Life history strategies of northern form Dolly Varden (*Salvelinus malma malma*) in the western Canadian Arctic

by

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Abstract

Northern form Dolly Varden char (*Salvelinus malma malma*) inhabit cold-water streams in the western Canadian Arctic. They are an important cultural and subsistence resource to local Aboriginal communities, yet little is known about their complex early life histories. Populations of Dolly Varden exhibit partial anadromy, where a portion of the population migrates to the ocean to feed in productive coastal waters (anadromous), while other individuals remain in freshwater year-round (residents). Residents are 'sneak' spawners and benefit from early maturation, while fish that migrate benefit from a larger size-at-maturation and thus a competitive advantage for spawning opportunities. According to classical life history theory, in populations that are partially anadromous, fast growing fish should migrate sooner and at smaller sizes than slow growing individuals, and the fastest growers in the population should remain as stream residents.

Dolly Varden were sampled from three river systems (Rat, Big Fish, and Babbage rivers) and otoliths were used to assess size-at-age and growth patterns through back-calculation, and age-at-migration through strontium analysis. Otoliths were used as proxy measures for fish growth and size-at-age due to their ability to record life history events throughout the lifetime of the fish. Initially, the fish length – otolith length relationship was observed in order to verify proportional growth between the fish and otolith. However, a decoupling was detected during first migration where fish size dramatically increased but otolith growth did not accrete material to the same extent. Modified back-calculation equations were developed to account for this decoupling based on discontinuous piecewise regressions. The new biological intercept

breakpoint method provided the most accurate representation of fish size-at-age throughout all life history stages when compared to known capture values in fish, although traditional back-calculation methods also reflected actual values for post-migratory fish. The decoupling indicates that factors other than somatic growth are important for otolith accretion. It is likely that physiological changes during smoltification that alter calcium uptake are affecting calcium deposition rates on otoliths during this short time period.

Back-calculated fish lengths for anadromous and resident fish were compared to determine how early growth influences migratory behaviour, and whether Dolly Varden exhibit life history strategies that follow predictions of classical life history theory. In accordance with predictions, results showed that early migrating fish were faster growers and migrated at smaller sizes than late migrating Dolly Varden. Size-at-migration varied between river systems, with fish from the Babbage River migrating earlier and at smaller sizes than those from the Rat and Big Fish rivers. Fish on the Big Fish River migrated at much larger sizes compared with the other systems, which was likely due to local adaptations to characteristics of this river, which are much different from most North Slope systems. Contrary to predictions of life history theory, no differences were observed in growth between resident and early migrating individuals, although a trend towards increased size-at-age was observed on the Rat and Big Fish rivers. These results indicate that factors other than growth are playing a role in life history 'decisions'. Future work on growth efficiencies and metabolic rates is needed to assess how they influence migratory and resident behaviours.

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Chapter 1: General Introduction

General Context

Life history traits are those that influence the variation observed in the life cycle of an organism, including size and age of important life stages such as birth, maturity and death, growth patterns, and reproductive investment. Together these traits comprise the life history and the strategy that an organism adopts in order to maximize its fitness or reproductive output (Gross 1987). Due to physiological, evolutionary and environmental constraints on traits, individuals must make trade-offs within and between traits in order to optimize fitness (Roff 1992, Roff 1996, Stearns 1992, 2000).

Within salmonids, variation in life history traits is common in many species and populations. In northern latitudes anadromous life histories have developed in order for fish to maximize growth and increase reproductive capacity (Hendry et al. 2004, Roff 1988, Stearns 1976), since in northern systems the productivity in ocean environments generally exceeds freshwater environments (Gross 1987). However, the trade-off for anadromy is increased mortality due to predation, stress and energy expenditure from migration and smoltification, and delayed maturation since anadromous individuals typically do not mature until after a few consecutive migrations. Jonsson and L'Abee-Lund (1993) examined brown trout (*Salmo trutta*) populations in 102 rivers and determined anadromous trout in more northern latitudes had decreased freshwater growth rates, smolted and matured at older ages, had decreased spawning frequencies but had increased lifespans. Regardless of latitudinal cline, resident salmonids (those that remain in freshwater and forgo ocean migration) benefit from earlier maturation than their anadromous counterparts and increased survival due to decreased predation risk in freshwater environments, yet experience decreased growth opportunities, and shorter lifespans (Hendry et al 2004; Jonsson and Jonsson 1993). Since anadromous fish utilize the increased productivity in northern marine environments, they tend to have increased growth rates and energy stores compared to their freshwater counterparts (Hendry et al. 2004). Through experimentation Nordeng (1983) showed that changing food availability in freshwater could change the

proportion of residents and anadromous Arctic char (*Salvelinus alpinus*) in a system, providing experimental evidence of the link between the degree of anadromy and marine versus freshwater productivity. Wysujack et al. (2009) also experimentally demonstrated that low food availability in the freshwater environment led to an increase in anadromous brown trout.

The benefits of an anadromous life history are generally more pronounced with females since female body size is directly correlated to reproductive output (Hendry et al. 2001, Loewen et al. 2010, Theriault et al. 2007); an increase in growth equates to a greater reproductive carrying capacity (more and/or larger eggs). In populations that exhibit both anadromous and resident life histories, males should dominate the resident life history, as size has a less direct impact on the ability to fertilize eggs (Hendry et al. 2004). Indirectly, small precocious males may compete with larger males in order to reproduce. Studies have indicated that a 'sneak' spawn strategy can be highly effective in fertilizing a large proportion of eggs (Hutchings and Myers 1988, Theriault et al. 2007), and that intermediate sized males have the least reproductive output since they are too large to adopt a "sneaking" strategy, yet too small to successfully compete against larger males (Fleming and Gross 1994).

General life history theory dictates that residents should have increased growth compared to pre-migratory anadromous individuals (Hendry et al. 2004, Stearns 1992, Thorpe et al. 1998). This is because an organism's goal is to reach maturity in order to reproduce and increase its individual fitness. Evidence suggests that maturation and smoltification cannot co-occur and that maturation is the preferred development pathway (Berglund et al. 1991, Thorpe 1994, Thorpe and Morgan 1980). Once a size threshold for maturation is reached, an individual should forgo growth and become reproductively mature (Metcalfe 1998, Thorpe et al. 1992). If an organism does not reach this maturation threshold in a given year, it can either wait until the following year or migrate to more productive habitats. Numerous studies have shown evidence for salmonids conforming to this general life history trajectory (Forseth et al. 1999, Morinville and Rasmussen 2003, Ricker 1938, Thorpe et al. 1998). However, other salmonid populations have been shown to adopt a reverse strategy where anadromous individuals experience higher growth rates compared to their resident counterparts (Loewen et al. 2010, Olsson et al. 2006, Rikardsen and Elliott 2000, Svenning et al. 1992). Whether or not a species' growth history conforms to general life history theory appears to be population-specific. Therefore, studying life history

theory for specific populations and systems is necessary to elucidate the mechanisms driving juvenile growth and maturation.

Dolly Varden

Dolly Varden (*Salvelinus malma*) are a species of char native to cold water habitats in northern latitudes of Asia and North America. Within North America, two subspecies have been identified, southern form (*S.m.lordi*) and northern form (*S.m.malma*). These subspecies are distinguished based on gill rakers, vertebrae (Behnke 1980), genetics (Phillips et al. 1999), and distribution (Kowalchuk et al. 2010; Figure 1.1). Southern form Dolly Varden occur in coastal watersheds from Washington State to the south side of the Alaskan Peninsula, while northern form Dolly Varden are found north of the Alaskan Peninsula and Aleutian Islands to the Mackenzie River, Northwest Territories.

Northern Dolly Varden, herein referred to as Dolly Varden, are associated with high gradient alpine streams, which are required for spawning, overwintering, and juvenile rearing (Reist and Sawatzky 2010). They have a limited distribution within the western Canadian Arctic due to the need for habitat consisting of perennial groundwater springs (Mochnacz et al. 2010). These springs provide areas of open water in systems that otherwise freeze solid in winter months. Genetically distinct northern Dolly Varden populations occur within at least seven different river systems in the Canadian Arctic including the Fish, Firth, Babbage, Big Fish, Rat, Peel, and Gayna rivers (Sandstrom 1995, Stewart et al. 2010, Harris et al. 2015; Figure 1.2).

Dolly Varden exhibit numerous life history strategies including anadromous, resident (from the same genetic populations as their anadromous counterparts), isolated stream residents, and lake residents (Armstrong and Morrow 1980). Residents do not migrate to the sea, but remain in freshwater year-round. They are typically males that adopt a 'sneak spawn' strategy in order to fertilize eggs of depositing females (McCart 1980). Residents are characterized by their small size, dark colour, visible parr marks, and early maturation. Spawning occurs from early September to late October before freeze-up, with fry emerging from the gravel in May and June (Stewart et al. 2010). Juveniles remain in freshwater from 1 to 5 years before beginning annual migrations to feed in productive marine waters (Craig 1977, Underwood et al. 1996, Yoshihara 1973 cited in McCart 1980, this study). Downstream migration to the sea begins during spring

freshet, which is typically in early to mid June, and can last until the beginning of August (McCart 1980). Upstream migration can begin as early as July and last until mid to October in some systems (McCart 1980; DeCicco 1989, Sandstrom et al. 2001). Mature spawning adults tend to return to natal streams first, while smolts are usually the last fish to return (Glova and McCart 1974, McCart 1980). Dolly Varden are iteroparous, with populations/individuals typically migrating and spawning either annually or biennially (Sandstrom and Harwood 2002, Sandstrom et al. 1997), however, some populations are known to skip both migration and spawning in some years (DeCicco 1989).

Thesis Overview

The underlying mechanisms of anadromy and residency are poorly understood in salmonids (Curry et al. 2010, Wysujack et al. 2009), and no studies to date have focused on early life history selection in Dolly Varden. Dolly Varden are an important component of North Slope ecosystems, and hold cultural and subsistence value to Aboriginal communities (Howland et al. 2012). Management of Dolly Varden typically focuses on the adult anadromous portion of specific populations, and studies on early ontogenetic stages are lacking. Since early life history trajectories appear to be species and population specific, and life history 'decisions' can shape populations, it is important to be able to have accurate information in regards to life history for a given species and population. Therefore, the overall objective of my thesis was to determine how early growth affects life history 'decisions' within Dolly Varden populations, specifically comparing growth and size-at-age of residents and early and late migrating fish to determine if Dolly Varden populations conform to general life history theory.

My thesis consists of two data chapters, which have been prepared as separate manuscripts. Chapter 2 assesses the Dolly Varden fish size-otolith size relationship and examines the decoupling that occurs during first migration. This chapter also describes a new back-calculation model that accounts for the decoupling that we witnessed within Dolly Varden populations. Chapter 3 compares factors that contribute to life history selection, specifically how growth influences migratory or resident behaviour. The final chapter concludes my thesis by reiterating the important details described within the two data chapters, highlighting the importance of and outlining the next steps for this research.

Study River Systems

This thesis covers research on Dolly Varden populations from three distinct river systems in the western Canadian Arctic: the Babbage, Big Fish, and Rat rivers (Figure 1.2), which all vary with respect to surrounding environment, water temperatures, water quality, availability of critical spawning and overwintering habitat, and distances between spawning/overwintering areas and the sea. Populations within these three systems show high fidelity to their natal spawning rivers and are known to be genetically distinct (Harris et al. 2015, Reist 1989).

The Babbage River makes up the eastern boundary of Ivvavik National Park. The river is located within the Inuvialuit Settlement Region (ISR) and flows north from the British Mountains to Phillips Bay along the Beaufort Sea Coast. Spawning and overwintering occur in Fish Hole Creek, a tributary to the Babbage River, in an area locally described as the "Fish Hole" (DFO 2003a). Mochnacz et al. (2010) provides a detailed description of habitat characterisitcs in Fish Hole Creek. A perennial freshwater thermal groundwater spring at the Fish Hole provides open water in the winter months and consistent water temperatures around 4°C. Spawning and overwintering habitat within this system is limited to 0.057km^2. The Babbage River contains both anadromous and resident individuals, along with an isolated resident population that occurs above falls on the mainstem of the river. There has been one recording of a female resident to date (Gallagher, unpublished data). During ice break up, fish undergoing migration swim downstream 145km from the overwintering site to the Beaufort Sea Coast.

The Big Fish River flows northeast from the Richardson Mountains into the Mackenzie Delta at Moose Channel. The river is within the ISR and crosses through both the Yukon and Northwest Territories. Spawning and overwintering occur at an area known as Fish Hole on Little Fish River, a tributary of the Big Fish River (DFO 2003b). Mochnacz et al. (2010) provides a detailed description of habitat characterisitcs on the Big Fish River. Spawning and overwintering habitat covers approximately 0.047km^2. A perennial groundwater spring, originating from sub-permafrost provides open water in the winter months. Unlike other river systems along the North Slope, the Big Fish River is characterized by a high mineral content, low oxygen levels, and warm water temperatures ranging from 8-16°C. The Big Fish River contains both anadromous and resident individuals, along with an isolated resident population

situated above falls on Little Fish River. No female residents have been observed in this system to date (Gallagher, unpublished data). During ice break up, fish undergoing migration swim downstream 131km from the overwintering site to the Beaufort Sea Coast.

The Rat River flows from the headwaters of the Richardson Mountains in the Northwest Territories and drains into Husky Channel of the Mackenzie River, north of the town of Fort McPherson. The river is located within the Gwich'in Settlement Area (GSA). Spawning and overwintering areas are found in Fish Creek, one of three main tributaries to the Rat River (Roux et al. 2012). Mochnacz et al. (2010) provides a detailed description of habitat characterisitcs on the Rat River. Perennial groundwater springs provide open water winter habitat with temperatures around 4-5°C. Known spawning and overwintering habitat covers an area of 0.089km^2. The Rat River contains both anadromous and resident individuals, with one record of a female resident to date (Gallagher, unpublished data). No isolated resident population has been recorded on this system. Dolly Varden in the Rat River undergo the longest seaward migration; starting during ice break up, fish swim downstream 316km from the overwintering site to the Beaufort Sea Coast.

Literature Cited

Armstrong, R.H., and Morrow, T.E. 1980. The Dolly Varden charr, *Salvelinus malma malma*. *In* Charrs, salmonid fishes of the genus *Salvelinus*. *Edited by* E.K. Balon. Hague: W. Junk, pp. 99-139.

Behnke, R.J. 1980. A systematic review of the genus *Salvelinus*. *In* Charrs, salmonid fishes of the genus *Salvelinus*. *Edited by* E.K. Balon. Hague: W. Junk, pp. 441-481.

Berglund, I., Hansen, L.P., Lundqvist, H., Jonsson, B., Eriksson, T., Thorpe, J.E., and Eriksson, L.O. 1991. Effects of elevated winter temperature on seawater adaptability, sexual rematuration, and downstream migratory behavior in mature male Atlantic salmon parr (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences **48**(6): 1041-1047.

COSEWIC. 2010. COSEWIC assessment and status report on the Dolly Varden *Salvelinus malma malma* (Western Arctic populations) in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. x + 65 pp.

Craig, P.C. 1977. Ecological studies of anadromous populations of arctic char in the canning river drainage and adjacent coastal waters of the Beaufort Sea, Alaska. *In* Fisheries investigations along the north slope and Beaufort sea coast in Alaska with emphasis on Arctic char. *Edited by* P.J. McCart. Canadian Arctic Gas Study Ltd., Calgary, Alberta, pp. 1-116.

Curry, R.A., Bernatchez, L., Whoriskey, F., and Audet, C. 2010. The origins and persistence of anadromy in brook charr. Reviews in Fish Biology and Fisheries **20**(4): 557-570.

DeCicco, A. 1989. Movements and spawning of adult Dolly Varden charr (*S. malma*) in Chukchi Sea drainages of northwestern Alaska: evidence for summer and fall spawning populations. Physical. Ecol. Japan. Spec. **1:** 229-238.

DFO. 2003a. Babbage River Dolly Varden. DFO Sci. Stock Status Report D5-62 (2002).

DFO. 2003b. Big Fish River Dolly Varden. DFO Sci. Stock Status Report D5-60 (2002).

Fleming, I.A., and Gross, M.R. 1994. Breeding competition in a pacific salmon (coho, *Oncorhynchus kisutch*): measures of natural and sexual selection. Evolution **48**(3): 637-657.

Forseth, T., Naesje, T.F., Jonsson, B., and Harsaker, K. 1999. Juvenile migration in brown trout: a consequence of energetic state. Journal of Animal Ecology **68**(4): 783-793.

Glova, G., and McCart, P.J. Life history of Arctic charr (*Salvelinus alpinus L.*) in the Firth River system, Yukon Territory. *In* Life histories of anadromous and freshwater fish in the western Arctic. *Edited by* P.J. McCart. Canadian Arctic Gas Study Ltd., Calgary, Alberta.

Gross, M.R. 1987. Evolution of diadromy in fishes. American Fisheries Society Symposium **1**:14-25.

Harris, L.N., Bajno, R., Gallagher, C.P., Koizumi, I., Johnson, L.K., Howland, K.L., Taylor, E.B., and Reist, J.D. 2015. Life-history characteristics and landscape attributes as drivers of genetic variation, gene flow, and fine-scale population structure in northern Dolly Varden (*Salvelinus malma malma*) in Canada. Canadian Journal of Fisheries and Aquatic Sciences **72**(10): 1477-1493.

Hendry, A.P., Bohlin, T., Jonsson, B., and Berg, O.K. 2004. To sea or not to sea? Anadromy versus non-anadromy in salmonids. *In* Evolution illuminated: salmon and their relatives. *Edited by* A.P. Hendry and S.C. Stearns. Oxford University Press, pp. 92-125.

Hendry, A.P., Day, T., and Cooper, A.B. 2001. Optimal size and number of propagules: Allowance for discrete stages and effects of maternal size on reproductive output and offspring fitness. American Naturalist **157**(4): 387-407.

Howland, K., Mochnacz, N., Gallagher, C., Tallman, R., Ghamry, H., Roux, M.J., Sandstrom, S., and Riest, J. 2012. Developing Strategies for Improved Assessment and Ecosystem-Based Management of Canadian Northern Dolly Varden. *In* Global Progress in Ecosystem-Based Fisheries Management. *Edited by* G.H. Kruse, H.I. Browman, K.L. Cochrane, D. Evans, G.S. Jamieson, P.A. Livingston, D. Woodby, and C.I. Zhang. Alaska Sea Grant, University of Alaska Fairbanks, pp. 169-188.

Hutchings, J.A., and Myers, R.A. 1988. Mating success of alternative maturation phenotypes in male Atlantic salmon, *Salmo salar*. Oecologia **75**(2): 169-174.

Jonsson, B., and Jonsson, N. 1993. Partial migration: niche shift versus sexual maturation in fishes. Reviews in Fish Biology and Fisheries **3**(4): 348-365.

Jonsson, B., and L'Abee-Lund, J.H. 1993. Latitudinal clines in life-history variables of anadromous brown trout in Europe. Journal of Fish Biology **43**: 1-16.

Kowalchuk, M.W., Sawatzky, C.D., and Reist, J.D. 2010. A Review of the Taxonomic Structure within Dolly Varden, *Salvelinus malma* (Walbaum 1792), of North America. Canadian Science Advisory Secretariat Research Document 013: i-vi, 1-16.

Loewen, T.N., Gillis, D., and Tallman, R.F. 2010. Maturation, growth and fecundity of Arctic charr, *Salvelinus alpinus* (L.), life-history variants co-existing in lake systems of Southern Baffin Island, Nunavut, Canada. Hydrobiologia **650**(1): 193-202.

McCart, P.J. 1980. A review of the systematics and ecology of Arctic char, *Salvelinus alpinus*, in the Western Arctic. Can. Tech. Rep. Fish. Aquat. Sci. 935: vii + 89p.

Metcalfe, N.B. 1998. The interaction between behavior and physiology in determining life history patterns in Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences **55**: 93-103.

Mochnacz, N.J., Schroeder, B.S., Sawatzky, C.D., and Reist, J.D. 2010. Assessment of northern Dolly Varden, *Salvelinus malma malma* (Walbaum, 1792), habitat in Canada. Canadian Manuscript Report of Fisheries and Aquatic Sciences 2926: i-vi, 1-48.

Morinville, G.R., and Rasmussen, J.B. 2003. Early juvenile bioenergetic differences between anadromous and resident brook trout (*Salvelinus fontinalis*). Canadian Journal of Fisheries and Aquatic Sciences **60**(4): 401-410.

Nordeng, H. 1983. Solution to the char problem based on Arctic char (*Salvelinus alpinus*) in Norway. Canadian Journal of Fisheries and Aquatic Sciences **40**(9): 1372-1387.

Olsson, I.C., Greenberg, L.A., Bergman, E., and Wysujack, K. 2006. Environmentally induced migration: the importance of food. Ecology Letters **9**(6): 645-651.

Phillips, R.B., Gudex, L.I., Westrich, K.M., and DeCicco, A.L. 1999. Combined phylogenetic analysis of ribosomal ITS1 sequences and new chromosome data supports three subgroups of Dolly Varden char (*Salvelinus malma*). Canadian Journal of Fisheries and Aquatic Sciences **56**(8): 1504-1511.

Reist, J.D. 1989. Genetic structuring of allopatric populations and sympatric life history types of charr, S*alvelinus alpinus/malma*, in the western Arctic, Canada. *In* Biology of Charrs and Masu Salmon, special volume 1. *Edited by* K. Hiroya, Y. Fumio and L.G.N. David. Physiology and Ecology Japan Editorial Office, Kyoto, Japan, pp.405-420.

Reist, J.D., and Sawatzky, C.D. 2010. Diversity and Distribution of Chars, Genus Salvelinus, in Northwestern North America in the Context of Northern Dolly Varden (*Salvelinus malma malma* (Walbaum 1792)). Canadian Science Advisory Secretariat Research Document 014: i-vi, 1-18.

Ricker, W.E. 1938. "Residual" and kokanee salmon in Cultus Lake. Journal of the Fisheries Research Board of Canada **4a**(3): 192-218.

Rikardsen, A.H., and Elliott, J.M. 2000. Variations in juvenile growth, energy allocation and life-history strategies of two populations of Arctic charr in North Norway. Journal of Fish Biology **56**(2): 328-346.

Roff, D.A. 1988. The evolution of migration and some life-history parameters in marine fishes. Environmental Biology of Fishes **22**(2): 133-146.

Roff, D.A. 1992. The evolution of life histories: theory and analysis. Chapman & Hall, New York.

Roff, D.A. 1996. The evolution of threshold traits in animals. Quarterly Review of Biology **71**(1): 3-35.

Roux, M.J., Howland, K., Gallagher, C.P., and Tallman, R.F. 2012. Synthesis of biological and harvest information used to assess populations of northern form Dolly Varden (*Salvelinus malma malma*) in Canada. Part I: Rat River. DFO Can. Sci. Advis. Sec. Res. Doc. 2011/132. viii + 77p.

Sandstrom, S.J. 1995. The effect of overwintering site temperature on energy allocation and life history characteristics of anadromous female Dolly Varden char (*Salvelinus malma*), from the Yukon and Northwest Territory North Slope, Canada. M.Sc. thesis, University of Manitoba, Winnipeg, MB.

Sandstrom, S.J., Chetkiewicz, C.B., and Harwood, L.A. 2001. Overwintering habitat of juvenile Dolly Varden (*Salvelinus malma*) (W.) in the Rat River, NT, as determined by radio telemetry. Canadian Science Advisory Secretariat 2001/092.

Sandstrom, S.J., and Harwood, L.A. 2002. Studies of anadromous Dolly Varden (*Salvelinus malma*) (W.), of the Big Fish River, NT, Canada 1972-1994. Canadian Manuscript Report of Fisheries and Aquatic Sciences 2603: i-vi, 1-31p.

Sandstrom, S.J., Lemieux, P.J., and Reist, J.D. 1997. Enumeration and biological data from the upstream migration of Dolly Varden charr (*Salvelinus malma*) (W.), from the Babbage River, Yukon north slope, 1990 to 1992. Canadian Data Report of Fisheries and Aquatic Sciences 1018: iv + 132p.

Stearns, S.C. 1976. Life history tactics: review of ideas. Quarterly Review of Biology **51**(1): 3-47.

Stearns, S.C. 1992. The evolution of life histories. Oxford University Press, New York.

Stearns, S.C. 2000. Life history evolution: successes, limitations, and prospects. Naturwissenschaften **87**(11): 476-486.

Stewart, D.B., Mochnacz, N.J., Reist, J.D., Carmichael, T.J., and Sawatzky, C.D. 2010. Fish life history and habitat use in the Northwest Territories: Dolly Varden (*Salvelinus malma*). Can. Manuscr. Rep. Fish. Aquat. Sci. 2915: vi + 63p.

Svenning, M.A., Smith-Nilsen, N., and M., J. 1992. Sea water migration of Arctic charr (*Salvelinus alpinus* L.): correlation between freshwater growth and seawater migration, based on back-calculation from otoliths. Nordic Journal of Freshwater Research **67**:18-26.

Theriault, V., Bernatchez, L., and Dodson, J.J. 2007. Mating system and individual reproductive success of sympatric anadromous and resident brook charr, *Salvelinus fontinalis*, under natural conditions. Behavioral Ecology and Sociobiology **62**(1): 51-65.

Thorpe, J.E. 1994. An alternative view of smolting in salmonids. Aquaculture **121**(1-3): 105-113.

Thorpe, J.E., Mangel, M., Metcalfe, N.B., and Huntingford, F.A. 1998. Modelling the proximate basis of salmonid life-history variation, with application to Atlantic salmon, *Salmo salar* L. Evolutionary Ecology **12**(5): 581-599.

Thorpe, J.E., Metcalfe, N.B., and Huntingford, F.A. 1992. Behavioural influences on life-history variation in juvenile Atlantic salmon, *Salmo salar*. Environmental biology of fishes **33**(4): 331-340.

Thorpe, J.E., and Morgan, R.I.G. 1980. Growth-rate and smolting-rate of progeny of male Atlantic salmon parr, *Salmo salar* L. Journal of Fish Biology **17**(4): 451-459.

Underwood, T.J., Millard, M.J., and Thorpe, L.A. 1996. Relative abundance, length frequency, age, and maturity of Dolly Varden in nearshore waters of the Arctic National Wildlife Refuge, Alaska. Transactions of the American Fisheries Society **125**(5): 719-728.

Wysujack, K., Greenberg, L.A., Bergman, E., and Olsson, I.C. 2009. The role of the environment in partial migration: food availability affects the adoption of a migratory tactic in brown trout *Salmo trutta*. Ecology of Freshwater Fish **18**(1): 52-59.

Yoshihara, H.T. 1973. Annual Progress Report for Monitoring and evaluation of Arctic waters with emphasis on the North Slope drainages. Alaska Dep. Fish Game, G-III-A, v.13, pp. 1-83.

