12313	Attawapiskat	CISC	migratory	6	16.60232
HBL25-5	12328	Attawapiskat	CISC	migratory	7	16.12022
HBL25-6	12329	Attawapiskat	CISC	migratory	5	18.02705
HBL26-1	12147	Severn	CISC	migratory	8	15.66351
HBL26-2	12241	Winisk	LKWH	migratory	31	13.59069
HBL26-3	12254	Winisk	LKWH	migratory	12	13.12295
HBL26-4	12160	Severn	CISC	migratory	4	15.81234
HBL26-5	12103	Attawapiskat	CISC	migratory	4	16.01586
HBL26-6	12102	Attawapiskat	CISC	migratory	7	16.98975
HBL27-1	12072	Attawapiskat	LKWH	migratory	4	16.73565
HBL27-2	12175	Severn	LKWH	migratory	4	14.33194
HBL27-3	12170	Severn	LKWH	migratory	5	13.7167
HBL27-4	12167	Severn	LKWH	migratory	4	14.37604
HBL27-5	12323	Attawapiskat	LKWH	migratory	8	14.64884
HBL27-6	12326	Attawapiskat	LKWH	migratory	3	14.88392
HBL28-1	12186	Severn	NRPK	migratory	6	9.718377
HBL28-2	12467	Severn	NRPK	non-migratory	4	9.902979
HBL28-3	12466	Severn	NRPK	non-migratory	3	9.091543
HBL28-4	12463	Severn	NRPK	non-migratory	3	7.079571
HBL28-5	12462	Severn	NRPK	non-migratory	4	7.088723
HBL28-6	12461	Severn	NRPK	non-migratory	6	8.398622
HBL29-1	12468	Severn	NRPK	migratory	4	10.84491
HBL29-2	12473	Severn	NRPK	non-migratory	3	10.10059
HBL29-3	12472	Severn	NRPK	non-migratory	3	13.42719
HBL29-4	12471	Severn	NRPK	non-migratory	3	16.8316
HBL29-5	12470	Severn	NRPK	non-migratory	4	6.369087
HBL29-6	12469	Severn	NRPK	non-migratory	5	8.385972
HBL30-1	12474	Severn	NRPK	non-migratory	3	9.737155
HBL30-2	12480	Severn	NRPK	non-migratory	3	4.897494
HBL30-3	12479	Severn	NRPK	non-migratory	3	7.51161
HBL30-4	12478	Severn	NRPK	non-migratory	5	11.48986
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Ring Position	Fish #	River	Species	Migratory group	Age	δ ³⁴ S (‰)
HBL30-5	12477	Severn	NRPK	migratory	4	16.87576
HBL30-6	12476	Severn	NRPK	migratory	5	1.927739
HBL31-1	12366	Winisk	NRPK	migratory	6	11.62868
HBL31-2	12371	Winisk	NRPK	non-migratory	5	12.96444
HBL31-3	12370	Winisk	NRPK	migratory	4	12.21657
HBL31-4	12369	Winisk	NRPK	non-migratory	5	8.574698
HBL31-5	12368	Winisk	NRPK	migratory	5	12.93058
HBL31-6	12367	Winisk	NRPK	migratory	6	12.30682
HBL32-1	12372	Winisk	NRPK	non-migratory	7	8.793586
HBL32-2	12378	Winisk	NRPK	non-migratory	5	8.667809
HBL32-3	12377	Winisk	NRPK	migratory	5	7.55473
HBL32-4	12376	Winisk	NRPK	migratory	5	9.997713
HBL32-5	12375	Winisk	NRPK	non-migratory	4	13.43288
HBL32-6	12373	Winisk	NRPK	non-migratory	2	9.468416
HBL33-1	12379	Winisk	NRPK	non-migratory	5	8.388713
HBL33-2	12385	Winisk	NRPK	non-migratory	6	5.403908
HBL33-3	12384	Winisk	NRPK	non-migratory	9	8.931266
HBL33-4	12383	Winisk	NRPK	migratory	10	11.34002
HBL33-5	12382	Winisk	NRPK	non-migratory	8	8.061046
HBL33-6	12381	Winisk	NRPK	non-migratory	3	8.745671
HBL33-7	12380	Winisk	NRPK	non-migratory	5	7.178556
HBL34-1	12411	Severn	CISC	migratory	5	15.37615
HBL34-2	12417	Severn	CISC	migratory	7	15.43117
HBL34-3	12416	Severn	CISC	migratory	10	15.1133