Figures

Figure 1.1 – Map showing the distribution of Dolly Varden (*Salvelinus malma*) in North America. Green shading represents southern form Dolly Varden (*S.m.lordi*) while black and red represents northern form Dolly Varden (*S.m.malma*). The red is a proposed intermediate subspecies that is currently identified as northern form (Source: COSEWIC 2010).
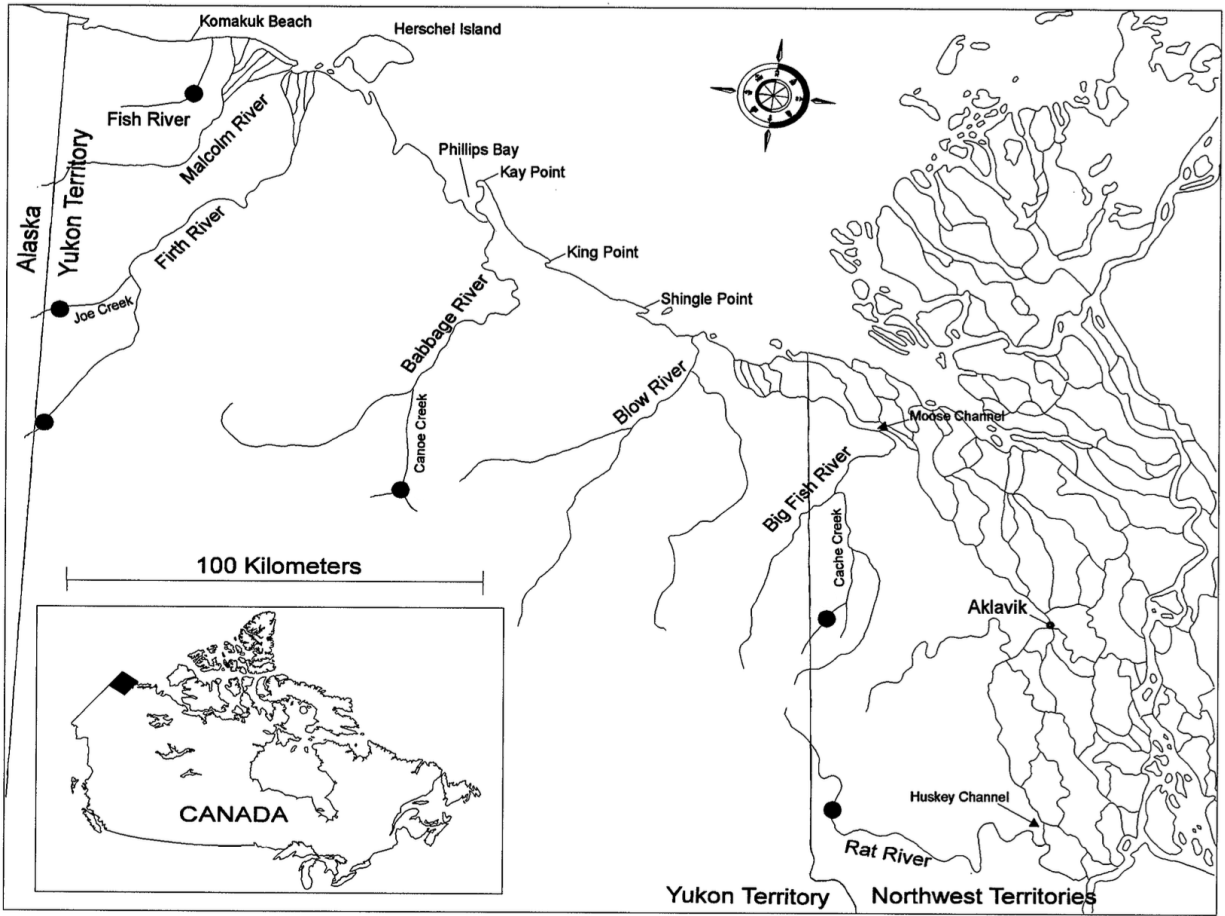
Figure 1.2 – Map of known Dolly Varden habitat in Canada. Dots represent known spawning/overwintering sites. Note that the Dolly Varden are found further south within the Mackenzie basin (Source: Sandstrom et al. 1995).

Chapter 2: Decoupling of otolith and somatic growth during migration in northern form Dolly Varden

Introduction

Back-calculating fish length using otoliths, scales, or other bony structures, is a common tool used by fisheries scientists. Growth increments in the form of daily, seasonal, or yearly rings on otoliths or other calcified structures often reflect the growth of the fish and can be used to reconstruct size-at-age and growth patterns within individuals (Francis 1990). First described by Lea (1910), back-calculation techniques have developed over the years to encompass many different growth patterns observed in fishes. Reviews of the different back-calculation models that have been developed have been covered extensively by Francis (1990) and Vigliola and Meekan (2009).

In order to apply back-calculation techniques to obtain previous size-at-age data from existing calcified structures, two main assumptions must be met: 1) the rate of accretion of measureable increments does not vary, and 2) that the fish length-otolith length relationship (FL – OL relationship) is linear and does not vary with the growth of the fish (Campana and Neilson 1985). This first assumption is usually verified experimentally (Geffen 1992). The second assumption is usually verified by constructing simple correlation plots between measures of fish size and otolith size. However, numerous studies have shown that this second assumption is often not met (Fey 2006, Mosegaard et al. 1988, Secor and Dean 1992, Wright et al. 1990). A 'growth effect' is often observed where slow growing fish have larger otoliths than faster growing fish of the same size, indicating individual variation in the FL – OL relationship within a species or population. Not mutually exclusive, an 'age effect' has also been described where otoliths will continue to accrue material despite somatic growth slowing down or stopping as fish age (Morita and Matsuishi 2001, Secor and Dean 1992). In order to account for the growth effect, Campana (1990) developed the biological intercept back-calculation method. This equation is a variation of the regression based Fraser-Lee method (Lee 1920), but it constrains the equation through a biologically known rather than a statistically determined intercept. Morita

and Matsuishi (2001) developed a proportionally based model that accounts for age effects in the FL – OL relationship. However, proportionally based models do not account for growth effects, and can thus give highly biased size-at-age estimates (Vigliola and Meekan 2009).

While the biological intercept model, age effect model, and numerous others incorporate measures that account for growth and/or age effects (Campana 1990, Finstad 2003, Morita and Matsuishi 2001, Sirois et al. 1998, Vigliola et al. 2000), these models will only provide accurate and precise estimates of size-at-age provided there are no other factors, other than the age or growth effects they account for, that are contributing to the decoupling of otolith and somatic growth. For example, independent decoupling is often observed in daily microstructure of larval fish, where changes in the FL – OL relationship are associated with the different ontogenetic stages experienced by larval fishes (Campana 1984, Gunther et al. 2012, Hare and Cowen 1995, Hobbs et al. 2007). Traditional back-calculation methods can be used in these situations when there is sufficient data to biologically estimate the transition zones, allowing for stage-specific back-calculation models. Hobbs et al. (2007) found that using stage-specific biological intercept models estimated size-at-age better then both the modified fry model (Vigliola et al. 2000) and the time varying growth model (Sirois et al. 1998). Laidig et al. (1991) used a segmented approach to back-calculate growth through four different ontogenetic stages in larval and juvenile shortbelly rockfish (*Sebastes jordani*) by modifying the body-size proportional method described in Francis (1990).

Decoupling episodes have also been observed in experiments that look at the effects temperature has on otolith accretion rates and the relationship to somatic growth. Mosegaard et al. (1988) found that an increase in temperature corresponded in an increase in otolith growth of Arctic char (*Salvelinus alpinus*) fry, whereas somatic growth decreased after reaching an optimal temperature. Barber and Jenkins (2001) found a decoupling in the FL – OL relationship in juvenile King George whiting (*Sillaginodes punctatus*) with temperature as the main driver in short-term otolith accretion and food availability as the primary driver in somatic growth. While these are examples of decoupling that is independent of growth and age effects, their focus is on the microstructure data in otoliths and daily growth patterns in juvenile and larval fishes.

Although migration has a large influence on somatic growth in fishes, to date, there are no studies that I could find that have demonstrated a possible decoupling associated with large changes in fish size during migration. Often, observed increases in otolith increment width

during migration are indicators of continued proportionality during migration periods. Yet, short-term feeding experiments frequently show a decoupling or lag time between otolith and somatic growth (Molony and Choat 1990, Wright et al. 1990) and evidence suggests that otolith accretion is not necessarily always regulated by somatic growth (Mosegaard et al. 1988, Wright 1991).

Northern form Dolly Varden char (*Salvelinus malma malma*) are a salmonid species that inhabit high gradient streams in the western Arctic, along the Alaskan coastline north of the Aleutian Islands, east to the Mackenzie Delta, NWT Canada (Reist and Sawatzky 2010). Anadromous populations of Dolly Varden migrate to coastal waters after river ice-melt where they feed in nearshore marine habitats before returning to natal streams to overwinter (Brown et al. 2014). Being iteroparaus, migrating individuals consist of juvenile smolts, maturing or ripening adults, and resting adults. While at sea, first time migrants exhibit rapid increases in growth during the short summer feeding season (Craig 1977). As an important cultural and subsistence resource to local communities, it is important to be able to provide accurate scientific information on Dolly Varden in order to properly manage the species. However, due to sampling constraints in northern latitudes, directly assessing populations is not often feasible. Otolith analysis provides an important resource in order to reconstruct environmental life histories of this species.

This study was part of a larger research program that uses otoliths to reconstruct early life histories within Dolly Varden and examine growth and migratory behaviour of northern Dolly Varden within western Canadian streams. In examining the FL – OL relationship I observed a decoupling that was occurring during the first year of migration, where fish growth was occurring at a much faster rate than otolith growth. The objectives of this chapter were: 1) to develop a modified back-calculation model to account for this discontinuity in the FL – OL relationship, and 2) to highlight the importance of verifying assumptions on the FL – OL relationship prior to back-calculating size-at-age in species with complex ontogenetic changes.

Materials and methods

Study area and field collection methods

Dolly Varden were sampled from three different river systems in the western Arctic; the Rat, Big Fish, and Babbage rivers (Figure 1.2). Field collection occurred between 1986 and 2016 (Table **2**.**1**) in conjunction with ongoing harvest monitoring that occurs along the Beaufort Sea coast at Shingle Point, sites along the Mackenzie Delta and the Rat River, and at the mouth of and spawning/overwintering site on the Big Fish River (Table **2.2**). Sampling at Shingle Point occurred from mid-July to early-August while Dolly Varden were moving along the coast prior to returning to freshwater after summer feeding. Samples from the Rat River stock were collected from late-July to early-September during which time the fish were returning to their spawning and overwintering sites. Sampling at the mouth of the Big Fish River occurred early to mid-August, when the fish were returning to spawning grounds, or at the overwintering site in late-October to early November after the fish had returned. Fish were captured along the coast and at the mouth of the rivers using either 90, 102, or 114 mm stretch-mesh gill nets with variable lengths and set times. Fish were captured at the overwintering site on the Big Fish River with a 16m-long modified seine net (see Sandstrom et al. 2009). Sample collection consisted of measuring and recording fork length (mm), weight (g), sex, and maturity stage. Sagittal otoliths were removed and placed in coin envelopes and a piece of fin tissue was stored in ethanol for DNA analysis (see Gallagher et al. 2013, Harris et al. 2015). All samples were collected with permission from Inuvialuit and Gwich'in harvesters.

Information pertaining to growth of tagged fish was obtained from 2007-2014 in conjunction with mark-recapture programs that occurred at the spawning and overwintering sites on the Rat, Big Fish, and Babbage Rivers (Table **2.2**). Fish were captured via a 16m-long modified seine net and tagged with numbered t-bar tags, which were inserted below the posterior end of the dorsal fin (Sandstrom et al. 2009). All captured fish, including recaptures, were assessed for fork-length (mm), sex (if determinable), and life history stage prior to release. Tagged fish used in growth analyses for this study were those recaptured during harvest monitoring programs and therefore had corresponding body lengths and otoliths.

Juvenile samples were collected during the mark-recapture program and stored frozen until lab analysis. Additional juvenile Dolly Varden samples were collected in late-August 2014 and early to mid-August 2016 from tributaries of the Rat River using a backpack electrofisher and stored frozen until lab analysis. Lab analysis included recording fork-length (mm), weight (g), sex, and removal of sagittal otoliths.

Otolith analysis

Wide opaque summer and narrow translucent winter growth zones, called annuli, represent yearly growth structures in the otolith. Age was determined by counting the translucent bands on whole otoliths following methods in described in Gallagher et al. (2016) and Chilton and Beamish (1982). Two experienced readers read Dolly Varden samples blind and followed Quality Assurance and Quality Control (QAQC) measures with a precision target of 5% agreement between readers.

Otolith lab preparation followed methods outlined in Gallagher et al. (2016). Otoliths were embedded in ColdCure^{TM} epoxy resin and left to harden for approximately 1 week. Embedded otoliths were sectioned across the nucleus perpendicular to the sulcus with a Buehler Isomet slow speed saw (Buehler Ltd., Lake Bluff, Illinois) with diamond wafering blades. Sectioned otoliths were then polished with 0.3, 9, and 30 μm lapping film and imaged using a Nikon DXM1200 digital camera (Nikon Instruments Inc., Melville, New York) attached to a dissecting microscope.

Analysis of otolith strontium (Sr) levels in otoliths can be used to determine migration history in anadromous species since Sr concentrations in otoliths reflect the salinity encountered by the fish throughout its life history (Zimmerman 2005). Dolly Varden otolith Sr concentrations were analyzed using laser ablation inductively coupled plasma mass spectrometry (LA-ICP-MS) conducted at the University of Manitoba's Geological Sciences Department (Winnipeg, Manitoba) following preparation methods outlined in Howland et al. (2001), Loewen et al. (2015), and Swanson et al. (2010). Otolith sections were embedded in 1-inch Lucite discs using ColdCure^{TM} epoxy, which were then polished with 0.3, 9, and 30 μm lapping film. A final polish was done on a Buehler polishing wheel (Buehler Ltd., Lake Bluff, Illinois) with 0.05μm diamond grit paste and the otolith discs were then ultrasonically cleaned in distilled water prior to analysis. Transects were ablated from the otolith core to the outer edge of the dorsal lobe, following marked transects overlaid on digital images, using a Thermo Finnigan Element 2 High Resolution-Inductively Coupled Plasma-Mass Spectrometer (HR-ICP-MS) (Thermo Fisher Scientific Inc., Mississauga, Ontario) in combination with a Merchantek LUV 213 laser ablation system (New Wave Research/Merchantek, Fremont, California). Vaterite, a polymorph of

calcium carbonate (Gauldie 1993), has a negative influence on Sr deposition (Gauldie 1996), and thus otoliths with vateritic inclusions were removed from analysis. Following LA-ICP-MS analyses, otoliths were imaged and Sr profiles were overlaid on the digital otolith images in order to align Sr concentrations with otolith annuli (Morris et al. 2005).

In order to determine age at first migration for each individual, threshold Sr concentrations were established by plotting the overall Sr concentration maximum against the overall Sr range (maximum – minimum Sr value) for otoliths of all anadromous and known freshwater individuals following methods derived from Brown et al. (2007), Howland et al. (2009), and Howland et al. (2001). Thresholds for freshwater Sr concentrations were obtained from mature freshwater residents, which were from the same population as anadromous individuals. Due to the high amount of naturally occurring winter NaCl in the Big Fish River (Clark et al. 2001), freshwater Sr values within all otoliths obtained from this system fluctuate on a yearly cycle, with high Sr levels in the winter that are comparable to Sr levels at ocean migration, and low Sr levels in the summer that reflect freshwater levels in other river systems. In order to account for this fluctuation within the maximum-range plots for the Big Fish River, the overall maximum mid-annular increment value that corresponds to summer Sr levels was taken instead of the overall maximum. Plots were examined to verify distinct groupings representing freshwater and anadromous life histories and to determine threshold values. A Mann-Whitney rank sum test was used to compare the mean ranges and maximums of the distinct groupings for each river system. Age at first migration was determined by examining the Sr profile overlaid on the otolith image, and at what annuli an individual transitioned to the anadromous Sr threshold group for each river system.

FL – OL Regressions

The imaging software ImageJ 1.44 (National Institutes of Health, Bethesda, MD, USA) was used to measure the otolith radius (mm) as well as the distance from the nucleus to each individual annulus. Measurements were taken at a 50-degree angle to the sulcus, from the center of the nucleus to the outer edge of the ventral lobe. Linear regression analysis was conducted on the FL – OL relationship in order to determine if constant proportional growth was observed throughout the life history of Dolly Varden. Fish size was recorded as fork length (mm) and

otolith size was recorded as otolith radius (mm). Due to the small sample size of freshwater juveniles within each system (Table 2.1), male and female juvenile samples were combined for all analyses.

Due to the observed jump in the FL – OL trajectory when plotting juveniles on the FL – OL regression, FL was fit to OL using a discontinuous piecewise regression model with an unknown change point. The change point, or jump, from juvenile to anadromous trajectory, was determined using an iterative approach (see Crawley 2013). All possible change points were fit to the formula L~O*I(O<jump)+O*I(O>=jump) where L is fish length (mm), O is otolith radius length (mm), and I(O<jump) and I(O>=jump) were dummy variables. Breakpoints were determined as being the fit with the lowest residual mean standard error (MSE). The middle value was taken as the breakpoint if there was more than one low MSE value. 95% confidence intervals for each parameter were determined with bootstrapping using 10000 bootstrap replicates. Using the determined breakpoints, discontinuous piecewise regressions were fit to the data for males and females (with juveniles combined) for each river system (Eqn. 2.1).

$$f(O) = \begin{array}{l} a1 + b1 * O \text{ if } O < \text{estimated change point} \\ a2 + b2 * O \text{ if } O \geq \text{estimated change point} \end{array} \qquad [2.1]$$

Due to the small sample size for juveniles (n=11) from the Big Fish River, we were unable to generate a biologically realistic regression fit for this river system and instead alternative models were examined based on proxy data from the Rat and Babbage river systems to determine what was most representative of Big Fish River males and females. The alternative models included [1] all the data combined from the three rivers, [2] all the male data combined from the three rivers, [3] all the female data combined from the three rivers, [4] post-migratory males from the Big Fish River with juveniles from all systems, and [5] post-migratory females from the Big Fish River with juveniles from all systems. The latter two models were also used to fit the Rat and Babbage rivers for comparison. The best model for the Big Fish River was determined based on r^2 values, confidence intervals around the slopes and intercepts, how well the data matched individual post-migratory regressions for the Big Fish River, and biologically realistic slopes and intercepts (intercepts that would be expected for size-at-hatch).

Back-calculations

Using the fit from the piecewise regressions, two new back-calculation models were derived from existing models; the biological intercept model (Campana 1990; Eqn. 2.2) and the modified fry model (Vigliola et al. 2000; Eqn. 2.3):

$$L_i = L_c + \frac{(O_i - O_c)(L_c - L_h)}{(O_c - O_h)} \qquad [2.2]$$

$$L_i = a + \exp\left(\ln(L_h - a) + \frac{[\ln(L_c - a) - \ln(L_h - a)][\ln(O_i) - \ln(O_h)]}{[\ln(O_c) - \ln(O_h)]}\right) \qquad [2.3]$$

where L_i is the back-calculated length at a given age, L_c is the fish length at capture, L_h is the fish length at hatch, O_i is the otolith size at a given age, O_c is the otolith size at capture, and O_h is the otolith size at hatch. Otolith size and fish size at hatch was taken from the literature to be 0.06 and 16.5 mm respectively (Armstrong and Morrow 1980, Blackett 1968, Radtke et al. 1996).

I chose the biological intercept (BI) model as a base model because it is one of the most commonly used models for fisheries back-calculations, and is based on a simple linear FL –OL relationship, which we see at each ontogenetic stage. The modified fry (MF) model is an extension of the BI, except it is based on an allometric FL – OL relationship and will give values similar to the BI when there is a linear FL – OL relationship (Vigliola et al. 2000). While it is possible for individuals to have an allometric FL – OL relationship yet generate a linear population FL – OL relationship (Wilson et al. 2009), we did not expect this to be the case but nevertheless included a modified fry model in order to test the applicability of our piecewise regression to two commonly used back-calculation techniques.

The new models based off of the BI model (Eqn. 2.4) and the MF model (Eqn. 2.5) incorporate an individually derived breakpoint based on population parameters from the piecewise regressions:

$$L_i = \begin{cases} L_c + \dfrac{(L_c - L_{j1})(O_i - O_c)}{(O_c - O_j)} & \text{if } j \geq O'j \\[3mm] L_{j2} + \dfrac{(L_{j2} - L_h)(O_i - O_j)}{(O_j - O_h)} & \text{if } j < O'j \end{cases} \qquad [2.4]$$

$$L_i = \begin{cases} a + \exp\left(ln(L_{j1} - a) + \dfrac{[ln(L_c - a) - ln(L_{j1} - a)][ln(O_i) - ln(O_j)]}{[ln(O_c) - ln(O_j)]} \right) & \text{if } j \geq O'j \\[3mm] d + \exp\left(ln(L_h - d) + \dfrac{[ln(L_{j2} - d) - \ln(L_h - d)][ln(O_i - \ln(O_h))]}{[ln(O_j) - ln(O_h)]} \right) & \text{if } j < O'j \end{cases} \qquad [2.5]$$

where L_{j1} is length at jump for post-migration, L_{j2} is length at jump for pre-migration, O_j is otolith size at the jump point, and O'j is the individual otolith size at the jump.

Back-calculated lengths using the BI method, the new biological intercept breakpoint (BI-BP) method, and the new modified fry breakpoint (MF-BP) method were compared to known juvenile size-at-age data using either analysis of variance (ANOVA) with a post hoc Tukey HSD test or a Kruskal-Wallis analysis of variance on ranks with post hoc Dunn's test. Because the time of capture takes place after annuli are laid down, I expected values for capture to be higher than back-calculated values. While fish captured at age 1 were included in the analysis, it is unknown whether these fish were on a trajectory to become either freshwater juveniles or stream residents.

Linear regression models were constructed to examine the relationship between known growth data obtained from mark-recapture studies and those back-calculated using the BI, BI-BP, and MF-BP methods. Back-calculated values were calculated to reflect actual time of tagging based on a linear relationship between capture and recapture. Regression analysis was used to compare results to those of a 1:1 relationship, with an intercept of 0 and a slope of 1.

Otolith annual increment widths

Based on the observed decoupling in the FL – OL relationship I was interested in determining whether there was an increase in otolith annual increment widths during first migration for individual Dolly Varden that corresponded with the larger increase in somatic growth. Individuals were separated by year of migration and then the annual increment widths were compared between pre-migrating, post-migrating, and first migrating individuals. Either a t-test or a Mann-Whitney rank sum test was used to compare increment widths. For the Babbage River females, an ANOVA with a post hoc Tukey HSD test was used for comparison since there were three migratory years with sufficient sample sizes for comparison.

General Analysis

All statistical analyses were completed in R Studio (RStudio Team, 2016). Normality and homogeneity of variance were determined with Shapiro-Wilk tests and Levene's tests respectively. Data was considered significant at alpha ≤ 0.05 in all cases. Data presentation was completed using both Sigmaplot 12.5 (Systat Software Inc.) and R Studio.

Results

Age at Migration

Sr maximum-range plots for each of the three river systems (Rat, Big Fish, and Babbage rivers; Figure 2.1) showed two distinct Sr groupings ($p<0.001$ for all comparisons), which I interpreted as freshwater (group 1) and anadromous (group 2). Although the Big Fish River showed less separation between the two groupings compared with the Rat and Babbage rivers, likely due to the high Sr levels during winter, two distinct groups were still observable. Based on the otoliths used in this study, anadromous Sr thresholds for the Rat, Babbage, and Big Fish river maxima values were $\geq$ 1986mg/kg, 2235mg/kg, and 1969mg/kg, and for the range were $\geq$ 1778mg/kg, 1994mg/kg, and 1092mg/kg, respectively. Based on the maximum-range plot thresholds, Sr profiles overlaid on otolith images, and otolith age estimates, the majority of

sampled individuals were undergoing their first migration at age 2 and 3 on the Babbage River, and age 3 and 4 on the Rat and Big Fish rivers (Table **2.3**).

Fish size-otolith size relationship: Linear regression

The fish size-otolith size relationship showed similar patterns for all three systems (Figure 2.2). For post-migratory individuals there were linear relationships observed for males and females within each river system (r^2=0.55-0.68, p<0.001 for all relationships). When plotting juveniles, a linear relationship was observed for the Rat (r^2=0.50, p<0.001) and Babbage (r^2=0.69, p<0.001) rivers. While the Big Fish River juvenile FL – OL linear relationship was marginally significant (r^2=0.30, p=0.043), limited sample size (n=11) and low power (0.592) likely contributed to this weaker result.

Including juveniles within the post-migratory FL – OL regressions improved r^2 values in all cases (r^2=0.71-0.89, p<0.001 for all relationships; **Error! Reference source not found.**Figure 2.2), indicating a better fit. However, observation of the FL – OL regression suggests that juveniles and post-migratory individuals follow separate growth trajectories, with juveniles jumping to the post-migratory trajectory during first migration. Prior to migration the average fish length of older aged juveniles was 145 ± 8mm (Rat: 3+yrs, n=14), 199mm (Big Fish: 3+yrs, n=2), and 1534 ± 12mm (Babbage: 2+yrs, n=23), whereas average length of first-year male and female migratory Dolly Varden was 349 ± 13mm (Rat males: n=13), 344 ± 66mm (Rat females: n=3), 342 ± 11mm (Big Fish males: n=13), 335 ± 10mm (Big Fish females: n=9), 336mm (Babbage males: n=2), and 325mm (Babbage females n=1). This is an almost doubling in size during first migration for individuals from these three rivers (Figure 2.3).

Fish size-otolith size relationship: Piecewise regression

Using river and sex specific data, I obtained statistically determined breakpoints for the Rat and Babbage rivers that differed between male (0.424mm, 0.421mm) and female populations (0.426mm, 0.451mm). Piecewise regressions between fish length and otolith radius using these breakpoints were significant (p<0.001 in all cases; Table **2.4**; Figure **2.4**), with r^2 values

(r^2=0.93-0.94) that were much higher than the results from the linear regressions. However, when juveniles from all rivers were combined for river- and sex-specific models, I observed a large increase in the slope and an unrealistically low y-intercept for the pre-migration portion of the regression, which based on 95% confidence intervals either did not overlap or only marginally overlapped with the above-described models that incorporated river specific juvenile data (Table **2**.4; **Error! Reference source not found.**Figure **2**.4). Similarly large slopes and low y-intercepts for the pre-migration portion of the piecewise regressions in the sex-specific Big Fish models that had juveniles from all systems combined led to their rejection. The model with all data combined also had an unrealistic pre-migration y-intercept and larger slope than the sex specific models using data combined from all river systems and was subsequently rejected. Thus, based on the higher r^2 values (r^2=0.89 and 0.90) the sex specific models incorporating data from all river systems were chosen to represent the Big Fish River for back-calculation. The sex specific models gave otolith breakpoints of 0.421mm (males) and 0.430mm (females), which when used in the piecewise regressions, produced significant relationships ($p<0.001$).

Back-calculations

When comparing back-calculated data for pre-migratory fish from the BI method with known capture data, I found that back-calculating size-at-age using the BI method overestimated pre-migratory juvenile size-at-age by a large margin in all three river systems (Kruskal-Wallis $p<0.001$) (Table **2**.5; Figure **2**.5). Back-calculated sizes-at-age 1 (141-166mm) were similar to capture data for older aged juveniles, while estimated lengths of aged 3 (281-302mm) and 4 (308-331mm) year old juveniles were closer in size to post-migratory individual sizes at capture.

For the BI-BP model, estimated pre-migratory size-at-age was similar to capture data for all ages from all river systems (Table **2**.5; Figure **2**.5). The BI-BP model generally gave average estimated sizes slightly below capture values, which was expected. The only time average estimates were above capture values was for ages 3 (BI-BP: 145mm, capture: 144mm) and 4 (BI-BP: 167mm, capture: 160mm) males and females from the Rat River; however these differences were not significant. Significant differences between capture and BI-BP values were observed in Babbage 1yr males (Kruskal-Wallis: $p<0.0001$; BI-BP: 86mm, capture: 116mm), and Big Fish

2yr males (Kruskal-Wallis: p<0.0001; BI-BP: 140mm, capture: 182mm) and females (Kruskal-Wallis: p<0.0001; BI-BP: 133mm, capture: 182mm).

For the MF-BP model, estimated pre-migratory size-at-age was generally similar to capture data for all ages from all river systems (Table **2**.**5**; Figure **2**.**5**). Similar to the BI-BP model, the MF-BP model generally gave average estimates below capture values, which was expected. Average estimates that were higher than capture values occurred for Rat River aged 1 males (BI-BP: 98mm, capture: 85mm) and females (BI-BP: 94mm, capture: 85mm), aged 3 males (BI-BP: 147mm, capture: 144mm) and females (BI-BP: 145mm, capture: 144mm) and aged 4 (BI-BP: 169mm, capture: 160mm) males and females, and Babbage River aged 1 (BI-BP: 145mm, capture: 116mm), 2 (BI-BP: 189mm, capture: 141mm), and 3 (BI-BP: 210mm, capture: 174mm) females. These differences were only significant for aged 2 Babbage River females (Kruskal-Wallis: p<0.001). A significant difference between capture and MF-BP values was also observed in Babbage 1 year males (Kruskal-Wallis: p<0.001; BI-BP: 93mm, capture: 116mm).

When comparing back-calculated data for post-migratory fish from the BI, BI-BP, and MF-BP models to known capture data, I found that all models gave fairly similar estimates of size-at-age relative to capture (Table **2**.**5**; Figure **2**.**5**). All average estimates of size-at-age were lower than average values at capture, which was expected. Significant differences between capture values and the BI, BI-BP, and MF-BP models occurred for Rat River aged 5 males (Kruskal-Wallis: p<0.001) and aged 4 females (ANOVA: p<0.001), Babbage aged 3 (Kruskal-Wallis: p<0.001), 4 (ANOVA: p<0.001), and 5 (ANOVA: p<0.001) males, and age 4 (ANOVA: p<0.001), 5 (ANOVA: p<0.001), and 6 (Kruskal-Wallis: p<0.001) females, and Big Fish aged 4 (ANOVA: p<0.001) and 5 (ANOVA: p<0.001) males and aged 5 (Kruskal-Wallis: p<0.001) females. Significant differences also occurred between the BI-BP model and capture for aged 5 Rat River females (Kruskal-Wallis: p<0.001), and between the BI model and capture for Rat River aged 6 females (ANOVA: p<0.001), Babbage aged 3 females (Kruskal-Wallis: p<0.001), and Big Fish aged 4 (Kruskal-Wallis: p<0.001) and 6 (ANOVA: p<0.001) females. Based on 25 average back-calculated estimates, the BI model produced estimates with the highest values compared to other models 13 times and the lowest values 12 times. The BI-BP model consistently produced estimates between the BI and the MF-BP models (18 out of 19 times), with a few estimates consistent with the MF-BP model (6 times), and the MF-BP model produced estimates with the highest values 8 times and the lowest values 10 times.

When back-calculated and known size-at-age information obtained from tagging studies were compared, there was a good fit to a 1:1 relationship for estimates based on all back-calculation models (Table **2**.**6**; Figure **2**.**6**), with the 1:1 relationship falling within prediction intervals. For the Rat River, the BI-BP model provided the smallest y-intercept and slope closest to 1, while the BI model had the largest y-intercept and slope value farthest from 1. For this system the BI model's slope and intercept were different from 1 and 0, respectively (slope: p=0.002, intercept: p=0.001). On the Babbage River, the BI model provided the smallest y-intercept and slope closest to 1, while the MF-BP model had the largest y-intercept and slope value farthest from 1. The slope of the MF-BP model was the only value that was marginally different from 1 (p=0.047). On the Big Fish River the BI model provided the smallest y-intercept, while the BI-BP model had a slope value closest to 1. The MF-BP model had the largest y-intercept and slope value farthest from 1.

Otolith increment widths

An examination of otolith annual increments widths provided inconclusive results (Figure **2**.**7**). Fish that migrated at a younger age from the Rat and Big Fish rivers on average had larger otolith increments compared to those that migrated the following year (p<0.001 in all cases). The average increment width in younger-age migrating individuals from the Babbage River were not found to be significantly different (p=0.274 and 0.063 for males and females, respectively), however the results indicated low power and an observed trend of on average slightly larger increment widths in migrating individuals compared to non-migrating fish. Older migrating male individuals from the Rat River also had larger otoliths compared to fish undergoing their second migration (p=0.001), however this result was not apparent in other systems.

Discussion

Back-calculations

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My results indicate that the BI-BP model produced the most reliable estimates of size-at-age for pre-migratory individuals compared to the BI and MF-BP models. It was the only model that produced estimates of juvenile size-at-age that were consistent with capture data. Estimates of size-at-age were generally below or similar to known average capture sizes, which was expected given the time of annuli formation and capture. Juvenile back-calculation results with the BI-BP model are consistent with Craig (1977), who found Dolly Varden in the Canning River (northeast Alaska) to have an average length of 85mm at age 1. Underwood et al. (1996) also found results similar to this study when looking at data collected on Dolly Varden populations in systems within the Arctic National Wildlife Refuge. Aged 1 fish ranged from 64-120mm (n=10) and aged 2 fish ranged from 102-184mm (n=22). Aged 3 (n=37) and 4 (n=70) fish were found to have a wider size range from 106-395mm and 171-420mm respectively. This is consistent with my findings, both from back-calculation using the BI-BP method and sizes of actual captured fish, which show large variation in length for 3 and 4 year-old fish when not taking year of smoltification into account. The BI-BP model should still be used with caution when back-calculating to age 1 since we had a limited sample of aged 1 fish, with the possibility of the fish being freshwater residents instead of future anadromous individuals.

Based on my results, the BI model should not be used to back-calculate size for pre-migratory fish. By back-calculating through the decoupling that occurs during first migration, the growth that occurs during this period is being accounted for in estimates of pre-migration juvenile size, thereby increasing size-at-age estimates to unrealistic values. Using any model that does not incorporate this decoupling is likely to highly overestimate size at age in Dolly Varden and any other species that undergo similar decoupling patterns during first migration.

In comparing the MF-BP model to capture data I found that the MF-BP model tended to give high estimates for sizes-at-age 1. With Babbage females the MF-BP model produced estimates that were similar to the BI model at age 1 and overestimated size-at-age at all juvenile ages, with estimated lengths larger then capture data. The MF-BP model incorporated a statistically determined breakpoint into the MF model derived by Vigliola et al. (2000). The MF model is based on an allometric FL – OL relationship, however when the FL – OL relationship is linear, as appears to be the case with Dolly Varden, the BI and the MF model should give the same estimate of size-at-age (Vigliola and Meekan 2009). Because the statistically determined breakpoint is the same for the BI-BP and MF-BP models, I would have expected the models to

produce similar, if not the same results, given that the FL – OL relationship appears linear within the juvenile stage. A possible explanation for why similar estimates in these models at younger ages is not being observed is that the statistically determined breakpoints were determined using a linear scale and then fit to the nonlinear allometric equation. Fitting the breakpoints using an allometric scale may produce different results and is recommended in populations that exhibit an allometric FL – OL relationship.

For post-migratory fish, size-at-capture was larger at all ages and for all back-calculation models. Larger size-at-capture was expected since time-at-capture occurred after annuli formation in all cases. The BI, BI-BP, and MF-BP all performed similarly when size-at-age estimates were compared to capture data, and our results indicate that any of the 3 models could be used to back-calculate size-at-age in post-migratory individuals. Results from tagging studies also indicated that no single model predicted size-at-age better than the other in all cases. Other than the BI model on the Rat River, all models gave intercept values close to 0 and slopes close to 1, indicating they fit a 1:1 relationship with capture data. These results should be interpreted with caution as the back-calculation values were altered along a linear scale to reflect time-of-capture and not time of annuli formation. Dolly Varden are not growing in a linear fashion within a year, and thus a sigmoidal curve between years more accurately reflects a yearly growth pattern (Fechhelm et al. 1997). However, there is currently no specific within-year growth information to fit such a curve, and many of the recaptures with corresponding otoliths occurred in non-consecutive years, so it is likely that the within-annuli estimated results are either over or underestimating length in relation to capture data. Further challenges in determining accuracy of back-calculation models for adults is the range of growth experienced by Dolly Varden within a single year. Data from tagging studies show a range of 0-155mm, 0-115mm, and 5-90mm of growth have occurred within a single year for individual fish from the Rat, Big Fish, and Babbage rivers respectively (DFO 2017a, b, Gallagher et al. 2013, Gallagher, unpublished data). With such large growth increases occurring over a short time period, it is possible that decoupling of otolith and somatic growth could also be occurring in some instances after first migration. Dolly Varden may skip spawning and also refrain from migrating in some years. Without knowing the maturation and migratory state of an individual at each back-calculated age, or the potential for decoupling, it is difficult to determine the accuracy of back-calculated models at the individual level.

Overall the BI-BP provided the best estimate of size-at-age. The MF-BP model gave estimates of size-at-age that were comparable to the BI-BP and BI models in adults, however the complex calculations involved in the MF-BP model make it a less desirable option for back-calculating size-at-age. While the age range used in this study was relatively small, the inclusion of older aged fish still gave a linear FL – OL relationship as opposed to an allometric relationship. For studies with species that have an allometric relationship, the MF-BP may be a better option for back-calculating in post-migratory fish. For pre-migratory fish with an allometric relationship, fitting the breakpoint using an allometric model as opposed to a linear model may be more desirable so as to not over-estimate fish length at young ages.

I have shown that decoupling does not appear to adversely affect BI back-calculation estimates in post-migratory individuals. Without information pertaining to the population or individual breakpoint, my results indicate that the BI model (with intercept at hatch) can be used with confidence to back-calculate Dolly Varden size-at-age for post-migratory individuals. This is useful since many populations of Dolly Varden and other anadromous species lack information on pre-migratory individuals to construct a breakpoint model. In Dolly Varden studies that require size information from otoliths on pre-migratory individuals, yet lack river-specific juvenile information to determine an accurate breakpoint regression, the model for the sex-specific regressions could be used in place of a river-specific model. For other species that undergo a decoupling during migration, validation of each model at different ontogenetic stages should be undertaken before back-calculating size-at-age in order to determine how well the model fits a given species.

Using stage-specific back-calculation equations has been recommended when there are ontogenetic shifts within the FL – OL relationship (Hare and Cowen 1995, Hobbs et al. 2007). However, this method only works if there is a large enough sample size to calculate a biological transition point and if there is limited variation in otolith and somatic size at that transition point. If there is large variation at transition, fitting the data to an average biological intercept will cause large over or under estimation in back-calculated lengths. While my model used statistically derived information to determine a population transition point, the actual transition is dependent on each individual fish and their specific otolith size at migration. As long as there is enough information to obtain a population regression, using a discontinuous piecewise model allows the variation around size at migration to be accounted for within the model. My approach

to back-calculation at the individual level is similar to Gunther et al. (2012) who derived a model that allowed for individual variation around the ontogenetic transition point in Baltic sprat (*Sprattus sprattus*) based on individual otolith size at the transition. Similar to our model, Laidig et al. (1991) also used a segmented approach for back-calculating shortbelly rockfish. However, in their model they assumed all fish transitioned from one ontogenetic stage to another over a small otolith and somatic size, thereby removing the possibility of large variation in individual fish at transition.

Otolith Increment widths

While no large increment increase was apparent on the otolith for individuals undergoing their first migration (Figure **2.8**), analysis of otolith increment widths indicated a possible increase during migration for earlier migrating individuals. While there is an apparent decoupling occurring in the FL – OL relationship, some of the increased growth occurring during first migration appears to be reflected in the otolith. Although few studies have been conducted on northern Dolly Varden, and specifically examining otolith patterns, Yoshihara (1973) (from McCart 1980) found that Dolly Varden from the Sagavanirktok drainage in Alaska had otolith increment widths that were on average larger at age 3, which is consistent with average age of seaward migration in this system. Decoupling during migration may be a species-specific occurrence that reflects the unique physiology and environmental history of Dolly Varden. However, any fish that undergoes physiological changes associated with migration, and large increases in growth under a short time frame, may exhibit decoupling to some extent, regardless of observable differences in otolith increment widths during first migration.

FL – OL Decoupling

Decoupling occurs when somatic growth and otolith growth fail to increase in a proportional manner. Observation of Dolly Varden growth in relation to otolith growth clearly demonstrated a decoupling occurring at the time of first migration where fish growth increases at a rate non-proportional to otolith growth. Both pre- and post-migratory fish demonstrated linear

growth before and after first migration respectively, with a clear jump in somatic growth during first migration. This is the first known reported evidence of decoupling occurring in this manner.

While I don't have actual length data from smolts used in this study, potential size ranges of smolts (taken from smolt aged juveniles) were 100-220mm. This is consistent with Fechhelm et al. (1997), who found the modal length of out-migrating Dolly Varden smolts in Prudhoe Bay, northeastern Alaska, to be 150-160mm. Fechhelm et al. (1997) found modal smolt length at the end of the summer to have increased to 200-240mm, which is much lower than lengths observed in my study that ranged from 296-370mm. While there have been a few instances of small anadromous fish captured during mark-recapture surveys, only one returning fish has been observed with a length below 250mm (measured at 225mm). The overall percentage of anadromous fish <300mm observed during mark-recapture programs is <0.001% on the Rat River (n=6115), 0.003% on the Big Fish River (n=4045), and 0.02% on the Babbage River (n=3517) (Gallagher, unpublished data). This discrepancy in growth of returning first time migrants could indicate a change in feeding habits or a change in ocean productivity, which may be affecting the summer growth in Dolly Varden. Alternatively, the differences may represent the different size structures and growth patterns observed within Dolly Varden populations from different river systems. However, my study examines three distinct populations of Dolly Varden, all of which have similar size structures at all ontogenetic stages despite differences in migration timing and river-specific characteristics. A study conducted by Underwood et al. (1996), which looked at Dolly Varden populations situated between Prudhoe Bay and the Babbage River, found that the majority of smolt-sized fish captured in July were in the modal length group of 190mm. This value increased to 220mm by early August indicating a growth trend similar to that observed by Fechhelm et al. (1997). However, after mid-August the observed length of the modal group fell to 210mm. This suggests the observed return smolt length of 200-240mm is likely not from the same group that outmigrated at 150-160mm, but may be a separate group that has yet to finish their coastal migration and summer growth potential. Jensen et al. (2012) observed similar results in migrating Arctic char, Atlantic salmon (*Salmo salar*), and brown trout (*S. trutta*) smolts, where an increase in migrating smolt length was followed by a decrease later in the summer. McCart (1980) found that returning immature Dolly Varden ranged in size between 250-350mm, which is consistent with my observations, and that the majority of fish in this size range were returning in late September, just prior to freeze-up. Similarly, juvenile Dolly

Varden within my study systems may not begin migrating upriver until late September (Sandstrom et al. 2001). Without strontium data to indicate seawater migration, it would be understandable that no larger fish (>250mm) would be classified as a smolt.

While there are numerous known physiological changes that occur during smoltification (Hoar 1988, McCormick and Saunders 1987), there is no information on smoltification in regards to its effect on otolith accretion rates, even though individual physiology is known to regulate otolith growth (Gauldie and Nelson 1990, Grønkjær 2016, Morales-Nin 2000). Studies that have focused on rates of otolith accretion indicate that metabolic processes and not somatic growth are the main drivers of otolith growth (Armstrong et al. 2004, Mosegaard et al. 1988, Wright 1991, Yamamoto et al. 1998). However, just how metabolic processes influence otolith growth has yet to be determined. Armstrong et al. (2004) found a correlation between otolith accretion and specific dynamic action in pike (*Esox lucius*), and Huuskonen and Karjalainen (1998) found a positive relationship between otolith increment width and specific dynamic action in whitefish (*Coregonus lavaretus*). In examining dominance hierarchies in masu salmon (*Oncorhynchus masou*), Yamamoto et al. (1998) found that resting metabolic rate was highly correlated with otolith increment width. Wright (1991) found similar results in a study on oxygen consumption and otolith increment width in Atlantic salmon. However, Wright et al. (2001) showed that otolith increment width and metabolic rate varied in their response to temperature change.

Temperatures experienced by over-wintering Dolly Varden ranges from 1-11°C (Mochnacz et al. 2010), while temperatures experienced by Dolly Varden in nearshore habitats have been shown to range from 0.5-15.5°C (Courtney et al. 2016). While I expect a temperature change associated with marine migration, it is unlikely that these differences would influence the dramatic changes observed in the FL – OL relationship. Within the three river systems in my study, there are very different temperature regimes (Mochnacz et al. 2010), yet we don't see large differences in the FL – OL relationship among systems. Studies that link food ration to temperature (Barber and Jenkins 2001, Baumann et al. 2005, Neat et al. 2008) often focus on otolith growth at starvation and no studies have examined otolith growth during large increases in somatic growth.

This pattern of decoupling in Dolly Varden otoliths is only occurring during first migration and not noticeably in any other consecutive migrations. While somatic growth,

temperature, and metabolism are most likely influencing otolith accretion, I expect that whatever is governing this decoupling episode is related to first time physiological changes due to smoltification, as smoltification alters hormones that regulate calcium homeostasis within fish (Loewen et al. 2016). Since otolith growth is governed by calcium accretion, it is possible that these hormonal changes are having short-term effects on the rate of calcium deposition, leading to the observed decoupling in the FL – OL relationship in Dolly Varden.

Literature Cited

Armstrong, J.D., Fallon-Cousins, P.S., and Wright, P.J. 2004. The relationship between specific dynamic action and otolith growth in pike. Journal of Fish Biology **64**(3): 739-749.

Armstrong, R.H., and Morrow, T.E. 1980. The Dolly Varden charr, *Salvelinus malma malma*. *In* Charrs, salmonid fishes of the genus *Salvelinus*. *Edited by* E.K. Balon. Hague: W. Junk, pp. 99-139.

Barber, M.C., and Jenkins, G.P. 2001. Differential effects of food and temperature lead to decoupling of short-term otolith and somatic growth rates in juvenile King George whiting. Journal of Fish Biology **58**(5): 1320-1330.

Baumann, H., Peck, M.A., and Herrmann, J.P. 2005. Short-term decoupling of otolith and somatic growth induced by food level changes in postlarval Baltic sprat, *Sprattus sprattus*. Marine and Freshwater Research **56**(5): 539-547.

Blackett, R.F. 1968. Spawning behavior, fecundity, and early life history of anadromous Dolly Varden, *Salvelinus malma* (Walbaum) in Southeastern Alaska. Alaska Department of Fish and Game Research Report **6**:1-85.

Brown, R.J., Bickford, N., and Severin, K. 2007. Otolith trace element chemistry as an indicator of anadromy in Yukon River drainage coregonine fishes. Transactions of the American Fisheries Society **136**(3): 678-690.

Brown, R.J., Loewen, M.B., and Tanner, T.L. 2014. Overwintering locations, migrations, and fidelity of radio-tagged Dolly Varden in the Hulahula River, Arctic National Wildlife Refuge, 2007-09. Arctic **67**(2): 149-158.

Campana, S.E. 1984. Microstructural growth-patterns in the otoliths of larval and juvenile starry flounder, *Platichthys-stellatus*. Canadian Journal of Zoology **62**(8): 1507-1512.

Campana, S.E. 1990. How reliable are growth back-calculations based on otoliths. Canadian Journal of Fisheries and Aquatic Sciences **47**(11): 2219-2227.

Campana, S.E., and Neilson, J.D. 1985. Microstructure of fish otoliths. Canadian Journal of Fisheries and Aquatic Sciences **42**(5): 1014-1032.

Chilton, D.E., and Beamish, R.J. 1982. Age determination methods for fishes studied by the Groundfish Program at the Pacific Biological Station. Can. Spec. Publ. Fish. Aquat. Sci. p.102.

Clark, I.D., Lauriol, B., Harwood, L., and Marschner, M. 2001. Groundwater contributions to discharge in a permafrost setting, Big Fish River, NWT, Canada. Arctic Antarctic and Alpine Research **33**(1): 62-69.

Courtney, M.B., Scanlon, B.S., Rikardsen, A.H., and Seitz, A.C. 2016. Marine behavior and dispersal of an important subsistence fish in Arctic Alaska, the Dolly Varden. Environmental Biology of Fishes **99**: 209-222.

Craig, P.C. 1977. Ecological studies of anadromous populations of arctic char in the canning river drainage and adjacent coastal waters of the Beaufort Sea, Alaska. *In* Fisheries investigations along the north slope and Beaufort sea coast in Alaska with emphasis on arctic char. *Edited by* P.J. McCart. Canadian Arctic Gas Study Ltd., Calgary, Alberta. pp. 1-116.

Crawley, M.J. 2013. The R book. Wiley, Chichester, West Sussex, U.K.

DFO. 2017a. Assessment of Dolly Varden from the Babbage River, Yukon Territory 2010–2014. DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2016/055.

DFO. 2017b. Assessment of Dolly Varden from the Rat River, Northwest Territories 2009–2014. DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2016/058.

Fechhelm, R.G., Bryan, J.D., Griffiths, W.B., and Martin, L.R. 1997. Summer growth patterns of northern Dolly Varden (*Salvelinus malma*) smolts from the Prudhoe Bay region of Alaska. Canadian Journal of Fisheries and Aquatic Sciences **54**(5): 1103-1110.

Fey, D.P. 2006. The effect of temperature and somatic growth on otolith growth: The discrepancy between two clupeid species from a similar environment. Journal of Fish Biology **69**(3): 794-806.

Finstad, A.G. 2003. Growth backcalculations based on otoliths incorporating an age effect: adding an interaction term. Journal of Fish Biology **62**(5): 1222-1225.

Francis, R. 1990. Back-calculation of fish length: a critical review. Journal of Fish Biology **36**(6): 883-902.

Gallagher, C.P., Howland, K.L., and Wastle, R.J. 2016. A comparison of different structures and methods for estimating age of northern-form Dolly Varden *Salvelinus malma malma* from the Canadian Arctic. Polar Biology **39**(7): 1257-1265.

Gallagher, C.P., K.L., R., Harris, L.N., Banjo, R., Sandstrom, S., Loewen, T., and Reist, J. 2013. Dolly Varden (*Salvelinus malma malma*) from the Big Fish River: abundance estimates, effective population size, biological characteristics, and contribution to the coastal mixed-stock fishery. DFO Can. Sci. Advis. Sec. Res. Doc. p. v + 46p.

Gauldie, R.W. 1993. Polymporphic crystalline-structure of fish otoliths. Journal of Morphology **218**(1): 1-28.

Gauldie, R.W. 1996. Effects of temperature and vaterite replacement on the chemistry of metal ions in the otoliths of *Oncorhynchus tshawytscha*. Canadian Journal of Fisheries and Aquatic Sciences **53**(9): 2015-2026.

Gauldie, R.W., and Nelson, D.G.A. 1990. Otolith growth in fishes. Comparative Biochemistry and Physiology **97**(2): 119-135.

Geffen, A.J. 1992. Validation of otolith increment deposition rate. Canadian Special Publication of Fisheries and Aquatic Sciences **117**: 101-113.

Grønkjær, P. 2016. Otoliths as individual indicators: a reappraisal of the link between fish physiology and otolith characteristics. Marine and Freshwater Research **67**(7): 881-888.

Gunther, C.C., Temming, A., Baumann, H., Huwer, B., Mollmann, C., Clemmesen, C., and Herrmann, J.P. 2012. A novel length back-calculation approach accounting for ontogenetic changes in the fish length - otolith size relationship during the early life of sprat (*Sprattus sprattus*). Canadian Journal of Fisheries and Aquatic Sciences **69**(7): 1214-1229.

Hare, J.A., and Cowen, R.K. 1995. Effect of age, growth-rate, and ontogeny on the otolith size - fish size relationship in bluefish, *Pomatomus saltatrix*, and the implications for back-calculation of size in fish early-life history stages. Canadian Journal of Fisheries and Aquatic Sciences **52**(9): 1909-1922.

Harris, L.N., Bajno, R., Gallagher, C.P., Koizumi, I., Johnson, L.K., Howland, K.L., Taylor, E.B., and Reist, J.D. 2015. Life-history characteristics and landscape attributes as drivers of genetic variation, gene flow, and fine-scale population structure in northern Dolly Varden (*Salvelinus malma malma*) in Canada. Canadian Journal of Fisheries and Aquatic Sciences **72**(10): 1477-1493.

Hoar, W.S. 1988. The Physiology of Smolting Salmonids. *In* Fish Physiology Volume XI Physiology of Developing Fish, Part B. *Edited by* W.S. Hoar and D.J. Randall. Academic Press, San Diego pp. 275-343.

Hobbs, J.A., Bennett, W.A., Burton, J.E., and Baskerville-Bridges, B. 2007. Modification of the biological intercept model to account for ontogenetic effects in laboratory-reared delta smelt (*Hypomesus transpacificus*). Fishery Bulletin **105**(1): 30-38.

Howland, K.L., Babaluk, J.A., Chiperzak, D., Tallman, R.F., and Low, G. 2009. Variability in diadromous behavior of a northern coregonid based on scanning proton microprobe analysis of otolith strontium. Challenges for Diadromous Fishes in a Dynamic Global Environment **69**: 121-134.

Howland, K.L., Tonn, W.M., Babaluk, J.A., and Tallman, R.F. 2001. Identification of freshwater and anadromous inconnu in the Mackenzie river system by analysis of otolith strontium. Transactions of the American Fisheries Society **130**(5): 725-741.