HBL34-4	12415	Severn	CISC	migratory	7	14.64988
HBL34-5	12414	Severn	CISC	migratory	5	15.15198
HBL34-6	12413	Severn	CISC	migratory	6	16.36556
HBL34-7	12412	Severn	CISC	migratory	5	15.13209
HBL35-1	12418	Severn	CISC	migratory	7	15.60464
HBL35-2	12424	Severn	CISC	migratory	6	15.42572
HBL35-3	12423	Severn	CISC	migratory	6	16.09765
HBL35-4	12422	Severn	CISC	migratory	5	15.92111
HBL35-5	12421	Severn	CISC	migratory	6	15.42927
HBL35-6	12420	Severn	CISC	migratory	5	15.80013
HBL35-7	12419	Severn	CISC	migratory	5	14.81356
HBL36-1	12451	Severn	CISC	migratory	5	16.22576
HBL36-2	12458	Severn	LKWH	migratory	6	16.44874
HBL36-3	12457	Severn	LKWH	migratory	5	15.10789
HBL36-4	12456	Severn	LKWH	migratory	5	13.83935
HBL36-5	12455	Severn	CISC	migratory	5	17.52767
HBL36-6	12454	Severn	CISC	migratory	4	15.83137

Ring Position	Fish #	River	Species	Migratory group	Age	δ ³⁴ S (‰)
HBL36-7	12453	Severn	CISC	migratory	4	15.13159
HBL36-8	12452	Severn	CISC	migratory	4	15.84799
HBL37-1	12410	Winisk	LKWH	migratory	13	16.42995
HBL37-2	12436	Severn	LKWH	migratory	7	15.21643
HBL37-3	12438	Severn	LKWH	migratory	6	13.62527
HBL37-4	12435	Severn	LKWH	migratory	4	14.49934
HBL37-5	12434	Severn	LKWH	migratory	5	13.99408
HBL37-6	12433	Severn	LKWH	migratory	5	13.89079
HBL37-7	12432	Severn	LKWH	migratory	5	13.9146
HBL37-8	12431	Severn	LKWH	migratory	9	13.68008
HBL38-1	12401	Winisk	LKWH	migratory	8	13.05842
HBL38-2	12403	Winisk	LKWH	migratory	11	12.42293
HBL38-3	12405	Winisk	LKWH	migratory	10	13.80503
HBL38-4	12407	Winisk	LKWH	migratory	19	13.75029
HBL38-5	12408	Winisk	LKWH	migratory	18	13.49396
HBL38-6	12409	Winisk	LKWH	migratory	13	13.55024
HBL38-7	12402	Winisk	LKWH	migratory	9	13.16492
HBL39-1	12386	Winisk	CISC	migratory	8	15.39008
HBL39-2	12220	Winisk	CISC	migratory	10	17.36756
HBL39-3	12219	Winisk	CISC	migratory	11	17.33219
HBL39-4	12404	Winisk	LKWH	migratory	9	19.58911
HBL39-5	12390	Winisk	CISC	migratory	10	16.35497
HBL39-6	12389	Winisk	CISC	migratory	11	17.00582
HBL39-7	12388	Winisk	CISC	migratory	14	15.99486
HBL39-8	12387	Winisk	CISC	migratory	11	15.03924
HBL40-1	12314	Attawapiskat	NRPK	migratory	6	11.91195
HBL40-2	12361	Winisk	NRPK	migratory	6	10.48431
HBL40-3	12275	Attawapiskat	NRPK	non-migratory	11	14.12963
HBL40-4	12274	Attawapiskat	NRPK	non-migratory	7	14.61822
HBL40-5	12315	Attawapiskat	NRPK	non-migratory	6	11.66684
HBL40-6	12316	Attawapiskat	NRPK	migratory	8	10.5726
HBL41-1	12425	Severn	CISC	migratory	5	15.83722
HBL41-2	12406	Winisk	LKWH	migratory	8	13.63428
HBL41-3	12312	Attawapiskat	CISC	migratory	6	17.6408
HBL41-4	12430	Severn	CISC	migratory	3	15.53476
HBL41-5	12429	Severn	CISC	migratory	5	15.68495
HBL41-6	12428	Severn	CISC	migratory	6	14.18561
HBL41-7	12427	Severn	CISC	migratory	5	15.94375
HBL41-8	12426	Severn	CISC	migratory	5	15.79116
HBL42-1	12391	Winisk	LKWH	migratory	18	13.00498
HBL42-2	12440	Severn	LKWH	migratory	5	13.82603