Huuskonen, H., and Karjalainen, J. 1998. A preliminary study on the relationships between otolith increment width, metabolic rate and growth in juvenile whitefish (*Coregonus lavaretus* L.). Archiv Fur Hydrobiologie **142**(3): 371-383.

Jensen, A.J., Finstad, B., Fiske, P., Hvidsten, N.A., Rikardsen, A.H., and Saksgard, L. 2012. Timing of smolt migration in sympatric populations of Atlantic salmon (*Salmo salar*), brown trout (*Salmo trutta*), and Arctic char (*Salvelinus alpinus*). Canadian Journal of Fisheries and Aquatic Sciences **69**(4): 711-723.

Laidig, T.E., Ralston, S., and Bence, J.R. 1991. Dynamics of growth in the early life-history of shortbelly rockfish *Sebastes jordani*. Fishery Bulletin **89**(4): 611-621.

Lea, E. 1910. On the methods used in the herring investigations. Publications de Circconstance Conseil Permanent Interational pour L'Exploration de la Mer **53**:7-25.

Lee, R.M. 1920. A review of the methods of age and growth determination in fishes by means of scales. Fishery Investigations London Series **4**(2): 1-34.

Loewen, T.N., Carriere, B., Reist, J.D., Halden, N.M., and Anderson, W.G. 2016. Linking physiology and biomineralization processes to ecological inferences on the life history of fishes. Comparative Biochemistry and Physiology A **202**: 123-140.

Loewen, T.N., Reist, J.D., Yang, P., Koleszar, A., Babaluk, J.A., Mochnacz, N., and Halden, N.M. 2015. Discrimination of northern form Dolly Varden Char (*Salvelinus malma malma*) stocks of the North Slope, Yukon and Northwest Territories, Canada via otolith trace elements and Sr-87/Sr-86 isotopes. Fisheries Research **170**: 116-124.

McCart, P.J. 1980. A review of the systematics and ecology of Arctic char, *Salvelinus alpinus*, in the Western Arctic. Can. Tech. Rep. Fish. Aquat. Sci. 935: vii + 89p.

McCormick, S.D., and Saunders, R.L. 1987. Preparatory physiological adaptations for marine life of salmonids: osmoregulation, growth, and metabolism. American Fisheries Symposium **1**:211-229.

Mochnacz, N.J., Schroeder, B.S., Sawatzky, C.D., and Reist, J.D. 2010. Assessment of northern Dolly Varden, *Salvelinus malma malma* (Walbaum, 1792), habitat in Canada. Canadian Manuscript Report of Fisheries and Aquatic Sciences 2926: i-vi, 1-48.

Molony, B.W., and Choat, J.H. 1990. Otolith increment widths and somatic growth-rate: the presence of a time-lag. Journal of Fish Biology **37**(4): 541-551.

Morales-Nin, B. 2000. Review of the growth regulation processes of otolith daily increment formation. Fisheries Research **46**(1-3): 53-67.

Morita, K., and Matsuishi, T. 2001. A new model of growth back-calculation incorporating age effect based on otoliths. Canadian Journal of Fisheries and Aquatic Sciences **58**(9): 1805-1811.

Morris, J.A., Rulifson, R.A., Babaluk, J.A., May, P.G., and Campbell, J.L. 2005. Use of micro-PIXE to investigate otolith Sr distributions of the anadromous striped bass, *Morone saxatilis*. X-Ray Spectrometry **34**(4): 301-305.

Mosegaard, H., Svedang, H., and Taberman, K. 1988. Uncoupling of somatic and otolith growth-rates in Arctic char (*Salvelinus alpinus*) as an effect of differences in temperature response. Canadian Journal of Fisheries and Aquatic Sciences **45**(9): 1514-1524.

Neat, F.C., Wright, P.J., and Fryer, R.J. 2008. Temperature effects on otolith pattern formation in Atlantic cod *Gadus morhua*. Journal of Fish Biology **73**(10): 2527-2541.

Otterlei, E., Folkvord, A., and Nyhammer, G. 2002. Temperature dependent otolith growth of larval and early juvenile Atlantic cod (*Gadus morhua*). Ices Journal of Marine Science **59**(2): 401-410.

Radtke, R.L., Fey, D.P., DeCicco, A.F., and Montgomery, A. 1996. Otolith microstructure in young-of-the-year Dolly Varden, *Salvelinus malma*, from American and Asian populations: Resolution of comparative life history characteristics. Arctic **49**(2): 162-169.

Reist, J.D., and Sawatzky, C.D. 2010. Diversity and distribution of chars, genus Salvelinus, in Northwestern North America in the context of Northern Dolly Varden (*Salvelinus malma malma* (Walbaum 1792)). Canadian Science Advisory Secretariat Research Document 014: i-vi, 1-18.

Sandstrom, S., Harwood, L., and Howland, K. 2009. Status of anadromous Dolly Varden char (*Salvelinus malma*) of the Rat River, Northwest Territories, as assessed through mark-recapture and live-sampling at the spawning and over-wintering site (1995-2007). Can. Tech. Rep. Fish. Aqua. Sci. p.75.

Sandstrom, S.J., Chetkiewicz, C.B., and Harwood, L.A. 2001. Overwintering habitat of juvenile Dolly Varden (*Salvelinus malma*) (W.) in the Rat River, NT, as determined by radio telemetry. Canadian Science Advisory Secretariat Res. Doc. 2001/092, p.16.

Secor, D.H., and Dean, J.M. 1992. Comparison of otolith-based back-calculation methods to determine individual growth histories of larval striped bass, *Morone saxatilis*. Canadian Journal of Fisheries and Aquatic Sciences **49**(7): 1439-1454.

Sirois, P., Lecomte, F., and Dodson, J.J. 1998. An otolith-based back-calculation method to account for time-varying growth rate in rainbow smelt (*Osmerus mordax*) larvae. Canadian Journal of Fisheries and Aquatic Sciences **55**(12): 2662-2671.

Swanson, H.K., Kidd, K.A., Babaluk, J.A., Wastle, R.J., Yang, P.P., Halden, N.M., and Reist, J.D. 2010. Anadromy in Arctic populations of lake trout (*Salvelinus namaycush*): otolith microchemistry, stable isotopes, and comparisons with Arctic char (*Salvelinus alpinus*). Canadian Journal of Fisheries and Aquatic Sciences **67**(5): 842-853.

Underwood, T.J., Millard, M.J., and Thorpe, L.A. 1996. Relative abundance, length frequency, age, and maturity of Dolly Varden in nearshore waters of the Arctic National Wildlife Refuge, Alaska. Transactions of the American Fisheries Society **125**(5): 719-728.

Vigliola, L., Harmelin-Vivien, M., and Meekan, M.G. 2000. Comparison of techniques of back-calculation of growth and settlement marks from the otoliths of three species of *Diplodus* from the Mediterranean Sea. Canadian Journal of Fisheries and Aquatic Sciences **57**(6): 1291-1299.

Vigliola, L., and Meekan, M.G. 2009. The back-calculation of fish growth from otoliths. *In* Tropical Fish Otoliths: Information for Assessment, Management and Ecology. *Edited by* B.S. Green, B.D. Mapstone, G. Carlos and G.A. Begg. Springer, Dordrecht pp. 174-211.

Wilson, J.A., Vigliola, L., and Meekan, M.G. 2009. The back-calculation of size and growth from otoliths: validation and comparison of models at an individual level. Journal of Experimental Marine Biology and Ecology **368**(1): 9-21.

Wright, P.J. 1991. The influence of metabolic rate on otolith increment width in Atlantic salmon parr, *Salmo salar* L. Journal of Fish Biology **38**(6): 929-933.

Wright, P.J., Fallon-Cousins, P., and Armstrong, J.D. 2001. The relationship between otolith accretion and resting metabolic rate in juvenile Atlantic salmon during a change in temperature. Journal of Fish Biology **59**(3): 657-666.

Wright, P.J., Metcalfe, N.B., and Thorpe, J.E. 1990. Otolith and somatic growth-rates in Atlantic salmon parr, *Salmo salar* L.: evidence against coupling. Journal of Fish Biology **36**(2): 241-249.

Yamamoto, T., Ueda, H., and Higashi, S. 1998. Correlation among dominance status, metabolic rate and otolith size in masu salmon. Journal of Fish Biology **52**(2): 281-290.

Yoshihara, H.T. 1973. Annual Progress Report for Monitoring and evaluation of Arctic waters with emphasis on the North Slope drainages. Alaska Dep. Fish Game, G-III-A, v.13, pp. 1-83.

Zimmerman, C.E. 2005. Relationship of otolith strontium-to-calcium ratios and salinity: experimental validation for juvenile salmonids. Canadian Journal of Fisheries and Aquatic Sciences **62**(1): 88-97.

Tables

Table 2.1 – Number of Dolly Varden samples used for analysis collected from 1986-2016 within the Rat, Babbage, and Big Fish rivers. Juveniles were collected at overwintering sites as pre-migratory fish. Anadromous samples were collected at either spawning/overwintering grounds, during coastal migration, or during return fall migration.

River	Life History	Sex	Sample Year												Total
			1986	1988	1991	2008	2009	2010	2011	2012	2013	2014	2015	2016	
Rat River	juvenile	Male		5								5	6		
		Female		3								4	7		31
		Unknown		1											
	anadromous	Male				3	1	3	5	28	8	30	27		105
		Female				1	8	5	25	29	6	33	20		127
Babbage River	juvenile	Male			18					1		2			
		Female			6										27
	anadromous	Male								44	6	21	1		72
		Female							1	42	8	28	1		80
Big Fish River	juvenile	Male	3										1		
		Female	5										1		11
		Unknown	1												
	anadromous	Male								5	14	22	31		72
		Female								2	36	22	27		87
		Unknown										1	3		4

Table 2.2 – Coordinates of where Dolly Varden samples were collected.

Sampling location	Coordinates	
	N	W
Shingle Point	68.99485	137.39708
	67.96425	135.34080
Mackenzie Delta & Rat River	67.74563	135.38124
	67.75958	135.13894
Rat overwintering site	67.76582	136.30533
Big Fish mouth	68.66290	135.87836
Big Fish overwintering site	68.30155	136.35761
Babbage overwintering site	68.60123	138.73581

Table 2.3 – Number of fish that migrated at a specific age for male and female Dolly Varden that were used in analysis from the Rat, Babbage, and Big Fish rivers. Age at migration was determined from Sr concentrations in otoliths.

River	Sex	Age at Migration			
		2	3	4	5
	males	1	34	63	1
Rat	females	1	35	60	3
	Total	2	69	123	4
	males	36	27	3	1
Babbage	females	35	29	7	0
	Total	71	56	10	1
	males	1	44	21	1
Big Fish	females	1	43	25	0
	Total	2	87	46	1

Table 2.4 – Results from the discontinuous piecewise regression of fish length (mm) on otolith radius length (mm) from samples of Dolly Varden collected on the Rat, Babbage, and Big Fish Rivers from 1986-2016. Male and female juveniles were combined for the analysis.

River	Sex	Juveniles from all systems combined or river specific	breakpoint	r2	p	Post-migration				Pre-migration			
						y-intercept	y-intercept 95%CI	slope	slope 95% CI	y-intercept	y-intercept 95%CI	slope	slope 95% CI
All	combined	combined	0.421	0.8538	<0.001	19	-17.7 53.2	718	663.4 778.3	-72	-161.0 -13.5	594	431 855
	males	combined	0.421	0.8945	<0.001	-69	-124.5 -17.6	869	785.9 961.7	-47	-93.3 9.2	518	368 649
	females	combined	0.430	0.9045	<0.001	55	-2.5 102.1	652	578.0 742.0	-49	-93.8 6.1	523	375 648
Rat	males	river specific	0.424	0.9300	<0.001	-26	-86.1 40.4	809	702.1 908.7	-14	-71.7 74.8	406	163 566
		combined	0.479	0.9249	<0.001	-41	-118.2 37.2	831	706.8 954.6	-151	-269.6 -68.2	819	587 819
	females	river specific	0.426	0.9409	<0.001	144	90.4 191.6	526	451.4 608.3	-14	-69.8 76.8	406	162 561
		combined	0.479	0.9316	<0.001	113	46.2 170.0	570	482.8 670.4	-136	-317.1 -43.3	777	511 1298
Babbage	males	river specific	0.421	0.9260	<0.001	-96	-203.3 -11.9	920	778.8 1097.9	-25	-85.1 43.7	462	272 632
		combined	0.478	0.9317	<0.001	-81	-188.3 11.1	894	740.2 1067.2	-123	-235.4 -47.9	741	529 1060
	females	river specific	0.451	0.9408	<0.001	34	-81.8 111.0	693	569.5 879.1	-33	-84.2 37.8	485	296 627
		combined	0.477	0.9412	<0.001	36	-78.0 119.1	688	554.5 865.3	-126	-271.8 -44.0	744	513 1151
Big Fish	males	combined	0.461	0.9228	<0.001	-39	-167.6 66.1	806	636.1 806.2	-82	-171.9 -26.9	620	470 882
	females	combined	0.479	0.9408	<0.001	69	-23.2 152.1	613	477.9 760.9	-101	-204.3 -36.3	675	494 965

Table 2.5 – Average Back-calculation results compared with known capture results for Dolly Varden on the Rat, Babbage, and Big Fish rivers. Back-calculation models used were the traditional biological intercept model (BI), the new biological intercept breakpoint model (BI-BP), and the new modified fry breakpoint model (MF-BP). Back-calculated lengths (mm) were calculated at each annuli for pre- and post-migration. Capture length (mm) is from known fish sizes at a given age, which correspond to a time period after annuli formation.

System	Sex	Model	Average back-calculated size-at-age																	
			Pre-migration								Post migration									
			1	95% CI	2	95% CI	3	95% CI	4	95% CI	3	95% CI	4	95% CI	5	95% CI	6	95% CI	7	95% CI
Rat	Males	Capture	85	1.4	126	8.1	144	8.1	160	-	326	74.5	394	19.3	459	13.6	530	69.4	568	31.8
		BI	142	5.4	223	5.4	288	6.6	329	8.4	-	-	378	15.1	411	11.7	487	30.8	535	25.6
		BI-BP	76	2.6	115	2.7	145	2.7	167	3.2	-	-	373	13.8	409	10.2	484	30.3	535	25.0
		MF-BP	98	1.2	121	2.0	147	2.6	169	3.5	-	-	372	13.6	407	9.8	481	30.0	535	24.9
	Females	Capture	85	1.4	126	8.1	144	8.1	160	-	368	648.0	426	21.2	441	10.0	508	26.1	532	38.9
		BI	141	5.2	224	5.5	286	5.8	324	7.5	-	-	370	11.9	399	9.1	463	20.1	503	32.3
		BI-BP	76	2.7	115	2.8	145	3.0	167	4.4	-	-	401	8.1	422	8.5	478	17.0	511	31.6
		MF-BP	94	1.3	119	2.1	145	3.0	169	5.2	-	-	401	8.2	423	8.8	479	16.9	512	31.7
Babbage	Males	Capture	116	4.4	141	12.2	174	18.4	-	-	367	12.4	424	17.0	476	11.5	512	67.1	565	51.5
		BI	152	6.5	246	6.9	298	12.2	-	-	329	9.9	381	11.8	437	17.8	487	33.5	534	51.1
		BI-BP	86	3.5	134	3.8	160	6.5	-	-	312	12.1	364	12.8	423	18.4	475	33.4	526	50.5
		MF-BP	93	3.5	138	3.5	161	5.7	-	-	312	11.2	361	12.3	419	18.0	470	33.0	522	50.1
	Females	Capture	116	4.4	141	12.2	174	18.4	-	-	359	14.9	422	24.3	452	13.1	484	15.3	488	22.6
		BI	147	5.8	235	6.5	284	9.4	314	25.3	321	8.3	365	8.1	407	8.9	444	12.8	460	23.9
		BI-BP	86	3.3	134	3.8	162	5.6	187	20.6	332	11.4	371	8.3	412	8.0	448	12.0	462	22.7
		MF-BP	145	3.7	189	3.0	210	3.7	225	12.5	345	11.6	379	7.6	416	7.7	450	11.7	464	22.2
Big Fish	Males	Capture	-	-	182	9.1	199	209.7	-	-	334	17.5	402	19.3	461	16.5	501	26.1	575	-
		BI	166	6.0	248	6.2	302	7.2	331	14.0	-	-	376	10.8	416	13.0	468	24.4	538	154.8
		BI-BP	96	3.5	140	3.8	169	4.0	186	7.8	-	-	364	9.7	406	11.7	460	23.1	533	135.6
		MF-BP	118	3.0	151	2.6	170	2.4	180	4.5	-	-	362	9.6	403	11.3	466	22.3	531	131.6
	Females	Capture	-	-	182	9.1	199	209.7	-	-	331	14.3	379	20.1	420	11.3	454	15.5	507	18.7
		BI	152	5.1	227	5.3	281	5.4	308	9.4	-	-	350	6.2	383	8.5	427	12.8	484	22.2
		BI-BP	91	2.9	133	3.4	163	3.5	178	6.3	-	-	367	6.1	393	7.5	432	11.6	481	20.4
		MF-BP	121	2.5	152	2.1	170	1.9	178	3.1	-	-	367	6.3	393	7.5	432	11.6	481	20.4

Table 2.6 – Known fish length (mm) from tagging studies regressed on back-calculated results for post-migratory individual Dolly Varden from the Rat, Babbage, and Big Fish rivers. Back-calculations used were the biological intercept method (BI), the biological intercept breakpoint method (BI-BP), and the modified fry breakpoint method (MF-BP).

River	Sample Size	Model	r2	p-value	y-intercept	intercept 95% CI	intercept p-value	slope	slope 95% CI	slope p-value
Rat	61	BI	0.627	<0.001	119	71.4	0.001	0.751	0.151	0.002
		BI-BP	0.612	<0.001	60	85.9	0.165	0.854	0.177	0.104
		MF-BP	0.600	<0.001	65	87.1	0.139	0.843	0.179	0.086
Babbage	16	BI	0.885	<0.001	30	93.4	0.502	0.973	0.200	0.779
		BI-BP	0.867	<0.001	-117	134.6	0.085	1.281	0.288	0.055
		MF-BP	0.848	<0.001	-137	150.4	0.070	1.327	0.322	0.047
Big Fish	26	BI	0.787	<0.001	28	100.0	0.571	1.022	0.224	0.843
		BI-BP	0.801	<0.001	40	93.3	0.388	0.997	0.209	0.975
		MF-BP	0.776	<0.001	52	97.9	0.279	0.972	0.220	0.794
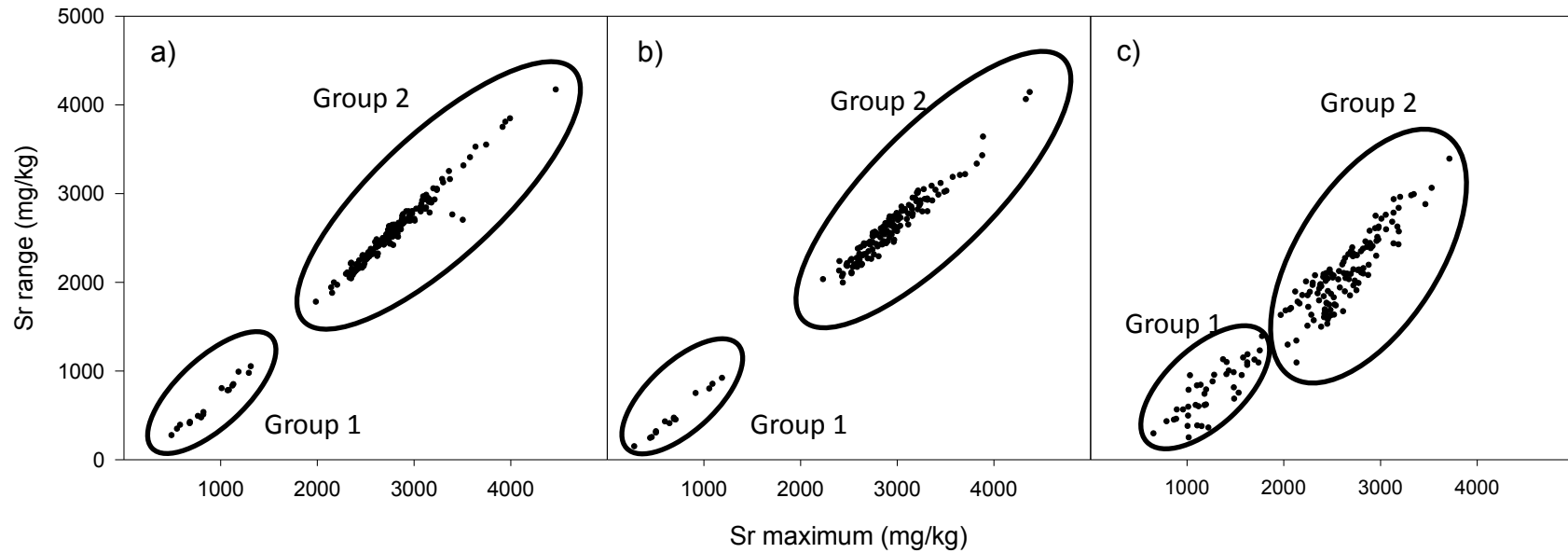
Figure 2.1 – Strontium (Sr) otolith concentration range versus maximum (mg/kg) plots for Dolly Varden from the a) Rat River, b) Babbage River, and c) Big Fish River. Group 1 denotes freshwater Sr concentrations while Group 2 denotes anadromous Sr concentrations.
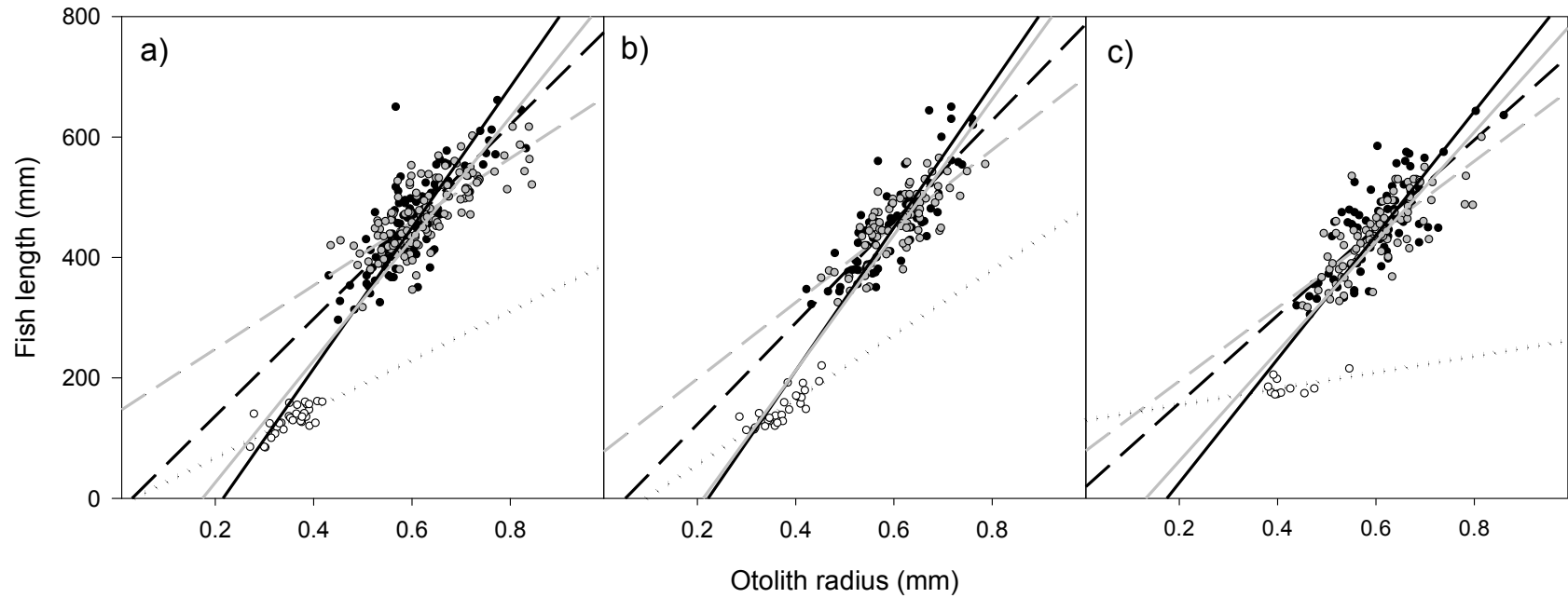
Figure 2.2 – Regressions of fish length (mm) on otolith radius (mm) for male (•), female (•), and pre-migratory juvenile (○) Dolly Varden from the a) Rat River, b) Babbage River, and c) Big Fish River. Dashed lines (- -, – –) represent post-migratory regressions, dotted lines (···) represent pre-migratory juvenile regressions, and solid lines (–, –) represent population regressions (pre- and post-migration combined).
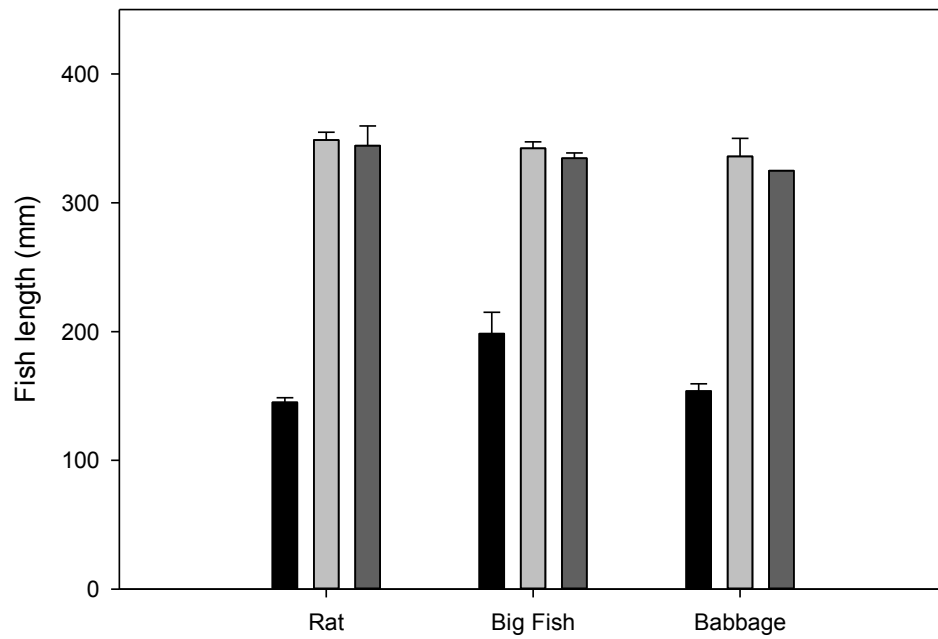
Figure 2.3 – Average fish length (mm) (±SE) of Dolly Varden from the Rat, Big Fish, and Babbage rivers for older pre-migratory juveniles (■), and males (□) and females (■) captured at sea during their first migration.
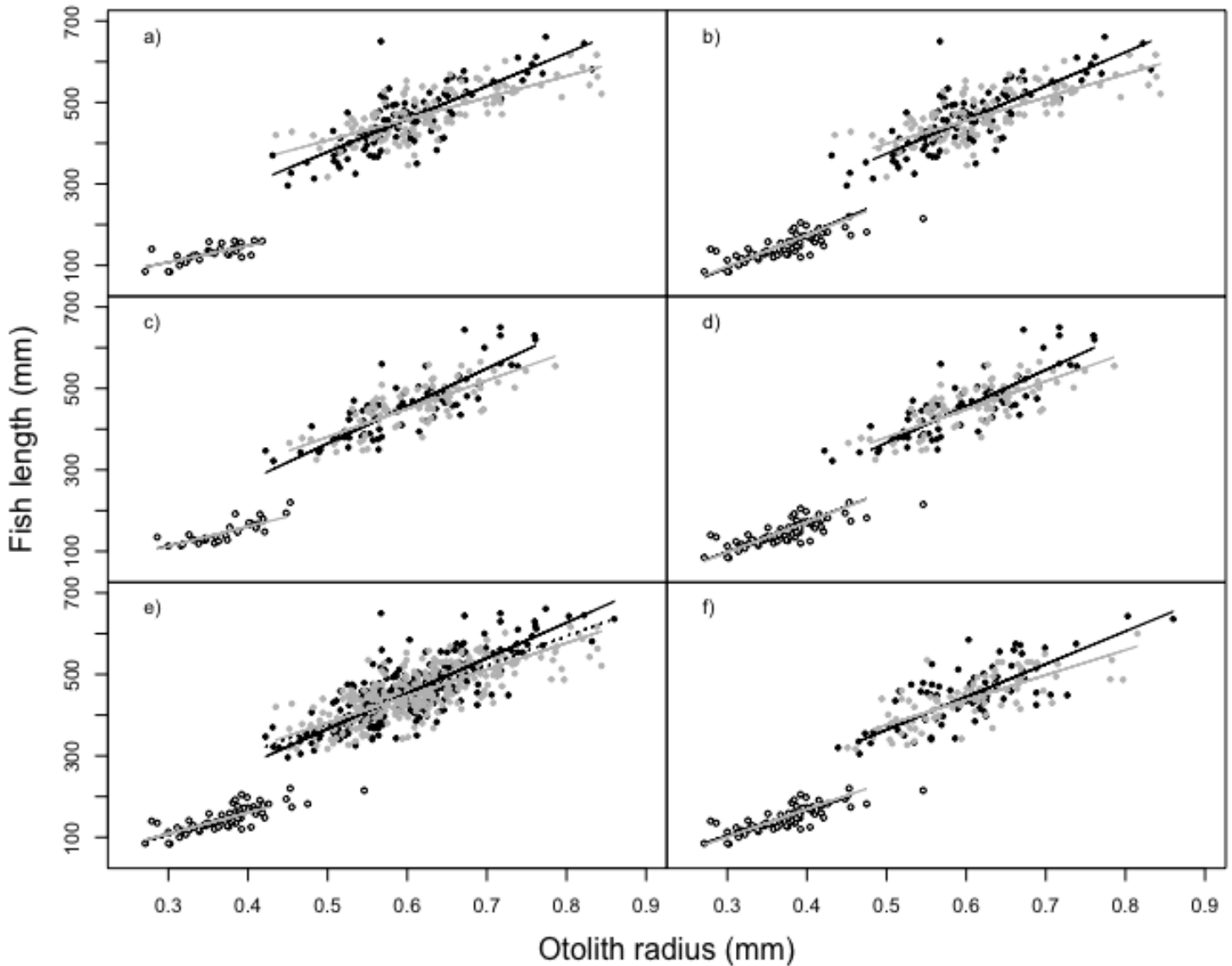
Figure 2.4 – Discontinuous piecewise regressions of fish length (mm) on otolith radius (mm) for Dolly Varden from the Rat, Babbage, and Big Fish rivers. (•) Denotes males, (•) denotes females, (◦) denotes pre-migratory juveniles. Regressions lines represent males (–), females (–), and male female combined (···). Regressions represent a) Rat River, b) Rat River with juveniles from all systems, c) Babbage River, d) Babbage River with juveniles from all systems, e) all systems, f) Big Fish River with juveniles from all systems.
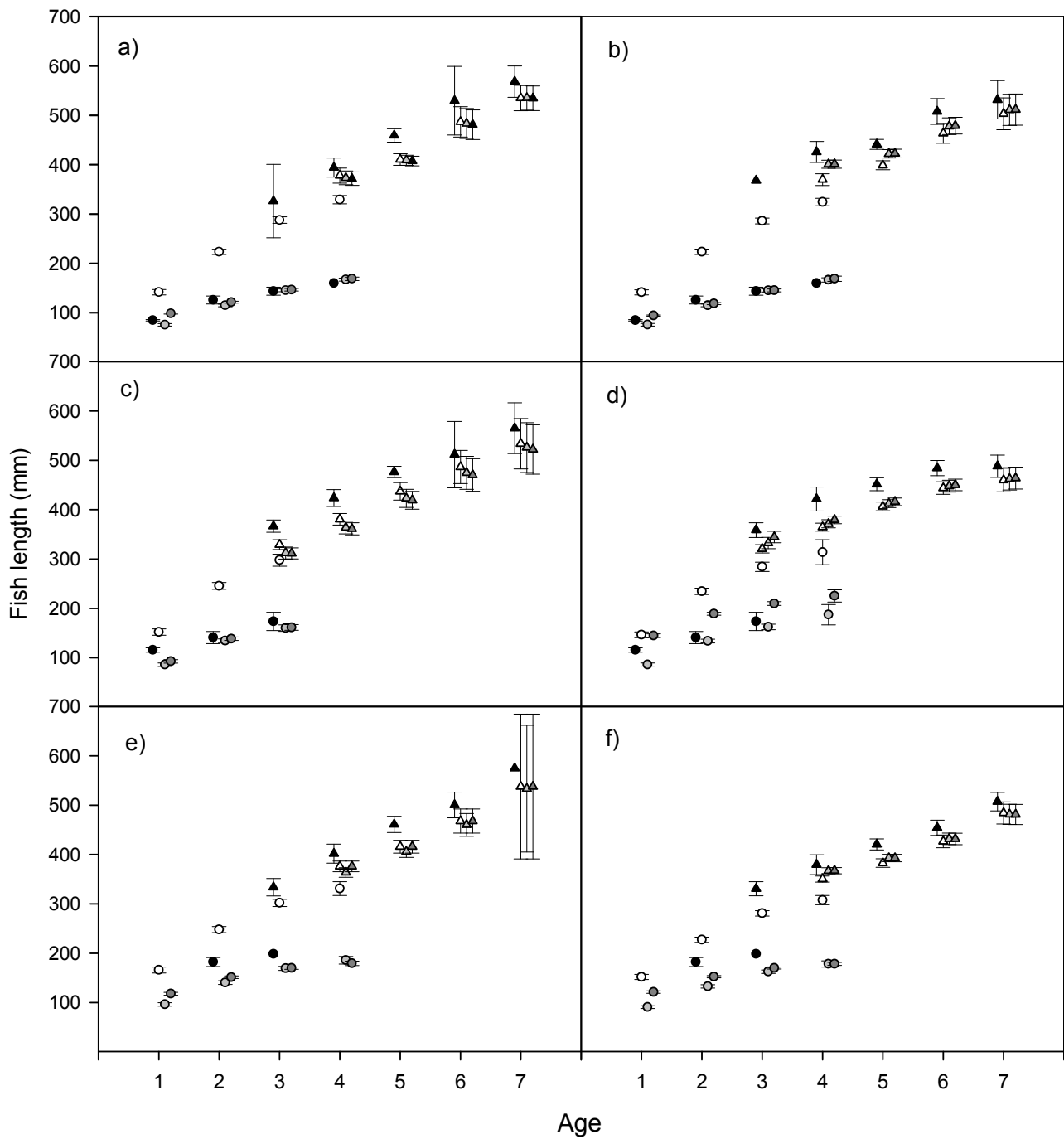
Figure 2.5 – Average size-at-age (±SE) of pre- (o) and post- (Δ) migratory Dolly Varden from capture data (■), and otolith back-calculations using the biological intercept method (□), the biological intercept breakpoint method (■), and the modified fry breakpoint method (■). Data is for: a) Rat River males, b) Rat River females, c) Babbage River males, d) Babbage River females, e) Big Fish River males, and f) Big Fish River females.
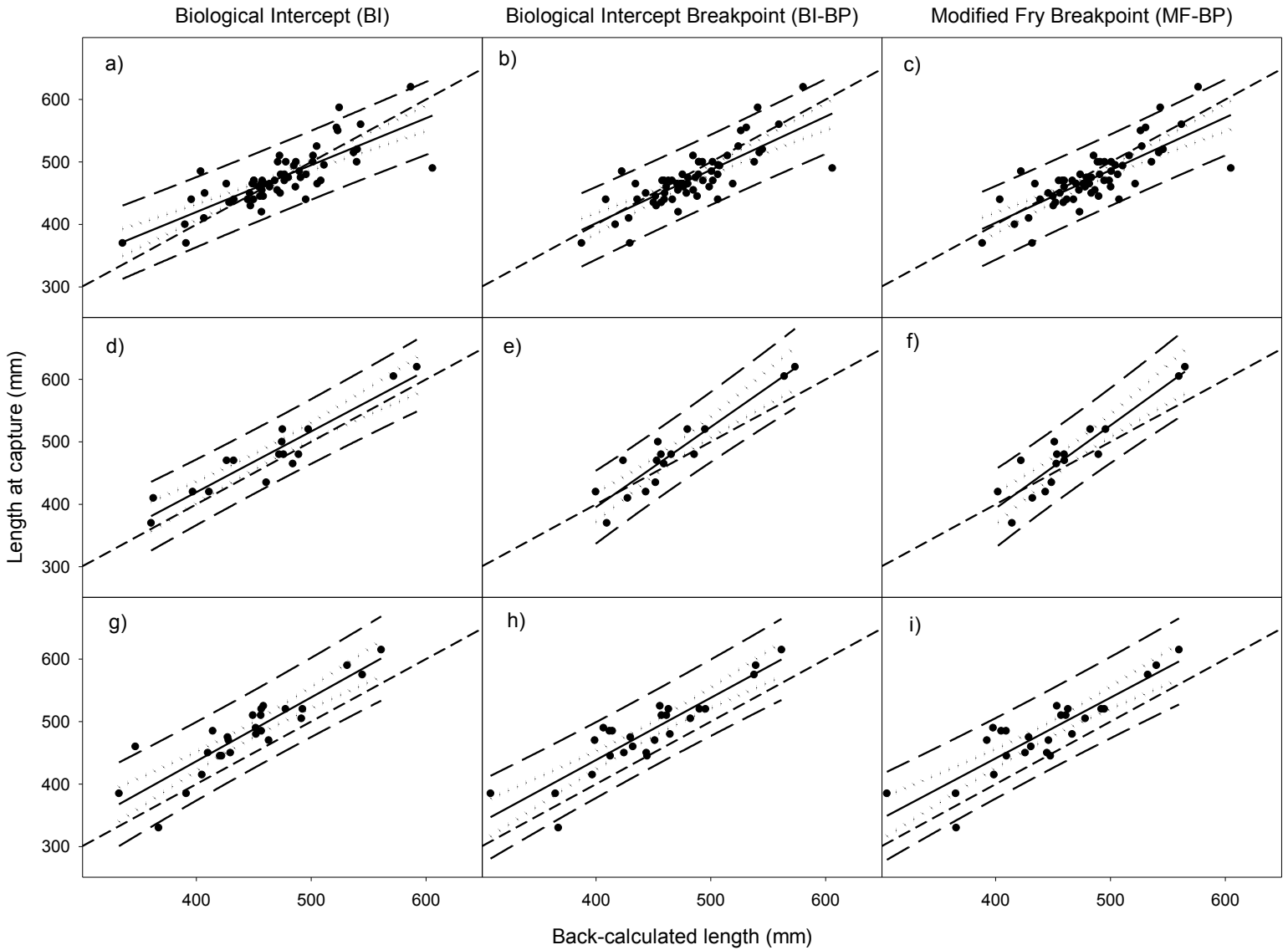
Figure 2.6 – Regressions of length at capture (mm) on back-calculated length (mm) using the biological intercept method (BI), the biological intercept breakpoint method (BI-BP), and the modified fry breakpoint method (MF-BP) for Dolly Varden from the a-c) Rat River, d-f) Babbage River, and g-i) Big Fish River. Solid lines (−) represent regressions, dotted lines (∙∙∙) represent 95% CI, long-dashed lines (– – –) represent prediction intervals, and short-dashed lines (- - -) represent a 1:1 relationship.
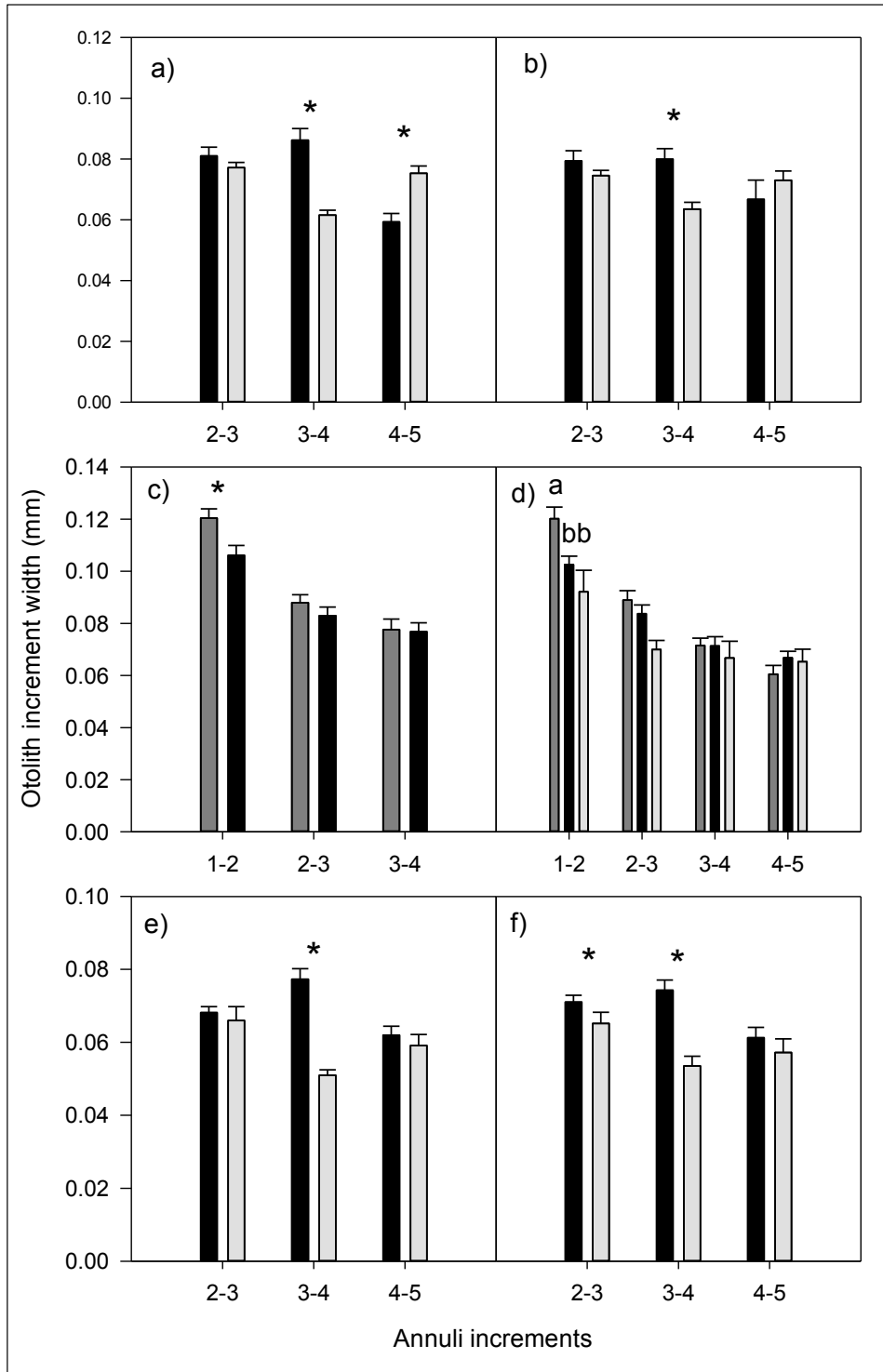
Figure 2.7 – Average Dolly Varden otolith increment widths (mm) (±SE) for a) Rat River males, b) Rat River females, c) Babbage River males, d) Babbage River females, e) Big Fish River males, and f) Big Fish River females. (■) Represents fish migrating at age 2, (■) represents fish migrating at age 3, and (■) represents fish migrating at age 4. * and letters represent significant differences (p<0.05).
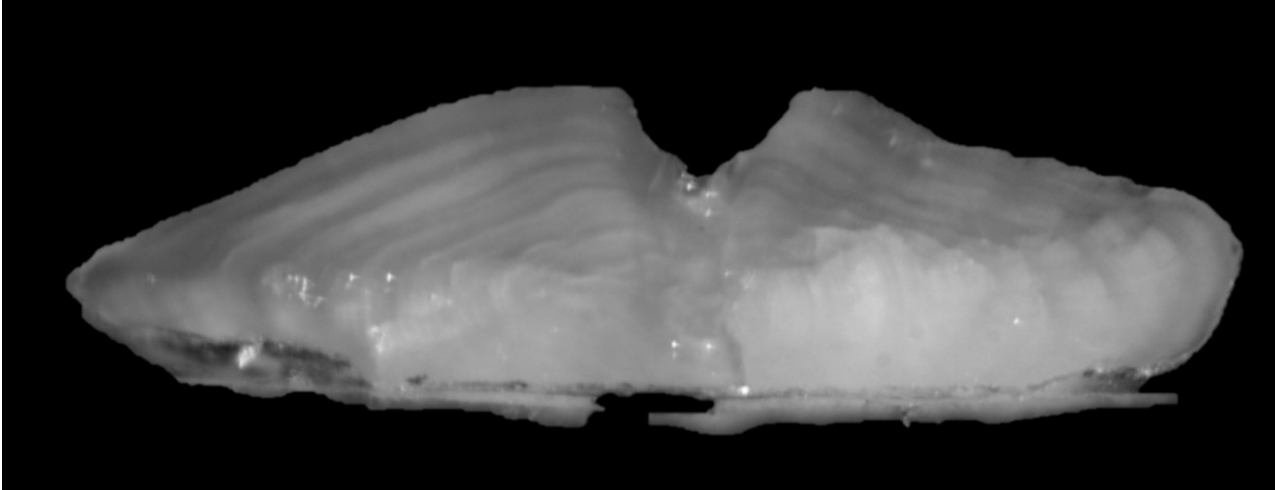
Figure 2.8 – Cross section of a Dolly Varden otolith from a 5-yr old that migrated at age 4.

Chapter 3: Assessing freshwater growth influences on life history 'decisions' in populations of northern form Dolly Varden

Introduction

Migration in salmonids is a well-studied phenomenon with the type and extent of migration varying among species and populations. Within species, populations can exhibit complete anadromy, complete residency, or partial anadromy. Partial anadromy (or partial migration) occurs when a proportion of the population migrate to sea (anadromous) while other individuals remain in freshwater as residents (Chapman et al. 2012, Jonsson and Jonsson 1993). This occurs in salmonid species such as Atlantic salmon (*Salmo salar*), brown trout (*S. trutta*), Arctic char (*Salvelinus alpinus*) (Klemetsen et al. 2003) and Dolly Varden (*S. malma*) (Armstrong and Morrow 1980). Partial migration has generally been viewed as a conditional mating tactic, where a single genotype can give rise to either resident or migratory individuals (Hendry et al. 2004, Jonsson and Jonsson 1993). Both forms may spawn together and produce either resident or anadromous offspring (Jonsson and Jonsson 1993, Nordeng 1983, Theriault et al. 2007).

Many populations that exhibit partial migration are polymorphic, with resident fish having slower growth, reaching smaller sizes, and displaying different morphologies than their anadromous counterparts (Jonsson and Jonsson 1993, Rikardsen and Elliott 2000). Anadromous individuals often delay maturity, but benefit from a longer lifespan, increased rate of growth, larger size at maturity, and increased reproductive output (Gross 1987, Hendry et al. 2004). However, disadvantages to anadromous behavior, include energy expenditure for migration and osmoregulation, and increased risk of predation. For example, a study conducted by Rikardsen et al. (1997) found a higher degree of mortality for anadromous Arctic char when in the marine environment compared with resident char in freshwater, although they found that generally anadromous char had longer lifespans than their resident counterparts.

In populations that exhibit partial anadromy, females tend to dominate the anadromous portion of the population, and males make up the larger proportion of residents (Hutchings and Jones 1998, Nordeng 1983). Jonsson et al. (2001), studying brown trout in 17 Norwegian

streams, determined that only 3.7% of adult females were resident, whereas male residents comprised almost 50% of the entire population. However, a 1:1 sex ratio is common in smolts in highly anadromous populations (Svennig et al. 1992, Rikardsen et al. 1997). A large size at maturity benefits females, which can produce more and/or larger eggs (Hendry et al. 2001, Loewen et al. 2010, Theriault et al. 2007), whereas in males reproductive output in the form of fertilization is dependent on the size, condition, and behavior of other males with whom they must compete (Hendry et al. 2004). While larger males are able to maintain a dominant position close to gravid females, and fight off competing males (Fleming and Gross 1994), precocious males that adopt a "sneak spawn" strategy are able to fertilize a substantial portion of eggs (Theriault et al. 2007) making migration potentially less beneficial to male salmonids.

It is still unclear as to why and when an individual 'decides' to adopt a migratory behaviour (Curry et al. 2010, Morinville and Rasmussen 2003, Wysujack et al. 2009) but migratory triggers are thought to occur early in life. An individual's 'decision' to migrate may be based on its condition, size, and/or status within the population (Hendry et al. 2004, Metcalfe et al. 1990), and is thought to relate to growth rates and metabolic processes (Jonsson and Jonsson 1993), however the observed patterns are equivocal. Generally fast growing fish from a population migrate earlier and at smaller sizes than slower growing individuals (Metcalfe et al. 1989, Metcalfe et al. 1990). Forseth et al. (1999) found that the fastest growing juvenile brown trout in a Norwegian stream migrated earlier and at smaller sizes than older juvenile migrants, and Theriault and Dodson (2003) found that larger individual brook trout (*Salvelinus fontinalis*) migrated earlier and determined that slow growth was associated with migration later in life at a larger size. When determining resident or anadromous behaviour, some studies have shown that faster growing fish become residents (Ricker 1938, Thorpe et al. 1998), while others have determined the opposite (Olsson et al. 2006, Rikardsen and Elliott 2000, Svenning et al. 1992). Rikardsen and Elliott (2000) found that in two populations of Arctic char, the largest fish became migrants at 4 years of age, medium-sized fish became migrants at 5 years of age, and the smallest fish matured as residents. Studying brook trout, Morinville and Rasmussen (2003) found that resident fish were larger by age 2 compared to their pre-migratory anadromous counterparts.

Not only do migratory behaviors vary among individuals within a population, but also between years and among populations (Hendry et al. 2004), indicating that environmental variation may be influential to determining migratory behaviour. Environmental variation occurs

in all systems, which differ in water chemistries, velocity, temperature, migration distance and elevation, area of suitable habitat, species composition, and overall productivity. For example, Forseth et al. (1999) found that the largest males from a population of brown trout in Norway remained in the stream as residents, while Jonsson (1985) found that the fastest and slowest growing brown trout within a different Norwegian lake system became anadromous, while medium growers became resident. Systems that vary in environmental conditions tend to produce populations with different migratory tendencies and also degrees of anadromy (Rikardsen et al. 1997). As an example, Curry et al. (2010) found that brook trout migratory patterns differed among three rivers systems, varying from almost complete anadromy to mainly resident.

Northern form Dolly Varden (*Salvenlinus malma malma*), herein referred to as Dolly Varden, are found in coldwater streams in Alaska, north of the Aleutian Islands, and the western Canadian Arctic, west of the Mackenzie Delta. Dolly Varden exhibit both anadromous and resident life histories within the same genetic population (Harris et al. 2015, McCart 1980, Reist 1989). During the summer months, after river ice-melt, anadromous Dolly Varden migrate to the Beaufort Sea where they feed in nearshore and offshore marine habitats (Brown et al. 2014, Courtney et al. 2016, Gallagher unpublished data), whereas resident Dolly Varden and pre-migratory juveniles remain within their natal streams. Females make up the larger proportion of the anadromous run, while resident populations are comprised almost entirely of males (Gallagher et al. 2012, McCart 1980).

While residents are an important component of these river systems, research has focused on the adult anadromous life history form and both resident and juvenile (pre-migratory) Dolly Varden in the western Arctic remain largely unstudied (Gallagher et al. 2012). Although both resident and anadromous life histories exist within Dolly Varden populations, the mechanisms behind individuals adopting one life history strategy over the other have not been examined. While studies in other salmonid species are more extensive, the mechanisms leading to different life history trajectories remain poorly understood (Curry et al. 2010, Morinville and Rasmussen 2003, Wysujack et al. 2009). Therefore, the objectives of my study are to 1) compare early freshwater growth in male resident and anadromous individuals from three river systems in the western Canadian Arctic in order to determine if and how growth influences residency and anadromy within Dolly Varden, and 2) determine whether or not there are differences in growth

patterns between Dolly Varden populations within different river systems in order to have population specific information to facilitate river specific co-management.

Materials and Methods

Study area and sampling methods

Dolly Varden were sampled from three genetically distinct stocks in the western Canadian Arctic: Rat, Big Fish, and Babbage rivers (Figure 1.2). Sampling of anadromous individuals occurred from 2012 to 2015 in conjunction with harvest monitoring programs that occur along the Beaufort Sea Coast at Shingle Point, sites along the Mackenzie Delta and the Rat River, and at the mouth of and spawning/overwintering site on the Big Fish River (Table **2.2**). Fish were captured along the coast and at the mouth of the rivers using either 90, 102, or 114 mm stretch-mesh gill nets with variable lengths and set times. Fish were captured at the overwintering site on the Big Fish River with a 16m-long modified seine net (see Sandstrom et al. 2009). Sample collection consisted of measuring and recording fork length (mm), weight (g), sex, and maturity stage. Sagittal otoliths were removed and placed in coin envelopes and a piece of fin tissue was stored in ethanol for DNA analysis (Gallagher et al. 2013, Harris et al. 2015).