Ring Position	Fish #	River	Species	Migratory group	Age	δ^{34} S (‰)
HBL42-3	12439	Severn	LKWH	migratory	11	13.62507
HBL42-4	12437	Severn	LKWH	migratory	11	12.95416
HBL42-5	12395	Winisk	LKWH	migratory	13	13.7332
HBL42-6	12394	Winisk	LKWH	migratory	14	13.79826
HBL42-7	12393	Winisk	LKWH	migratory	16	13.59651
HBL42-8	12392	Winisk	LKWH	migratory	14	14.49194
HBL43-1	12187	Severn	NRPK	non-migratory	8	13.19008
HBL43-2	12482	Severn	NRPK	non-migratory	2	4.596685
HBL43-3	12483	Severn	NRPK	non-migratory	2	5.985626
HBL43-4	12481	Severn	NRPK	migratory	2	8.503013
HBL43-5	12475	Severn	NRPK	non-migratory	4	12.645
HBL43-6	12178	Severn	NRPK	non-migratory	4	12.2438
HBL43-7	12177	Severn	NRPK	non-migratory	3	7.803164
HBL44-1	12265	Winisk	NRPK	non-migratory	6	10.52288
HBL44-2	12364	Winisk	NRPK	non-migratory	5	10.90747
HBL44-3	12365	Winisk	NRPK	non-migratory	5	9.109832
HBL44-5	12362	Winisk	NRPK	non-migratory	8	9.633381
HBL44-6	12266	Winisk	NRPK	non-migratory	5	9.65431
HBL45-1	12109	Attawapiskat	CISC	migratory	6	17.42499
HBL45-2	12342	Winisk	CISC	migratory	5	16.14508
HBL45-3	12341	Winisk	CISC	migratory	6	15.73917
HBL45-4	12400	Winisk	CISC	migratory	9	15.58672
HBL45-5	12398	Winisk	CISC	migratory	11	15.39038
HBL45-6	12399	Winisk	CISC	migratory	10	16.30675
HBL45-7	12226	Winisk	CISC	non-migratory	11	5.863351
HBL45-8	12104	Attawapiskat	CISC	migratory	4	16.15151
HBL45-9	12108	Attawapiskat	CISC	migratory	5	16.29836
HBL46-1	12344	Winisk	CISC	migratory	7	15.60641
HBL46-2	12359	Winisk	LKWH	migratory	11	12.74656
HBL46-3	12352	Winisk	LKWH	migratory	17	12.67923
HBL46-4	12354	Winisk	LKWH	migratory	18	13.23655
HBL46-5	12070	Attawapiskat	LKWH	migratory	4	15.0423
HBL46-6	12357	Winisk	LKWH	migratory	12	13.1187
HBL46-7	12221	Winisk	CISC	migratory	10	16.62296
HBL46-8	12345	Winisk	CISC	migratory	6	16.13003
HBL46-9	12346	Winisk	CISC	migratory	6	16.16304
HBL47-1	12441	Severn	LKWH	migratory	5	15.4869
HBL47-2	12298	Attawapiskat	LKWH	migratory	3	16.20759
HBL47-3	12349	Winisk	CISC	migratory	16	14.35628
HBL47-4	12347	Winisk	CISC	migratory	8	15.4295
HBL47-5	12397	Winisk	CISC	migratory	8	16.70155
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Ring Position	Fish #	River	Species	Migratory group	Age	δ ³⁴ S (‰)
HBL47-6	12442	Severn	LKWH	non-migratory	9	5.94778
HBL47-7	12460	Severn	LKWH	migratory	6	15.66421
HBL47-8	12459	Severn	LKWH	migratory	4	16.03276
HBL48-1	12162	Severn	LKWH	migratory	8	13.66467
HBL48-2	12363	Winisk	NRPK	non-migratory	8	8.402329
HBL48-3	12396	Winisk	CISC	migratory	12	15.03581
HBL48-4	12340	Winisk	CISC	migratory	10	15.66332
HBL49-1	12260	Winisk	NRPK	non-migratory	5	6.79865
HBL49-2	12317	Attawapiskat	NRPK	non-migratory	2	8.954667
HBL49-3	12464	Severn	NRPK	non-migratory	2	8.568048
HBL49-4	12287	Attawapiskat	NRPK	non-migratory	1	11.34794
HBL49-5	12465	Severn	NRPK	non-migratory	2	4.829976
HBL49-6	12318	Attawapiskat	NRPK	migratory	13	10.58753