Sampling of resident individuals occurred in the fall from 2012-2016 at the spawning/overwintering sites on the Rat, Big Fish, and Babbage rivers (Table **2.2**) in conjunction with mark-recapture programs. Fish were captured via a 16m-long modified seine net (see Sandstrom et al. 2009) and stored frozen until lab analysis, which included recording fork-length (mm), weight (g), sex, and removal of sagittal otoliths. All resident and anadromous samples were collected with permission from Inuvialuit and Gwich'in harvesters.

Otolith analysis

Due to the difficulties of sampling in remote northern regions, and obtaining individual growth information from small fish in the wild, otoliths were used in order to compare life history trajectories. Otoliths were aged whole following methods described by Gallagher et al.

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(2016) and Chilton and Beamish (1982). Age was determined by counting the narrow translucent winter growth bands (annuli) on each individual otolith. Otoliths were read by two separate readers with a Quality Assurance and Quality Control (QAQC) precision target of 5% between readers.

Otolith cross-sections were prepared following methods outlined in Gallagher et al. (2016). Otoliths were embedded in ColdCure[TM] epoxy resin, and once hardened, otoliths were sectioned across the nucleus, perpendicular to the sulcus with a Buehler Isomet slow speed saw (Buehler Ltd., Lake Bluff, Illinois) and diamond wafering blades. Otolith sections were polished with 0.3, 9, and 30 μm lapping film and imaged using a Nikon DXM1200 digital camera (Nikon Instruments Inc., Melville, New York) attached to a dissecting microscope.

Otolith Sr analysis was conducted in order to determine migratory patterns in anadromous individuals since otolith Sr concentrations can be used to infer the salinity levels encountered throughout the life of a fish (Zimmerman 2005). Sr concentrations in otoliths were analyzed using laser ablation inductively coupled plasma mass spectrometry (LA-ICP-MS) conducted at the University of Manitoba's Geological Sciences Department (Winnipeg, Manitoba) following preparation methods outlined in Howland et al. (2001), Loewen et al. (2015), and Swanson et al. (2010). Otolith sections were embedded in 1-inch Lucite discs using ColdCure[TM] epoxy, which were polished with 0.3, 9, and 30 μm lapping film with a final polish on a Buehler polishing wheel (Buehler Ltd., Lake Bluff, Illinois) with 0.05μm diamond grit paste. Prior to analysis, otolith discs were ultrasonically cleaned in distilled water. Transects were ablated from the otolith core to the outer edge of the dorsal lobe, following marked transects overlaid on digital images, using a Thermo Finnigan Element 2 High Resolution-Inductively Coupled Plasma-Mass Spectrometry (HR-ICP-MS) (Thermo Fisher Scientific Inc., Mississauga, Ontario) in combination with a Merchantek LUV 213 laser ablation system (New Wave Research/Merchantek, Fremont, California). Following LA-ICP-MS analyses, otoliths were imaged and Sr profiles were overlaid on the digital otolith images in order to align Sr concentrations with otolith annuli (Morris et al. 2005).

Back-calculation was conducted on otolith cross-sections in order to determine previous size-at-age for the first four years of life for resident fish and up until age at first migration for anadromous individuals. ImageJ 1.44 (National Institutes of Health, Bethesda, MD, USA) was used to measure the distance from the center of the nucleus to each annular increment along the

ventral lobe following a linear transect at 50-degree angle from the sulcus. Based on a linear relationship between fish length and otolith radius in resident fish, the biological intercept model (Campana 1990; Eqn. 3.1) was used to back-calculate size-at-age for resident individuals:

$$L_i = L_c + \frac{(O_i - O_c)(L_c - L_h)}{(O_c - O_h)} \qquad [3.1]$$

where L_i is the back-calculated length at a given age, L_c is the fish length at capture, L_h is the fish length at hatch, O_i is the otolith size at a given age, O_c is the otolith size at capture, and O_h is the otolith size at hatch. Otolith size and fish size at hatch was taken from the literature to be 0.06 and 16.5 mm, respectively (Armstrong and Morrow 1980, Blackett 1968, Radtke et al. 1996).

During first migration, there is a decoupling that occurs in the fish length – otolith length relationship, and therefore traditional back-calculation models overestimate size-at-age for anadromous individuals during the pre-migratory ontogenetic stage (Chapter 2). In order to accurately back-calculate size-at-age for post-migratory anadromous Dolly Varden, the newly derived biological intercept breakpoint method (Eqn. 3.2) was used:

$$L_i = \begin{cases} L_c + \dfrac{(L_c - L_{j1})(O_i - O_c)}{(O_c - O_j)} & \text{if } j \geq O'j \\[2em] L_{j2} + \dfrac{(L_{j2} - L_h)(O_i - O_j)}{(O_j - O_h)} & \text{if } j < O'j \end{cases} \qquad [3.2]$$

where L_{j1} is length at jump for post-migration, L_{j2} is length at jump for pre-migration, O_j is otolith size at the jump point, , and $O'j$ is individual otolith size at the jump. Individual jump points from pre- to post-migration were determined by individual otolith size at migration.

Statistical analysis

Age at migration was determined by examining Sr profiles overlaid on otolith images, and from threshold otolith Sr concentrations of anadromous and resident individuals by plotting overall Sr concentration maximum versus overall Sr range (maximum – minimum Sr) following

methods derived from Brown et al. (2007), Howland et al. (2009), and Howland et al. (2001). Natural occurring high levels of winter NaCl on the Big Fish River (Clark et al. 2001) produces Sr fluctuations in otoliths, with high Sr levels in the winter that are comparable to Sr levels at ocean migration, and low Sr levels in the summer that reflect freshwater levels in other river systems. The high-level winter Sr levels were accounted for by taking the mid-annuli values that reflect summer Sr levels instead of the overall maximum values. A Mann-Whitney rank sum test was used to compare mean ranges and maximums of distinct groupings representing freshwater and anadromous life histories. Age at first migration for an individual was determined by examining the Sr profile overlaid on the otolith image, and what group the individual fell into at each annuli for each river system based on the Sr concentration thresholds.

In order to determine differences in size at migration a 2-way ANOVA was run on size-at-age data, with river, and life history (early or late migration) as main effects, followed by post hoc Tukey HSD tests. Normality was determined with a Shapiro-Wilk test and equality of variance was determined with a Levene's test. Results were considered significant at alpha $\leq$ 0.05. Size at migration was based on size at annuli formation in the year an individual underwent its first migration, and not the specific size at out-migration.

Fish growth was determined by subtracting previous size-at-age from size-at-age for the year in question. The mixed effects model by Weisberg et al. (2010) was used to determine growth differences among life history trajectories and river systems while controlling for cohort and individual variation in growth. The model is as follows:

$$y_{cka} = i_a + yg_{ck} + yj_{ck} + h_{c+a-1} + (ih)_{a,c+a-1} + f_{ck} + e_{cka} \qquad [3.3]$$

where y_{cka} is the ath annual increment for the kth fish from cohort c, i_a is the annual increment at year of life a, yg_{ck} is the life history trajectory for individual k, yj_{ck} is used to represent the river system for individual k, h_{c+a-1} represents random environmental effects, $(ih)_{a,c+a-1}$ is a random effects interaction term, f_{ck} denotes random fish effects, and e_{cka} represents independent errors with mean zero and common variance σ^2. Linear models with different levels of fixed effects and fixed effect interactions were calculated using maximum likelihood estimation and compared using Akaike information criteria in order to determine the best fit model for describing growth at age (Zuur et al. 2009). The best fit model was then calculated using restricted maximum

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likelihood estimation. Interaction comparisons were conducted with post hoc Tukey HSD with significance determined at alpha ≤ 0.05.

All statistical analyses were completed in R Studio (RStudio Team, 2016). Data presentation was completed using Sigmaplot 12.5 (Systat Software Inc.). Only male fish were used in the study due to the limited number of female resident samples (n=2).

Results

Age and size at migration

Sr maximum-range plots for the Rat, Babbage, and Big Fish rivers showed distinct freshwater (group 1) and anadromous (group 2) groupings (p<0.001; Table **3**.**1**; Figure 2.1). Anadromous Sr thresholds for the Rat, Babbage, and Big Fish River maxima values were ≥ 1986mg/kg, 2235mg/kg, and 1969mg/kg, and for the range were ≥ 1778mg/kg, 1994mg/kg, and 1092mg/kg respectively. Based on the Sr maximum-range plot thresholds, age estimates derived from otoliths, and Sr profiles overlain on otolith images, the majority of individuals undergoing their first migration occurred at age 2 and 3 on the Babbage River, and age 3 and 4 on the Big Fish and Rat rivers (Table **3**.**2**). Based on age-at-migration, early migrants were classified as individuals that migrated at 2 years on the Babbage River and 3 years on the Big Fish and Rat rivers, while late migrants were classified as individuals that migrated at 3 years on the Babbage River and 4 years on the Big Fish and Rat rivers. Age 2 (Big Fish and Rat rivers), age 4 (Babbage River) and age 5 (all systems) were not included in further analysis due to small sample sizes (Big Fish and Rat age 2 n=2; Babbage age 4 n=3; all systems age 5 n=3).

Results (Figure **3**.**1**) indicated that differences in size at migration occurred among river systems (2-way ANOVA, $F_{2,206}=61.2$, p<0.001), with all rivers exhibiting different average sizes at migration (Babbage – Big Fish: p<0.0001; Babbage – Rat: p=0.007; Big Fish – Rat: p<0.0001), ranging from largest in the Big Fish River to smallest on the Babbage River (average size at migration ± SE: 158±2mm on the Rat, 179±2mm on the Big Fish, and 151±2mm on the Babbage). There were also differences between early and late migrants (2-way ANOVA: $F_{1,206}=67.2$, p<0.001), with early migrants being smaller than late migrants (average size at

migration ± SE: 149mm ± 3mm for early and 167mm ± 2mm for late on the Rat River, 172mm ± 2mm for early, and 186mm ± 3mm for late on the Big Fish River, and 142mm ± 2mm for early and 160mm ± 3mm for late on the Babbage River). The smallest size at migration was recorded as 113mm from an early migrant from the Babbage River, while the largest was 209mm from a late migrant from the Big Fish River. The river*migration interactions was not significant (2-way ANOVA: $F_{2,206}$=0.5, p=0.624).

Life history and river differences

The best model for describing growth (determined by the lowest AIC value) included age, life history (resident, early migrant, late migrant), river system, and interaction terms between age and life history, and between age and river, all while controlling for variation among cohorts and individuals (Table **3.3**). This model indicated that yearly juvenile growth differed significantly among ages (F=3267.4, p<0.0001), among life history trajectories (F=25.9, p<0.0001), and among river systems (F=78.2, p<0.0001). It also indicated that growth differences among the rivers and life history trajectories depended on age (F=34.7, p<0.0001 and F=7.6, p<0.0001, respectively).

When comparing life history trajectories across ages, I found that at age 1 there was no difference between resident and early migrating individuals (t_{1475}=-1.8, p=0.814). However, there is an observable trend of residents having a higher average growth compared to early migrating Dolly Varden on the Rat River at age 1 (Figure **3.2**). Late migrating fish had the slowest growth at age 1 compared to early migrants (t_{1466}=6.1, p<0.0001) and residents (t_{1272}=-8.4, p<0.0001) in all rivers. No difference was found between early and late migrating (t_{1466}=0.437, p=1.0) and between early migrating and resident (t_{1475}=-3.1, p=0.0799) Dolly Varden at age 2. However, Figure **3.2** suggests a trend towards increased growth at age 2 for residents compared to early migrants on the Rat River and for early migrants compared to late migrants on the Babbage River. Across the river systems, late migrating fish had lower growth at age 2 compared to residents (t_{1272}=-3.3, p=0.0426). No differences in growth were observed at ages 3 and 4, although Figure **3.2** indicates a trend towards increased growth in aged 3 residents on the Big Fish River. Based on the observed growth trajectories residents had the largest size-at-age. However, there is considerable overlap with early migrants, especially in the Babbage River at

all ages, and age 1 on the Rat and Big Fish rivers (Figure **3**.**2**). Late migrating fish consistently had smaller size-at-age compared to early migrating and resident Dolly Varden.

In overall comparisons among rivers, age 1 Dolly Varden from the Big Fish River had the highest average growth compared to fish from the Babbage (t_{1479}=-8.6, p<0.0001) and Rat (t_{1476}=14.6, p<0.0001) rivers, with fish from the Rat River having the lowest average growth (t_{1459}=5.2, p<0.0001). At age 2, Babbage River fish had the highest average growth compared to fish from the Big Fish (t_{1479}=3.9, p=0.0057) and Rat (t_{1459}=7.4, p<0.0001) rivers, while again the Rat River had the lowest average growth (t_{1476}=3.8, p=0.0098). However, this pattern was not noticeable in late migrating fish, where Figure **3**.**3** indicates growth for age 2 fish is the same between the Big Fish and Babbage rivers. No statistical differences in growth were observed at ages 3 and 4. However, Figure **3**.**3** indicates higher growth for age 3 late migrating fish and age 4 residents on the Babbage River. Based on the observed growth trajectories, Rat River Dolly Varden have the smallest size-at-age compared to Dolly Varden from the Big Fish and Babbage rivers (Figure **3**.**3**). While Babbage River size-at-age was initially smaller than Big Fish River, increased growth between years 1 and 2 and possibly later shows Babbage River reaching comparable size trajectories by age 2 for early migrants and age 3 for resident and late migrants (Figure **3**.**3**).

Discussion

Age and size at migration

Reconstructing growth patterns and size-at-age from Dolly Varden otoliths demonstrated the fastest growing fish in a population became either resident or early migrants while slow growth was associated with migrating later in life. This pattern of size differences between early and late migrating Dolly Varden is consistent with numerous studies on other salmonids such as Arctic char (Rikardsen and Elliott 2000, Svenning et al. 1992), brook trout (Morinville and Rasmussen 2003, Theriault and Dodson 2003), brown trout (Forseth et al. 1999, Jonsson 1985), and Atlantic salmon (Jonsson et al. 1998, Metcalfe et al. 1988). Anadromous migration is often considered a size-dependent tactic since a certain threshold size is needed for osmoregulation

(Conte and Wagner 1965, McCormick and Saunders 1987). Even after reaching threshold sizes, smaller-sized individuals have higher costs associated with energy expenditure for migration and osmoregulation, as well as an increase in predation mortality (Hendry et al. 2004). Therefore, slower growing fish benefit from delaying migration until the following year.

Within each river system the fish that had the least growth by age 1 delayed migration and migrated at 3+ on the Babbage River, and 4+ on the Big Fish and Rat rivers. However, size-at-migration appears to differ by river system, with individuals on the Big Fish River undergoing first migration at much larger sizes compared to those on the Babbage and Rat rivers. While initially experiencing increased growth, Big Fish Dolly Varden reach similar pre-migration size-at-age compared to those on the Babbage River, indicating similar freshwater growth potentials and productivity between the two systems. Differences in age and size at migration may be due to genetic differences among populations. Evidence suggests that there is a genetic basis for the timing of within-year smolt migration (Achord et al. 2007, Nielsen et al. 2001, Stewart et al. 2006, Thorstad et al. 2012), which may extend to genetic difference between years. Okland et al. (1993) suggested that fish with lower metabolic rates have increased difficulties with osmoregulation in marine environments. While the extent of metabolic differences among populations is unknown, it is likely that there are genetic differences due to local adaptations.

Adaptation to local environmental conditions in the Big Fish River has possibly led to a slight increase in size-at-migration due to increased costs associated with smoltification. While the Big Fish and Babbage rivers have similar migration distance (131km and 145km respectively), they differ in relation to freshwater environments. The Babbage River exhibits winter water temperatures around 4°C, while the Big Fish River is characterized by warm winter water temperatures ranging from 8-16°C, a high mineral content, and low oxygen levels (Mochnacz et al. 2010). The process of smoltification requires sufficient dissolved oxygen (DO) (Stefansson et al. 2008), and while DO levels do not appear to hamper the onset of smoltification, low DO levels may be playing a role in the delayed migration observed on the Big Fish River. Evidence also suggests that water quality can influence smoltification (McCormick and Saunders 1987, Stefansson et al. 2008). Other plausible reasons for this size discrepancy in migration is that the Big Fish River may experience higher predation rates (Gallagher, unpublished data), thus larger fish may be at an advantage during first migration compared to smaller individuals, leading to a genetic shift in size-at-migration.

Similarities were found between size-at-migration of Dolly Varden from the Rat and Babbage rivers, with Rat River individuals taking an extra year to reach similar migrating sizes compared to individuals on the Babbage River. While migration distance is vastly different on these systems, 316km and 145km for the Rat and Babbage rivers respectively, downstream migration is associated with low energy expenditure, as fish can passively drift downstream with high velocity flows (Stefansson et al. 2008), thus large differences in migration size were not expected between these systems. Delayed age at migration on the Rat River compared to the Babbage appears to be a function of size and growth and not related to fish age, suggesting that the Rat River has a lower productivity compared to the Babbage River.

Overall results indicate that a threshold size must be obtained prior to the onset of smoltification in Dolly Varden, and that age is not a determining factor for first migration. Reaching this threshold size however, does not guarantee smoltification. There also appears to be a strong environmental and/or genetic component governing size-at-first migration, which differs among river system.

Resident versus anadromous life history

Comparing between resident and anadromous Dolly Varden indicate that resident individuals do not differ in growth compared to early migrants. This is consistent with findings by Morinville and Rasmussen (2003) and Theriault and Dodson (2003). However, residents from the Rat and Big Fish rivers had a trend towards increased size at age 1 and 2, and age 2 and 3, respectively. This discrepancy among rivers is likely due to local genetic adaptations and different environmental characteristics that lead to different growth patterns among systems and life histories. Similar to our findings on the Rat and Big Fish rivers, Morinville and Rasmussen (2003) found that although no statistical differences were observed between resident and anadromous growth rates, there was an observable trend of larger size-at-age in resident fish compared with their anadromous counterparts.

Growth simulations by Hutchings and Jones (1998) indicate that early growth favours early maturation instead of migration. According to Thorpe (1994) maturation at a young age is the goal of an individual in order to maximize fitness. Therefore, once a threshold size has been reached, an individual should mature and become a resident. This coincides with general life

history theory about maximizing fitness by maturing at a young age. Since size in males does not necessarily bring about an advantage in fitness potential (Hendry et al. 2004), migration becomes a less desirable tactic. Thorpe et al.'s (1998) model of maturation versus migration is slightly more complex with numerous thresholds being met at given time periods. Those individuals who do not meet certain maturation size thresholds can choose to migrate and benefit by having a better competitive advantage for reproduction once mature, due to an increase in growth obtained during marine migration. However, this tactic carries the risk of increased predation and delays maturation by a considerable number of years. Resident Dolly Varden have been known to mature as young as age 2, while maturation in anadromous individuals often does not occur until a couple years after first migration at ages 5-6 (McCart 1980).

My findings of similar growth and size-at-age between resident and pre-migratory juveniles indicates that growth is not the only driver of life history 'decisions'. Studies have suggested that other factors, such as metabolic rate, social status, growth efficiencies, and lipid stores may also contribute to migratory 'decisions' (Jonsson and Jonsson 2003, Metcalfe 1998, Metcalfe et al. 1989, Metcalfe et al. 1995, Morinville and Rasmussen 2003, Rowe et al. 1991). Morinville and Rasmussen (2003) studied brook trout and found that although residents had increased size-at-age, future anadromous individuals had consumption rates 1.4 times higher than residents but lower growth efficiencies and higher total metabolic costs. The pre-migratory anadromous brook char in their study allocated 38-53% of their energy towards metabolism compared to 25-45% by residents. Forseth et al. (1999) studied freshwater migration and residency of brown trout and determined that while there were no differences in growth, consumption rates were higher in migrating trout compared to residents, and metabolic costs were considerably higher in migrating individuals. Morinville and Rasmussen (2003) proposed that the variation in metabolic rates seen in resident and anadromous individuals could either be results of differences in activity levels, or differences in standard metabolic rate. Aggressive behaviour is often linked to early migrating individuals as opposed to residents or late migrants (Lahti et al. 2002, Metcalfe et al. 1995, Metcalfe and Thorpe 1992). Metcalfe (1998) suggested that dominant individuals tend to be more aggressive, which leads to energetic costs and a decrease in growth potential. Metcalfe et al. (1995) also demonstrated that fish with lower standard metabolic rates migrate later in life compared to early migrants, indicating that metabolic differences are also likely between residents and early migrants. Fish that migrate

early, and do not remain as stream residents, may become growth limited and thus migrate to more productive habitats in order to satisfy metabolic costs.

Conclusions

With climate change bringing warmer temperatures, there is a potential for changing growth patterns in fishes occupying northern freshwater systems. Increased growth in these systems may lead to a change in size and age at migration, or an increase in residency over anadromy. However, this will be dependent on evolutionary 'switch points' within a population, the potential for density-dependent fitness, as well as the importance of metabolic drivers of life history trajectories. Studies have shown that increasing stream productivity can lead to a decrease in anadromy (Jonsson et al. 2013, Nordeng 1983, Olsson et al. 2006, Wysujack et al. 2009). The *Salvelinus* genus is known to be the 'least' anadromous compared to the *Oncorynchus* and *Salmo* genera (Rounsfell 1958), indicating that a decrease in anadromy is highly possible in Dolly Varden populations if climate change were to bring increased productivity to the region (barring any other detrimental effects to river systems in the region).

My study suggests that growth is an important factor in determining life history trajectories, specifically between early and late migration. Numerous factors can influence growth rate, such as egg size, time of hatch, time of emergence, first feeding, habitat availability, and climate variability. Any change in these factors has the potential to influence a population's growth rate and potentially life history trajectories. While Dolly Varden in my study showed a difference in growth between early and late migratory individuals, there was still considerable overlap in growth at age, indicating that other factors besides growth control an individual's migratory 'decisions'. Likewise, this research provides further evidence to support the importance of factors other than growth between anadromy and residency, such as growth efficiencies and metabolic rate. Further research on the contribution of metabolic rate to life history 'decisions' is needed in order to accurately reflect all factors that influence life history trajectories.

Literature Cited

Achord, S., Zabel, R.W., and Sandford, B.P. 2007. Migration timing, growth, and estimated parr-to-smolt survival rates of wild snake river spring-summer Chinook salmon from the salmon river basin, Idaho, to the Lower Snake River. Transactions of the American Fisheries Society **136**(1): 142-154.

Armstrong, R.H., and Morrow, T.E. 1980. The Dolly Varden charr, *Salvelinus malma malma*. *In* Charrs, salmonid fishes of the genus *Salvelinus*. *Edited by* E.K. Balon. Hague: W. Junk, pp. 99-139.

Blackett, R.F. 1968. Spawning behavior, fecundity, and early life history of anadromous Dolly Varden, *Salvelinus malma* (Walbaum) in Southeastern Alaska. Alaska Department of Fish and Game Research Report **6**:1-85.

Brown, R.J., Bickford, N., and Severin, K. 2007. Otolith trace element chemistry as an indicator of anadromy in Yukon River drainage coregonine fishes. Transactions of the American Fisheries Society **136**(3): 678-690.

Brown, R.J., Loewen, M.B., and Tanner, T.L. 2014. Overwintering locations, migrations, and fidelity of radio-tagged Dolly Varden in the Hulahula River, Arctic National Wildlife Refuge, 2007-09. Arctic **67**(2): 149-158.

Campana, S.E. 1990. How reliable are growth back-calculations based on otoliths. Canadian Journal of Fisheries and Aquatic Sciences **47**(11): 2219-2227.

Chapman, B.B., Hulthen, K., Brodersen, J., Nilsson, P.A., Skov, C., Hansson, L.A., and Bronmark, C. 2012. Partial migration in fishes: causes and consequences. Journal of Fish Biology **81**(2): 456-478.

Chilton, D.E., and Beamish, R.J. 1982. Age determination methods for fishes studied by the Groundfish Program at the Pacific Biological Station. Can. Spec. Publ. Fish. Aquat. Sci. p. 102.

Conte, F.P., and Wagner, H.H. 1965. Development of osmotic and ionic regulation in juvenile steelhead trout *Salmo gairdneri*. Comparative Biochemistry and Physiology **14**(4): 603-620.

Courtney, M.B., Scanlon, B.S., Rikardsen, A.H., and Seitz, A.C. 2016. Marine behavior and dispersal of an important subsistence fish in Arctic Alaska, the Dolly Varden. Environmental Biology of Fishes **99**: 209-222.

Curry, R.A., Bernatchez, L., Whoriskey, F., and Audet, C. 2010. The origins and persistence of anadromy in brook charr. Reviews in Fish Biology and Fisheries **20**(4): 557-570.

Fleming, I.A., and Gross, M.R. 1994. Breeding competition in a Pacific salmon (coho, *Oncorhynchus kisutch*): measures of natural and sexual selection. Evolution **48**(3): 637-657.

Forseth, T., Naesje, T.F., Jonsson, B., and Harsaker, K. 1999. Juvenile migration in brown trout: a consequence of energetic state. Journal of Animal Ecology **68**(4): 783-793.

Gallagher, C.P., Howland, K.L., and Wastle, R.J. 2016. A comparison of different structures and methods for estimating age of northern-form Dolly Varden *Salvelinus malma malma* from the Canadian Arctic. Polar Biology **39**(7): 1257-1265.

Gallagher, C.P., K.L., R., Harris, L.N., Banjo, R., Sandstrom, S., Loewen, T., and Reist, J. 2013. Dolly Varden (*Salvelinus malma malma*) from the Big Fish River: abundance estimates, effective population size, biological characteristics, and contribution to the coastal mixed-stock fishery. DFO Can. Sci. Advis. Sec. Res. Doc. p. v + 46 p.

Gallagher, C.P., Roux, M.J., Howland, K.L., and Tallman, R.F. 2012. Synthesis of biological and harvest information used to assess populations of northern form Dolly Varden (*Salvelinus malma*

malma) in Canada. Part III: Comparison among populations. . DFO Can. Sci. Advis. Sec. Res. . p. vi + 81 p.

Gross, M.R. 1987. Evolution of diadromy in fishes. American Fisheries Society Symposium **1**:14-25.

Harris, L.N., Bajno, R., Gallagher, C.P., Koizumi, I., Johnson, L.K., Howland, K.L., Taylor, E.B., and Reist, J.D. 2015. Life-history characteristics and landscape attributes as drivers of genetic variation, gene flow, and fine-scale population structure in northern Dolly Varden (*Salvelinus malma malma*) in Canada. Canadian Journal of Fisheries and Aquatic Sciences **72**(10): 1477-1493.

Hendry, A.P., Bohlin, T., Jonsson, B., and Berg, O.K. 2004. To sea or not to sea? Anadromy versus non-anadromy in salmonids. *In* Evolution illuminated: salmon and their relatives. *Edited by* A.P. Hendry and S.C. Stearns. Oxford University Press, pp.92-125.

Hendry, A.P., Day, T., and Cooper, A.B. 2001. Optimal size and number of propagules: Allowance for discrete stages and effects of maternal size on reproductive output and offspring fitness. American Naturalist **157**(4): 387-407.

Howland, K.L., Babaluk, J.A., Chiperzak, D., Tallman, R.F., and Low, G. 2009. Variability in diadromous behavior of a northern coregonid based on scanning proton microprobe analysis of otolith strontium. Challenges for Diadromous Fishes in a Dynamic Global Environment **69**: 121-134.

Howland, K.L., Tonn, W.M., Babaluk, J.A., and Tallman, R.F. 2001. Identification of freshwater and anadromous inconnu in the Mackenzie river system by analysis of otolith strontium. Transactions of the American Fisheries Society **130**(5): 725-741.

Hutchings, J.A., and Jones, M.E.B. 1998. Life history variation and growth rate thresholds for maturity in Atlantic salmon, *Salmo salar*. Canadian Journal of Fisheries and Aquatic Sciences **55**: 22-47.

Jonsson, B. 1985. Life-history patterns of fresh-water resident and sea-run migrant brown trout in Norway. Transactions of the American Fisheries Society **114**(2): 182-194.

Jonsson, B., and Jonsson, N. 1993. Partial migration: niche shift versus sexual maturation in fishes. Reviews in Fish Biology and Fisheries **3**(4): 348-365.

Jonsson, B., Jonsson, N., Brodtkorb, E., and Ingebrigtsen, P.J. 2001. Life-history traits of brown trout vary with the size of small streams. Functional Ecology **15**(3): 310-317.

Jonsson, B., Jonsson, N., and Finstad, A.G. 2013. Effects of temperature and food quality on age and size at maturity in ectotherms: an experimental test with Atlantic salmon. Journal of Animal Ecology **82**(1): 201-210.

Jonsson, N., and Jonsson, B. 2003. Energy allocation among developmental stages, age groups, and types of Atlantic salmon (*Salmo salar*) spawners. Canadian Journal of Fisheries and Aquatic Sciences **60**(5): 506-516.

Jonsson, N., Jonsson, B., and Hansen, L.P. 1998. Long-term study of the ecology of wild Atlantic salmon smolts in a small Norwegian river. Journal of Fish Biology **52**(3): 638-650.

Klemetsen, A., Amundsen, P.A., Dempson, J.B., Jonsson, B., Jonsson, N., O'Connell, M.F., and Mortensen, E. 2003. Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories. Ecology of Freshwater Fish **12**(1): 1-59.

Lahti, K., Huuskonen, H., Laurila, A., and Piironen, J. 2002. Metabolic rate and aggressiveness between brown trout populations. Functional Ecology **16**(2): 167-174.

Loewen, T.N., Gillis, D., and Tallman, R.F. 2010. Maturation, growth and fecundity of Arctic charr, *Salvelinus alpinus* (L.), life-history variants co-existing in lake systems of Southern Baffin Island, Nunavut, Canada. Hydrobiologia **650**(1): 193-202.

Loewen, T.N., Reist, J.D., Yang, P., Koleszar, A., Babaluk, J.A., Mochnacz, N., and Halden, N.M. 2015. Discrimination of northern form Dolly Varden Char (*Salvelinus malma malma*) stocks of the North Slope, Yukon and Northwest Territories, Canada via otolith trace elements and Sr-87/Sr-86 isotopes. Fisheries Research **170**: 116-124.

McCart, P.J. 1980. A review of the systematics and ecology of Arctic char, Salvelinus alpinus, in the Western Arctic. Can. Tech. Rep. Fish. Aquat. Sci. 935: vii + 89p.

McCormick, S.D., and Saunders, R.L. 1987. Preparatory physiological adaptations for marine life of salmonids: osmoregulation, growth, and metabolism. American Fisheries Symposium **1**:211-229.

Metcalfe, N.B. 1998. The interaction between behavior and physiology in determining life history patterns in Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences **55**: 93-103.

Metcalfe, N.B., Huntingford, F.A., Graham, W.D., and Thorpe, J.E. 1989. Early social status and the development of life-history strategies in Atlantic salmon. Proceedings of the Royal Society Series B-Biological Sciences **236**(1282): 7-19.

Metcalfe, N.B., Huntingford, F.A., and Thorpe, J.E. 1988. Feeding intensity, growth rates, and the establishment of life-history patterns in juvenile Atlantic salmon *Salmo salar*. Journal of Animal Ecology **57**(2): 463-474.

Metcalfe, N.B., Huntingford, F.A., Thorpe, J.E., and Adams, C.E. 1990. The effetcs of social status on life history variation in juvenile salmon. Canadian Journal of Zoology **68**(12): 2630-2636.

Metcalfe, N.B., Taylor, A.C., and Thorpe, J.E. 1995. Metabolic rate, social status and life history strategies in Atlantic salmon. Animal Behaviour **49**(2): 431-436.

Metcalfe, N.B., and Thorpe, J.E. 1992. Early predictors of life-history events: the link between 1st feeding date, dominance and seaward migration in Atlantic salmon *Salmo salar* L.. Journal of Fish Biology **41**: 93-99.

Mochnacz, N.J., Schroeder, B.S., Sawatzky, C.D., and Reist, J.D. 2010. Assessment of northern Dolly Varden, Salvelinus malma malma (Walbaum, 1792), habitat in Canada. Canadian Manuscript Report of Fisheries and Aquatic Sciences 2926: i-vi, 1-48.

Morinville, G.R., and Rasmussen, J.B. 2003. Early juvenile bioenergetic differences between anadromous and resident brook trout (Salvelinus fontinalis). Canadian Journal of Fisheries and Aquatic Sciences **60**(4): 401-410.

Morris, J.A., Rulifson, R.A., Babaluk, J.A., May, P.G., and Campbell, J.L. 2005. Use of micro-PIXE to investigate otolith Sr distributions of the anadromous striped bass, *Morone saxatilis*. X-Ray Spectrometry **34**(4): 301-305.

Nielsen, C., Holdensaard, G., Petersen, H.C., Bjornsson, B.T., and Madsen, S.S. 2001. Genetic differences in physiology, growth hormone levels and migratory behaviour of Atlantic salmon smolts. Journal of Fish Biology **59**(1): 28-44.

Nordeng, H. 1983. Solution to the char problem based on arctic char (*Salvelinus alpinus*) in Norway. Canadian Journal of Fisheries and Aquatic Sciences **40**(9): 1372-1387.

Okland, F., Jonsson, B., Jensen, A.J., and Hansen, L.P. 1993. Is there a threshold size regulating seaward migration of brown trout and Atlantic salmon. Journal of Fish Biology **42**(4): 541-550.

Olsson, I.C., Greenberg, L.A., Bergman, E., and Wysujack, K. 2006. Environmentally induced migration: the importance of food. Ecology Letters **9**(6): 645-651.

Radtke, R.L., Fey, D.P., DeCicco, A.F., and Montgomery, A. 1996. Otolith microstructure in young-of-the-year Dolly Varden, *Salvelinus malma*, from American and Asian populations: Resolution of comparative life history characteristics. Arctic **49**(2): 162-169.

Reist, J.D. 1989. Genetic structuring of allopatric populations and sympatric life history types of charr, *Salvelinus alpinus/malma*, in the western Arctic, Canada. *In* Biology of Charrs and Masu Salmon, special volume 1. Edited by K. Hiroya, Y. Fumio and L.G.N. David Physiology and Ecology Japan Editorial Office, Kyoto, Japan, pp.405-420.

Ricker, W.E. 1938. "Residual" and kokanee salmon in Cultus lake. Journal of the Fisheries Research Board of Canada **4a**(3): 192-218.

Rikardsen, A.H., and Elliott, J.M. 2000. Variations in juvenile growth, energy allocation and life-history strategies of two populations of Arctic charr in North Norway. Journal of Fish Biology **56**(2): 328-346.

Rikardsen, A.H., Svenning, M.A., and Klemetsen, A. 1997. The relationships between anadromy, sex ratio and parr growth of Arctic charr in a lake in North Norway. Journal of Fish Biology **51**(3): 447-461.

Rounsfell, G.A. 1958. Anadromy in North American Salmonidae. Fish. Bull. Wildl. Serv. pp. 171-185.

Rowe, D.K., Thorpe, J.E., and Shanks, A.M. 1991. Role of fat stores in the maturation of male atlantic salmon (*Salmo salar*) parr. Canadian Journal of Fisheries and Aquatic Sciences **48**(3): 405-413.

Sandstrom, S., Harwood, L., and Howland, K. 2009. Status of anadromous Dolly Varden char (*Salvelinus malma*) of the Rat River, Northwest Territories, as assessed through mark-recapture and live-sampling at the spawning and over-wintering site (1995-2007). Can. Tech. Rep. Fish. Aqua. Sci. p.75.

Stefansson, S.O., Björnsson, B.T., Ebbesson, L.O.E., and McCormick, S.D. 2008. Smoltification. *In* Fish Larval Physiology. *Edited by* R.N. Finn and B.G. Kapoor, B.G. Science Publishers, Enfield, NH, pp. 639-681.

Stewart, D.C., Middlemas, S.J., and Youngson, A.F. 2006. Population structuring in Atlantic salmon (*Salmo salar*): evidence of genetic influence on the timing of smolt migration in sub-catchment stocks. Ecology of Freshwater Fish **15**(4): 552-558.

Svenning, M.A., Smith-Nilsen, N., and M., J. 1992. Sea water migration of arctic charr (*Salvelinus alpinus* L.) - Correlation between freshwater growth and seawater migration, based on back-calculation from otoliths. Nordic Journal of Freshwater Research **67:**18-26.

Swanson, H.K., Kidd, K.A., Babaluk, J.A., Wastle, R.J., Yang, P.P., Halden, N.M., and Reist, J.D. 2010. Anadromy in Arctic populations of lake trout (*Salvelinus namaycush*): otolith microchemistry, stable isotopes, and comparisons with Arctic char (*Salvelinus alpinus*). Canadian Journal of Fisheries and Aquatic Sciences **67**(5): 842-853.

Theriault, V., Bernatchez, L., and Dodson, J.J. 2007. Mating system and individual reproductive success of sympatric anadromous and resident brook charr, Salvelinus fontinalis, under natural conditions. Behavioral Ecology and Sociobiology **62**(1): 51-65.

Theriault, V., and Dodson, J.J. 2003. Body size and the adoption of a migratory tactic in brook charr. Journal of Fish Biology **63**(5): 1144-1159.

Thorpe, J.E. 1994. An alternative view of smolting in salmonids. Aquaculture **121**(1-3): 105-113.

Thorpe, J.E., Mangel, M., Metcalfe, N.B., and Huntingford, F.A. 1998. Modelling the proximate basis of salmonid life-history variation, with application to Atlantic salmon, *Salmo salar* L. Evolutionary Ecology **12**(5): 581-599.

Thorstad, E.B., Whoriskey, F., Uglem, I., Moore, A., Rikardsen, A.H., and Finstad, B. 2012. A critical life stage of the Atlantic salmon *Salmo salar*: behaviour and survival during the smolt and initial post-smolt migration. Journal of Fish Biology **81**(2): 500-542.

Weisberg, S., Spangler, G., and Richmond, L.S. 2010. Mixed effects models for fish growth. Canadian Journal of Fisheries & Aquatic Sciences **67**(2): 269-277.

Wysujack, K., Greenberg, L.A., Bergman, E., and Olsson, I.C. 2009. The role of the environment in partial migration: food availability affects the adoption of a migratory tactic in brown trout *Salmo trutta*. Ecology of Freshwater Fish **18**(1): 52-59.

Zimmerman, C.E. 2005. Relationship of otolith strontium-to-calcium ratios and salinity: experimental validation for juvenile salmonids. Canadian Journal of Fisheries and Aquatic Sciences **62**(1): 88-97.

Zuur, A.F., Ieno, E.N., N., W., Saveliev, A.A., and Smith, G.M. 2009. Mixed effects models and extensions in ecology with R. Springer, New York.

Tables

Table 3.1 – Strontium (Sr) concentration ranges and maximums from freshwater and anadromous Dolly Varden otoliths from the Rat, Babbage, and Big Fish rivers.

River	Group	Mean Maximum	95% CI	Maximum range (mg/kg)	Mean Range	95% CI	Range range (mg/kg)
Rat	Freshwater (Group 1)	907	136	493-1313	641	129	275-1050
	Anadromous (Group 2)	2807	59	1986-4467	2581	60	1778-4172
Babbage	Freshwater (Group 1)	698	156	279-1188	485	142	148-919
	Anadromous (Group 2)	2965	60	2235-4371	2626	60	1994-4134
Big Fish	Freshwater (Group 1)	1261	90	654-1776	774	92	249-1390
	Anadromous (Group 2)	2635	59	1969-3713	2099	72	1092-3393

Table 3.2 – Number of fish that migrated at a specific age (with % in brackets) for male Dolly Varden that were used in analysis from the Rat, Babbage, and Big Fish rivers. Age at migration was determined from Sr concentrations in otoliths.

River	Age at Migration							
	2		3		4		5	
Rat	1	(1.0)	34	(34.3)	63	(63.6)	1	(1.0)
Babbage	36	(53.7)	27	(40.3)	3	(4.5)	1	(1.5)
Big Fish	1	(1.5)	44	(65.7)	21	(31.3)	1	(1.5)

Table 3.3 – Annual growth in Dolly Varden from the Rat, Big Fish, and Babbage rivers was determined from the following mix effect models. Random effects are in parentheses with * denoting an interaction effect. AIC values were determined from maximum likelihood estimation.

Model parameters	AIC	Δ AIC
growth = age + life history + river + age*life history + age*river + life history*river + age*life history*river + (cohort + individual)	11180.51	9.12
growth = age + life history + river + age*life history + age*river + life history*river + (cohort + individual)	11173.11	1.72
growth = age + life history + river + age*life history + age*river + (cohort + individual)	11171.39	0
growth = age + life history + river + age*life history + life history*river + (cohort + individual)	11328.41	157.02
growth = age + life history + river + age*river + life history*river + (cohort + individual)	11200.56	29.17
growth = age + life history + river + age*life history + (cohort + individual)	11325.55	154.16
growth = age + life history + river + age*river + (cohort + individual)	11199.18	27.79
growth = age + life history + river + life history*river + (cohort + individual)	11379.83	208.44
growth = age + life history + river + (cohort + individual)	11378.97	207.58

Figures
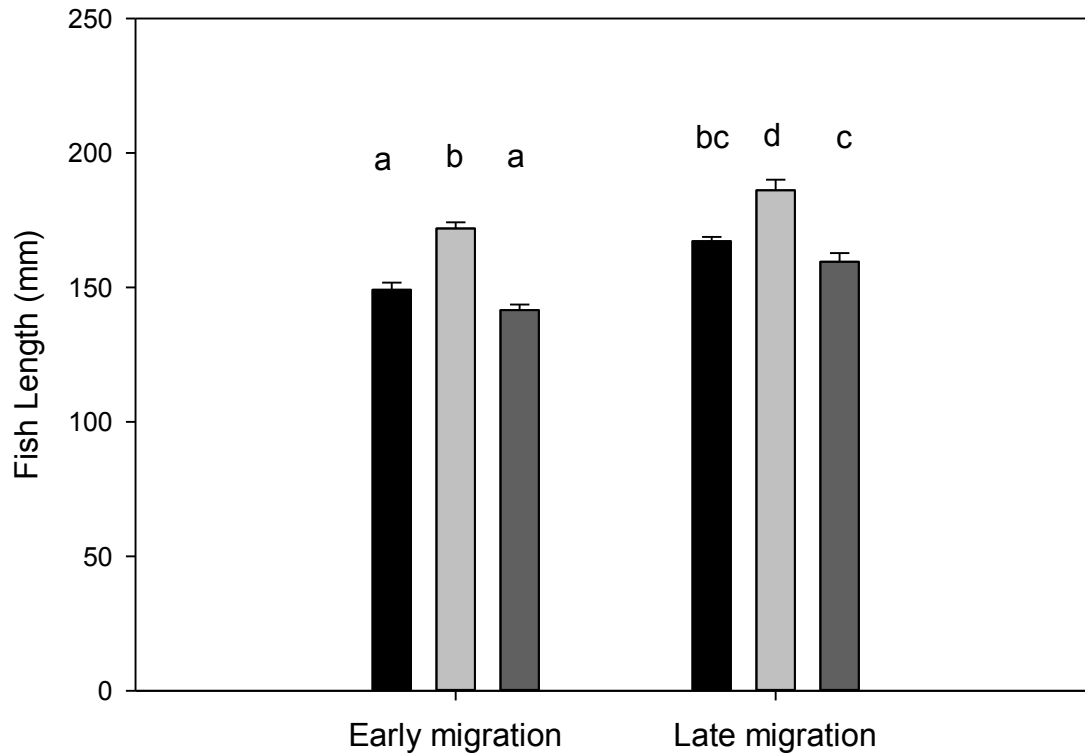
Figure 3.1 – Average fish size (mm) at migration (±SE) for early and late migrating Dolly Varden from the Rat River (■), Big Fish River (■), and Babbage River (■). Letters represent significant differences (p<0.05).
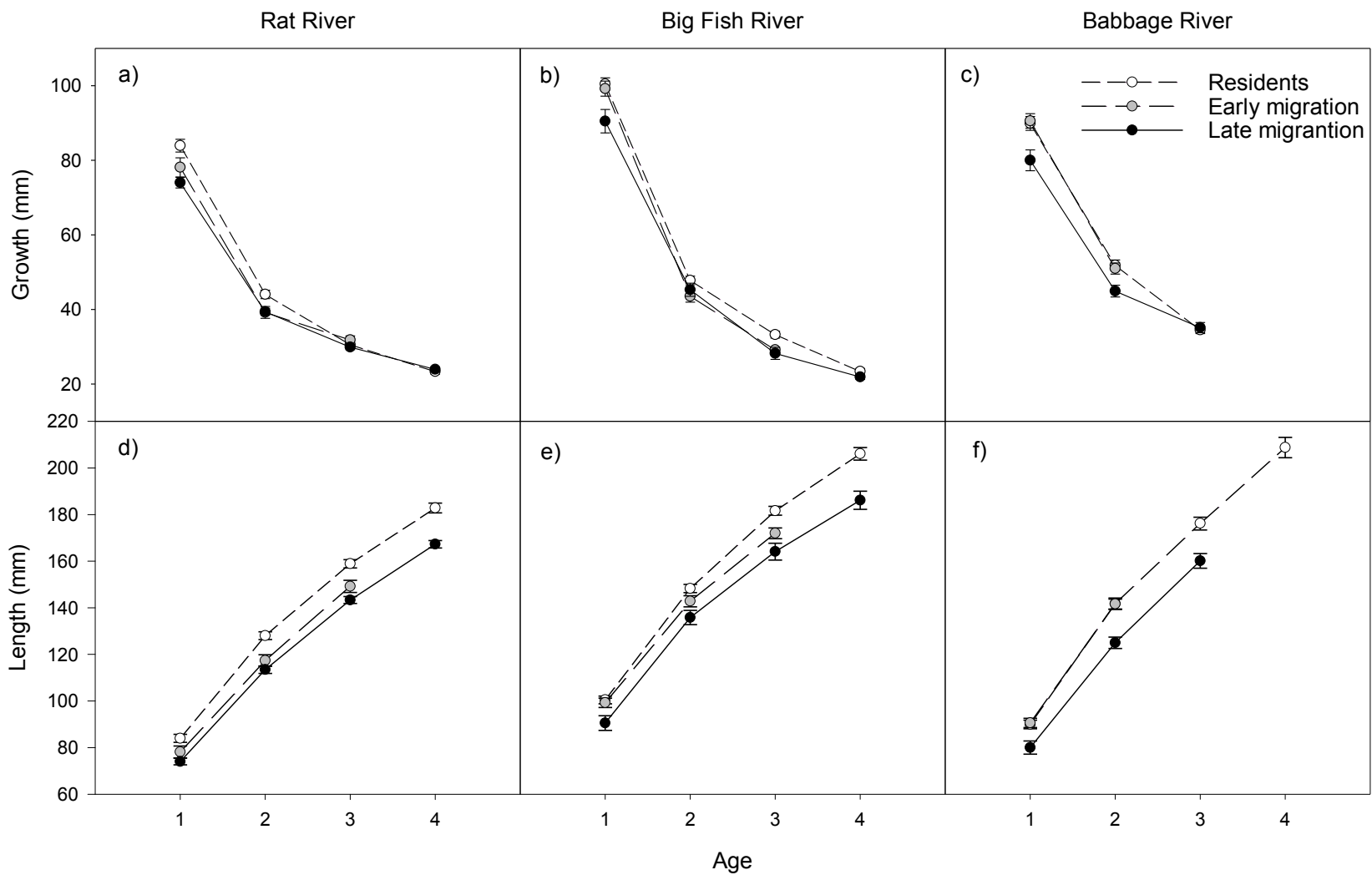
Figure 3.2 – Average a-c) growth-at-age (mm) (±SE), and d-f) average size-at-age (mm) (±SE) for resident (○, - -), early migrant (•, − −), and late migrant (•, −) Dolly Varden males on the Rat, Big Fish, and Babbage rivers.
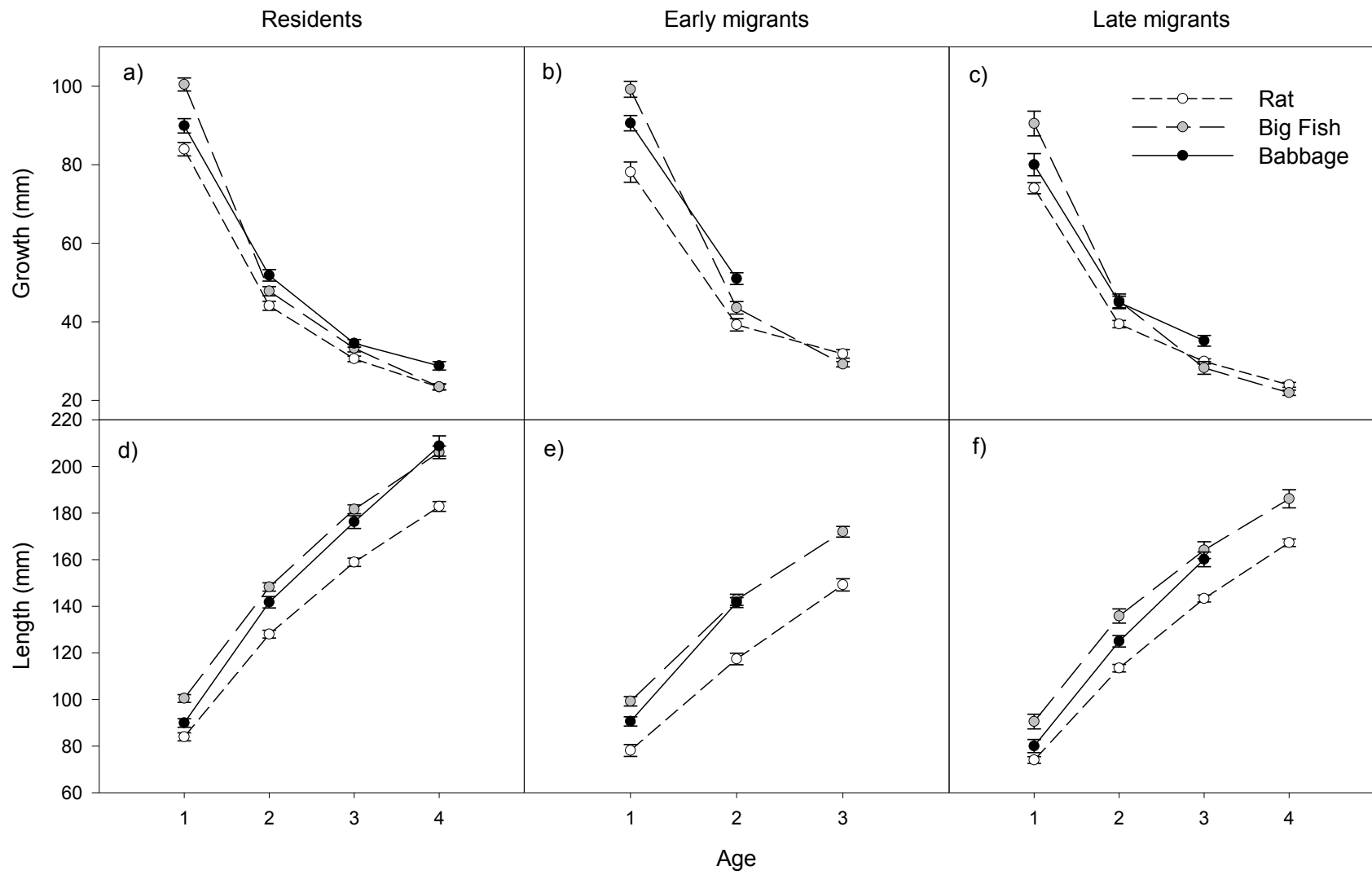
Figure 3.3 – Average a-c) growth-at-age (mm) (±SE), and d-f) average size-at-age (mm) (±SE) for Rat River (○, - -), Big Fish River (●, − −), and Babbage River (●, −) Dolly Varden resident, early migrating, and late migrating males.

Chapter 4: General Conclusions

Summary

Partial anadromy is common in salmonids, where a portion of the population forgoes migration and opts to remain in freshwater as stream residents (Chapman et al. 2012, Jonsson and Jonsson 1993). Fish that migrate to more productive habitat benefit from an increase in size, which leads to a competitive advantage during spawning (Gross 1987, Hendry et al. 2004). However, costs to migrating fish include increased mortality due to predation, energy expenditure for upstream migration, and delayed maturity. Females tend to dominate migration in populations that are partially migratory due to fitness benefits associated with increased reproductive capacity as size increases (Hendry et al. 2001, Hutchings and Jones 1998, Loewen et al. 2010, Nordeng 1983, Theriault et al. 2007). Reproductive success for males does not directly relate to size, with small males having the ability to 'sneak spawn' and fertilize a potentially substantial portion of deposited eggs. Classical life history theory predicts that as long as the benefit of size does not outweigh the costs of migration, in partially migratory populations fish will forgo migration and opt to mature in freshwater, thus increasing their fitness potential by maturing early and having more spawning opportunities (Roff 1992, Stearns 1992, Thorpe et al. 1998). Likewise, since fish size is important for migration, with larger individuals having more energy for smoltification and predator avoidance, smaller individuals should delay migration. This delay in migration will generally lead to younger fish migrating at a smaller size than older individuals.

Dolly Varden are a species of char that inhabit cold water stream systems in the western Arctic. Populations of Dolly Varden exhibit partial anadromy, with males making up almost the entire resident population (McCart 1980). Since Dolly Varden research is generally focused on the anadromous adult life history stages, the aim of this study was to focus on residents and early ontogenetic life stages. Specifically, the goal of my thesis was to assess how early growth influences life history 'decisions'. In order to get at life history questions, otoliths were used due to their applicability in reconstructing individual life histories.

Chapter 2 assessed the fish length – otolith length (FL – OL) relationship in order to determine if traditional otolith back-calculations could be used as a model for fish size-at-age. Results showed a decoupling that was occurring during first migration in otoliths of anadromous individuals, indicating that, while fish were more than doubling in size during first migration, the otolith was not growing in a proportional manner. This is the first known observation of decoupling during first migration to have been recorded in the literature to date. This decoupling that is occurring between Dolly Varden otolith and somatic growth is likely due to physiological changes during smoltification that alter the amount of calcium that is deposited onto the otolith. Since, a major goal for this thesis was to be able to reconstruct size-at-age from otoliths of anadromous Dolly Varden, modified back-calculation models were constructed that were based on the biological intercept model by Campana (1990) and the modified fry model by Vigliola et al. (2000). When compared to actual fish measurements, the modified version of the biological intercept model (biological intercept breakpoint) gave the most accurate values of fish size during all ontogenetic stages and was thus the chosen model for back-calculating size-at-age in Dolly Varden.

Chapter 3 used the biological intercept breakpoint model constructed in Chapter 2 as well as the traditional biological intercept model by Campana (1990) to back-calculate size-at-age in anadromous and resident male individuals. Within year growth was then compared between life histories, ages, and three river systems, while controlling for cohort and individual variation, using a mixed effects model derived from Weisberg et al. (2010). Results showed that there was variation in growth among populations from the Rat, Big Fish, and Babbage rivers. Similar to numerous other studies (Forseth et al. 1999, Jonsson 1985, Jonsson et al. 1998, Metcalfe et al. 1988, Morinville and Rasmussen 2003, Rikardsen and Elliott 2000, Svenning et al. 1992, Theriault and Dodson 2003), and classical life history theory (Roff 1992, Stearns 1992), slow growth was consistent with delayed migration and larger size at migration compared to earlier migrants. Comparisons of resident and anadromous individuals showed that there was no difference in growth between residents and early migrating individuals, although a trend towards larger residents was observed on the Rat and Big Fish Rivers. These results indicate that while growth is important, other factors such as growth efficiencies and metabolic rates may be significant contributors to life history 'decisions'

Future Directions

With the development of a new back-calculation equation that accounts for the decoupling observed in the FL – OL relationship (Chapter 2), Dolly Varden size-at-age and growth patterns can be accurately estimated using otoliths. Further research in this area could explore other Dolly Varden populations along the Yukon North Slope as well as populations along the Alaska coastline to determine how prevalent this pattern is within Dolly Varden otoliths. Increasing juvenile samples for each river system could also help to strengthen the results from the piecewise regressions in order to provide increased confidence in parameters being used in back-calculation equations for a specific population. This would be especially beneficial on the Big Fish River where a lack of juvenile samples led to using non-river-specific parameters to back-calculate size-at-age in this system.

Decoupling of fish and otolith size outside of growth and age effects is not a commonly known occurrence in adult otoliths. The majority of decoupling events are found in larval fish and focus on daily growth structures (Campana 1984, Gunther et al. 2012, Hare and Cowen 1995, Hobbs et al. 2007). The decoupling that is occurring in Dolly Varden otoliths is during first time migration and is likely due to physiological changes due to smoltification. While is it surprising that this decoupling has not been observed in other salmonids that undergo similar migration patterns, there is the possibility that it occurs to such a small extent in other species that it has not been recorded. Extensive reviews of otoliths of other fish species would be beneficial to determine how prevalent decoupling associated with smoltification is, and whether or not this is a species-specific phenomenon.

Smoltification initiates numerous physiological changes within a fish (Hoar 1988, McCormick and Saunders 1987, Stefansson et al. 2008). How this affects otolith accretion however, has never been studied. Otolith accretion is governed by calcium uptake, which is regulated through hormones that can be altered during smolting and osmoregulation events (Loewen et al. 2016). Whether or not this causes changes in otolith accretion should be the next step in research in regards to FL – OL decoupling during smoltification.

One of the largest difficulties in assessing differences between resident and anadromous fish is their morphological similarity. Prior to the 'decision' to migrate or mature no observable differences have been recorded between the life histories. Thorpe et al. (1998) has also indicated

that the 'decision' to migrate can occur prior to the actual onset of either maturation or migration, which makes it difficult to determine when morphological differences first appear between the life histories. For this reason, otoliths become a very useful tool in reconstructing life histories of fish at important life stages. Metabolic rates have been shown to be important contributors to life history decisions (Metcalfe et al. 1995, Morinville and Rasmussen 2003). However, directly comparing metabolic rates is difficult if the main goal is to assess when differences begin to occur. Assessing otolith carbon ratios as a measure of metabolic rate is a new technique in the field of otolith research (Kalish 1991, Solomon et al. 2006). This technique may allow otolith researchers the ability to infer metabolic rates at a given point along an otolith trajectory, which would then correspond to a specific time point in the life of the fish.

While growth efficiencies have been studied in brook trout (Morinville and Rasmussen 2003), no studies have been conducted on Dolly Varden. It is likely that differences in growth efficiencies exist between resident and anadromous individuals and future research to test this would be advisable. Furthering that goal, assessing the feeding behaviour of pre-smolt juveniles and residents would be useful in determining whether different food intake behaviours are playing a role in life history 'decisions'. Morinville and Rasmussen (2003) have found that pre-migratory juveniles tend to utilize within channel currents to catch downward drifting food, while residents prefer to remain in calmer pools. Tying all this information together with metabolic work from otoliths would provide a more complete picture as to the mechanism for life history 'decisions' within Dolly Varden.

Lastly, since growth is an important factor that drives migration, it is important to be able to have actual size information pertaining to smoltification. This current study could not directly assess size-at-smoltification but instead provided size at annuli formation for the year in which a fish migrated. While little to no growth is expected from the time of annuli formation to actual smoltification, knowing actual smolt size would enable researchers to accurately project migration size thresholds and have a baseline for determining potential future changes that may occur due to climate change in the region.

Implications

Dolly Varden are an important subsistence and cultural resource to many coastal Aboriginal communities (Howland et al. 2012). Historically, Inuvialuit and Gwich'in peoples regularly fished for Dolly Varden from the Rat, Big Fish, and Babbage rivers along the Beaufort Sea coastline, at the river mouths, and at overwintering sites. Population declines of Dolly Varden, particularly on the Rat and Big Fish rivers have led to voluntary fisheries closures and concern over the future viability of these stocks (Sandstrom et al. 2009, Sandstrom and Harwood 2002). While populations have rebounded in the Rat River and stabilized in the Big Fish River, concerns over declines and unknowns associated with a changing climate are still a priority in co-management and have led to Dolly Varden being listed as Special Concern under the Species at Risk Act (SARA) (Peter Rodger, unpublished data).

While population numbers is one of the main concerns for managing these stocks in a sustainable manner, other factors such as habitat and juvenile recruitment are also key foci. Within Dolly Varden populations one of the key concerns is the lack of data on juvenile life history stages as well as the influences of life history 'decisions', specifically the 'decision' in males to adopt resident or anadromous life history trajectories. This research provides key information on how growth influences migratory and resident behaviour within Dolly Varden populations. It also outlines a new back-calculation model that will allow researchers to use otoliths to answer biological questions on Dolly Varden life history. While the findings are regionally important, the overall mechanisms should be applicable to other northern Dolly Varden populations throughout Alaska and Eurasia, as well as to other salmonid species that exhibit similar anadromous and resident life history strategies and/or otolith decoupling events. The underlying mechanisms of anadromy and residency are poorly understood in salmonids (Curry et al. 2010, Wysujack et al. 2009), with most of the work focusing on Atlantic salmon and Arctic char (Klemetsen et al. 2003). Few studies to date have focused on Dolly Varden, with no studies conducted on life history trajectories or otolith back-calculation. This research addresses knowledge gaps for Dolly Varden as well as adding to the limited general knowledge base on life history in salmonids. It can also act as a starting point for more discussion on what governs otolith accretion and how physiological changes can influence otolith deposition.

Literature Cited

Campana, S.E. 1984. Microstructural growth patterns in the otoliths of larval and juvenile starry flounder, *Platichthys stellatus*. Canadian Journal of Zoology **62**(8): 1507-1512.

Campana, S.E. 1990. How reliable are growth back-calculations based on otoliths. Canadian Journal of Fisheries and Aquatic Sciences **47**(11): 2219-2227.

Chapman, B.B., Hulthen, K., Brodersen, J., Nilsson, P.A., Skov, C., Hansson, L.A., and Bronmark, C. 2012. Partial migration in fishes: causes and consequences. Journal of Fish Biology **81**(2): 456-478.

Curry, R.A., Bernatchez, L., Whoriskey, F., and Audet, C. 2010. The origins and persistence of anadromy in brook charr. Reviews in Fish Biology and Fisheries **20**(4): 557-570.

Forseth, T., Naesje, T.F., Jonsson, B., and Harsaker, K. 1999. Juvenile migration in brown trout: a consequence of energetic state. Journal of Animal Ecology **68**(4): 783-793.

Gross, M.R. 1987. Evolution of diadromy in fishes. American Fisheries Society Symposium **1:**14-25.

Gunther, C.C., Temming, A., Baumann, H., Huwer, B., Mollmann, C., Clemmesen, C., and Herrmann, J.P. 2012. A novel length back-calculation approach accounting for ontogenetic changes in the fish length - otolith size relationship during the early life of sprat (*Sprattus sprattus*). Canadian Journal of Fisheries and Aquatic Sciences **69**(7): 1214-1229.

Hare, J.A., and Cowen, R.K. 1995. Effect of age, growth rate, and ontogeny on the otolith size-fish size relationship in bluefish, *Pomatomus saltatrix*, and the implications for back-calculation of size in early life history stages. Canadian Journal of Fisheries and Aquatic Sciences **52**(9): 1909-1922.

Hendry, A.P., Bohlin, T., Jonsson, B., and Berg, O.K. 2004. To sea or not to sea? Anadromy versus non-anadromy in salmonids. *In* Evolution illuminated: salmon and their relatives. *Edited by* A.P. Hendry and S.C. Stearns. Oxford University Press, pp.92-125.

Hendry, A.P., Day, T., and Cooper, A.B. 2001. Optimal size and number of propagules: Allowance for discrete stages and effects of maternal size on reproductive output and offspring fitness. American Naturalist **157**(4): 387-407.

Hoar, W.S. 1988. The Physiology of Smolting Salmonids. *In* Fish Physiology Volume XI Physiology of Developing Fish, Part B. *Edited by* W.S. Hoar and D.J. Randall. Academic Press, San Diego pp. 275-343.

Hobbs, J.A., Bennett, W.A., Burton, J.E., and Baskerville-Bridges, B. 2007. Modification of the biological intercept model to account for ontogenetic effects in laboratory-reared delta smelt (*Hypomesus transpacificus*). Fishery Bulletin **105**(1): 30-38.

Howland, K., Mochnacz, N., Gallagher, C., Tallman, R., Ghamry, H., Roux, M.J., Sandstrom, S., and Riest, J. 2012. Developing Strategies for Improved Assessment and Ecosystem-Based Management of Canadian Northern Dolly Varden. *In* Global Progress in Ecosystem-Based Fisheries Management. *Edited by* G.H. Kruse, H.I. Browman, K.L. Cochrane, D. Evans, G.S. Jamieson, P.A. Livingston, D. Woodby, and C.I. Zhang. Alaska Sea Grant, University of Alaska Fairbanks, pp. 169-188.

Hutchings, J.A., and Jones, M.E.B. 1998. Life history variation and growth rate thresholds for maturity in Atlantic salmon, *Salmo salar*. Canadian Journal of Fisheries and Aquatic Sciences **55**: 22-47.

Jonsson, B. 1985. Life history patterns of freshwater resident and sea-run migrant brown trout in Norway. Transactions of the American Fisheries Society **114**(2): 182-194.

Jonsson, B., and Jonsson, N. 1993. Partial migration: niche shift versus sexual maturation in fishes. Reviews in Fish Biology and Fisheries **3**(4): 348-365.

Jonsson, N., Jonsson, B., and Hansen, L.P. 1998. Long-term study of the ecology of wild Atlantic salmon smolts in a small Norwegian river. Journal of Fish Biology **52**(3): 638-650.

Kalish, J.M. 1991. C-13 and O-18 isotopic disequilibria in fish otoliths: metabolic and kinetic effects. Marine Ecology Progress Series **75**(2-3): 191-203.

Klemetsen, A., Amundsen, P.A., Dempson, J.B., Jonsson, B., Jonsson, N., O'Connell, M.F., and Mortensen, E. 2003. Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories. Ecology of Freshwater Fish **12**(1): 1-59.

Loewen, T.N., Carriere, B., Reist, J.D., Halden, N.M., and Anderson, W.G. 2016. Linking physiology and biomineralization processes to ecological inferences on the life history of fishes. Comparative Biochemistry and Physiology A **202**: 123-140.

Loewen, T.N., Gillis, D., and Tallman, R.F. 2010. Maturation, growth and fecundity of Arctic charr, *Salvelinus alpinus* (L.), life-history variants co-existing in lake systems of Southern Baffin Island, Nunavut, Canada. Hydrobiologia **650**(1): 193-202.

McCart, P.J. 1980. A review of the systematics and ecology of Arctic char, Salvelinus alpinus, in the Western Arctic. Can. Tech. Rep. Fish. Aquat. Sci. 935: vii + 89p.

McCormick, S.D., and Saunders, R.L. 1987. Preparatory physiological adaptations for marine life of salmonids: osmoregulation, growth, and metabolism. American Fisheries Symposium **1**:211-229.

Metcalfe, N.B., Huntingford, F.A., and Thorpe, J.E. 1988. Feeding intensity, growth rates, and the establishment of life-history patterns in juvenile Atlantic salmon *Salmo salar*. Journal of Animal Ecology **57**(2): 463-474.

Metcalfe, N.B., Taylor, A.C., and Thorpe, J.E. 1995. Metabolic rate, social status and life history strategies in Atlantic salmon. Animal Behaviour **49**(2): 431-436.

Morinville, G.R., and Rasmussen, J.B. 2003. Early juvenile bioenergetic differences between anadromous and resident brook trout (*Salvelinus fontinalis*). Canadian Journal of Fisheries and Aquatic Sciences **60**(4): 401-410.

Nordeng, H. 1983. Solution to the char problem based on Arctic char (*Salvelinus alpinus*) in Norway. Canadian Journal of Fisheries and Aquatic Sciences **40**(9): 1372-1387.

Rikardsen, A.H., and Elliott, J.M. 2000. Variations in juvenile growth, energy allocation and life-history strategies of two populations of Arctic charr in North Norway. Journal of Fish Biology **56**(2): 328-346.

Roff, D.A. 1992. The evolution of life histories : theory and analysis. Chapman & Hall, New York.

Sandstrom, S., Harwood, L., and Howland, K. 2009. Status of anadromous Dolly Varden char (*Salvelinus malma*) of the Rat River, Northwest Territories, as assessed through mark-recapture and live-sampling at the spawning and over-wintering site (1995-2007). Can. Tech. Rep. Fish. Aqua. Sci. p. 75.

Sandstrom, S.J., and Harwood, L.A. 2002. Studies of anadromous Dolly Varden (*Salvelinus malma*) (W.), of the Big Fish River, NT, Canada 1972-1994. Canadian Manuscript Report of Fisheries and Aquatic Sciences 2603: i-vi, 1-31p.

Solomon, C.T., Weber, P.K., Cech, J.J., Ingram, B.L., Conrad, M.E., Machavaram, M.V., Pogodina, A.R., and Franklin, R.L. 2006. Experimental determination of the sources of otolith carbon and associated isotopic fractionation. Canadian Journal of Fisheries and Aquatic Sciences **63**(1): 79-89.

Stearns, S.C. 1992. The evolution of life histories. Oxford University Press, New York.

Stefansson, S.O., Björnsson, B.T., Ebbesson, L.O.E., and McCormick, S.D. 2008. Smoltification. *In* Fish Larval Physiology. *Edited by* R.N. Finn and B.G. Kapoor, B.G. Science Publishers, Enfield, NH, pp. 639-681.

Svenning, M.A., Smith-Nilsen, N., and M., J. 1992. Sea water migration of Arctic charr (*Salvelinus alpinus* L.): correlation between freshwater growth and seawater migration, based on back-calculation from otoliths. Nordic Journal of Freshwater Research **67:**18-26.

Theriault, V., Bernatchez, L., and Dodson, J.J. 2007. Mating system and individual reproductive success of sympatric anadromous and resident brook charr, *Salvelinus fontinalis*, under natural conditions. Behavioral Ecology and Sociobiology **62**(1): 51-65.

Theriault, V., and Dodson, J.J. 2003. Body size and the adoption of a migratory tactic in brook charr. Journal of Fish Biology **63**(5): 1144-1159.

Thorpe, J.E., Mangel, M., Metcalfe, N.B., and Huntingford, F.A. 1998. Modelling the proximate basis of salmonid life-history variation, with application to Atlantic salmon, *Salmo salar* L. Evolutionary Ecology **12**(5): 581-599.

Vigliola, L., Harmelin-Vivien, M., and Meekan, M.G. 2000. Comparison of techniques of back-calculation of growth and settlement marks from the otoliths of three species of *Diplodus* from the Mediterranean Sea. Canadian Journal of Fisheries and Aquatic Sciences **57**(6): 1291-1299.

Weisberg, S., Spangler, G., and Richmond, L.S. 2010. Mixed effects models for fish growth. Canadian Journal of Fisheries & Aquatic Sciences **67**(2): 269-277.

Wysujack, K., Greenberg, L.A., Bergman, E., and Olsson, I.C. 2009. The role of the environment in partial migration: food availability affects the adoption of a migratory tactic in brown trout *Salmo trutta*. Ecology of Freshwater Fish **18**(1): 52-59.

References

Achord, S., Zabel, R.W., and Sandford, B.P. 2007. Migration timing, growth, and estimated parr-to-smolt survival rates of wild snake river spring-summer Chinook salmon from the salmon river basin, Idaho, to the Lower Snake River. Transactions of the American Fisheries Society **136**(1): 142-154.

Armstrong, J.D., Fallon-Cousins, P.S., and Wright, P.J. 2004. The relationship between specific dynamic action and otolith growth in pike. Journal of Fish Biology **64**(3): 739-749.

Armstrong, R.H., and Morrow, T.E. 1980. The Dolly Varden charr, *Salvelinus malma malma*. *In* Charrs, salmonid fishes of the genus *Salvelinus*. *Edited by* E.K. Balon. Hague: W. Junk, pp. 99-139.

Barber, M.C., and Jenkins, G.P. 2001. Differential effects of food and temperature lead to decoupling of short-term otolith and somatic growth rates in juvenile King George whiting. Journal of Fish Biology **58**(5): 1320-1330.

Baumann, H., Peck, M.A., and Herrmann, J.P. 2005. Short-term decoupling of otolith and somatic growth induced by food level changes in postlarval Baltic sprat, *Sprattus sprattus*. Marine and Freshwater Research **56**(5): 539-547.

Behnke, R.J. 1980. A systematic review of the genus *Salvelinus*. *In* Charrs, salmonid fishes of the genus *Salvelinus*. *Edited by* E.K. Balon. Hague: W. Junk, pp. 441-481.

Berglund, I., Hansen, L.P., Lundqvist, H., Jonsson, B., Eriksson, T., Thorpe, J.E., and Eriksson, L.O. 1991. Effects of elevated winter temperature on seawater adaptability, sexual rematuration, and downstream migratory behavior in mature male Atlantic salmon parr (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences **48**(6): 1041-1047.

Blackett, R.F. 1968. Spawning behavior, fecundity, and early life history of anadromous Dolly Varden, *Salvelinus malma* (Walbaum) in Southeastern Alaska. Alaska Department of Fish and Game Research Report **6**:1-85.

Brown, R.J., Bickford, N., and Severin, K. 2007. Otolith trace element chemistry as an indicator of anadromy in Yukon River drainage coregonine fishes. Transactions of the American Fisheries Society **136**(3): 678-690.

Brown, R.J., Loewen, M.B., and Tanner, T.L. 2014. Overwintering locations, migrations, and fidelity of radio-tagged Dolly Varden in the Hulahula River, Arctic National Wildlife Refuge, 2007-09. Arctic **67**(2): 149-158.

Campana, S.E. 1984. Microstructural growth-patterns in the otoliths of larval and juvenile starry flounder, *Platichthys-stellatus*. Canadian Journal of Zoology **62**(8): 1507-1512.

Campana, S.E. 1990. How reliable are growth back-calculations based on otoliths. Canadian Journal of Fisheries and Aquatic Sciences **47**(11): 2219-2227.

Campana, S.E., and Neilson, J.D. 1985. Microstructure of fish otoliths. Canadian Journal of Fisheries and Aquatic Sciences **42**(5): 1014-1032.

Chapman, B.B., Hulthen, K., Brodersen, J., Nilsson, P.A., Skov, C., Hansson, L.A., and Bronmark, C. 2012. Partial migration in fishes: causes and consequences. Journal of Fish Biology **81**(2): 456-478.

Chilton, D.E., and Beamish, R.J. 1982. Age determination methods for fishes studied by the Groundfish Program at the Pacific Biological Station. Can. Spec. Publ. Fish. Aquat. Sci. p.102.

Clark, I.D., Lauriol, B., Harwood, L., and Marschner, M. 2001. Groundwater contributions to discharge in a permafrost setting, Big Fish River, NWT, Canada. Arctic Antarctic and Alpine Research **33**(1): 62-69.

Conte, F.P., and Wagner, H.H. 1965. Development of osmotic and ionic regulation in juvenile steelhead trout *Salmo gairdneri*. Comparative Biochemistry and Physiology **14**(4): 603-620.

COSEWIC. 2010. COSEWIC assessment and status report on the Dolly Varden *Salvelinus malma malma* (Western Arctic populations) in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. x + 65 pp.

Courtney, M.B., Scanlon, B.S., Rikardsen, A.H., and Seitz, A.C. 2016. Marine behavior and dispersal of an important subsistence fish in Arctic Alaska, the Dolly Varden. Environmental Biology of Fishes **99**: 209-222.

Craig, P.C. 1977. Ecological studies of anadromous populations of arctic char in the canning river drainage and adjacent coastal waters of the Beaufort Sea, Alaska. *In* Fisheries investigations along the north slope and Beaufort sea coast in Alaska with emphasis on Arctic char. *Edited by* P.J. McCart. Canadian Arctic Gas Study Ltd., Calgary, Alberta, pp. 1-116.

Crawley, M.J. 2013. The R book. Wiley, Chichester, West Sussex, U.K.

Curry, R.A., Bernatchez, L., Whoriskey, F., and Audet, C. 2010. The origins and persistence of anadromy in brook charr. Reviews in Fish Biology and Fisheries **20**(4): 557-570.

DeCicco, A. 1989. Movements and spawning of adult Dolly Varden charr (*S. malma*) in Chukchi Sea drainages of northwestern Alaska: evidence for summer and fall spawning populations. Physical. Ecol. Japan. Spec. **1:** 229-238.

DFO. 2003a. Babbage River Dolly Varden. DFO Sci. Stock Status Report D5-62 (2002).

DFO. 2003b. Big Fish River Dolly Varden. DFO Sci. Stock Status Report D5-60 (2002).

DFO. 2017a. Assessment of Dolly Varden from the Babbage River, Yukon Territory 2010–2014. DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2016/055.

DFO. 2017b. Assessment of Dolly Varden from the Rat River, Northwest Territories 2009–2014. DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2016/058.

Fechhelm, R.G., Bryan, J.D., Griffiths, W.B., and Martin, L.R. 1997. Summer growth patterns of northern Dolly Varden (*Salvelinus malma*) smolts from the Prudhoe Bay region of Alaska. Canadian Journal of Fisheries and Aquatic Sciences **54**(5): 1103-1110.

Fey, D.P. 2006. The effect of temperature and somatic growth on otolith growth: The discrepancy between two clupeid species from a similar environment. Journal of Fish Biology **69**(3): 794-806.

Finstad, A.G. 2003. Growth backcalculations based on otoliths incorporating an age effect: adding an interaction term. Journal of Fish Biology **62**(5): 1222-1225.

Fleming, I.A., and Gross, M.R. 1994. Breeding competition in a pacific salmon (coho, *Oncorhynchus kisutch*): measures of natural and sexual selection. Evolution **48**(3): 637-657.

Forseth, T., Naesje, T.F., Jonsson, B., and Harsaker, K. 1999. Juvenile migration in brown trout: a consequence of energetic state. Journal of Animal Ecology **68**(4): 783-793.

Francis, R. 1990. Back-calculation of fish length: a critical review. Journal of Fish Biology **36**(6): 883-902.

Gallagher, C.P., Howland, K.L., and Wastle, R.J. 2016. A comparison of different structures and methods for estimating age of northern-form Dolly Varden *Salvelinus malma malma* from the Canadian Arctic. Polar Biology **39**(7): 1257-1265.

Gallagher, C.P., K.L., R., Harris, L.N., Banjo, R., Sandstrom, S., Loewen, T., and Reist, J. 2013. Dolly Varden (*Salvelinus malma malma*) from the Big Fish River: abundance estimates, effective population size, biological characteristics, and contribution to the coastal mixed-stock fishery. DFO Can. Sci. Advis. Sec. Res. Doc. p. v + 46p.

Gallagher, C.P., Roux, M.J., Howland, K.L., and Tallman, R.F. 2012. Synthesis of biological and harvest information used to assess populations of northern form Dolly Varden (*Salvelinus malma malma*) in Canada. Part III: Comparison among populations. . DFO Can. Sci. Advis. Sec. Res. . p. vi + 81 p.

Gauldie, R.W. 1993. Polymporphic crystalline-structure of fish otoliths. Journal of Morphology **218**(1): 1-28.

Gauldie, R.W. 1996. Effects of temperature and vaterite replacement on the chemistry of metal ions in the otoliths of *Oncorhynchus tshawytscha*. Canadian Journal of Fisheries and Aquatic Sciences **53**(9): 2015-2026.

Gauldie, R.W., and Nelson, D.G.A. 1990. Otolith growth in fishes. Comparative Biochemistry and Physiology **97**(2): 119-135.

Geffen, A.J. 1992. Validation of otolith increment deposition rate. Canadian Special Publication of Fisheries and Aquatic Sciences **117**: 101-113.

Glova, G., and McCart, P.J. Life history of Arctic charr (*Salvelinus alpinus L.*) in the Firth River system, Yukon Territory. *In* Life histories of anadromous and freshwater fish in the western Arctic. *Edited by* P.J. McCart. Canadian Arctic Gas Study Ltd., Calgary, Alberta.

Grønkjær, P. 2016. Otoliths as individual indicators: a reappraisal of the link between fish physiology and otolith characteristics. Marine and Freshwater Research **67**(7): 881-888.

Gross, M.R. 1987. Evolution of diadromy in fishes. American Fisheries Society Symposium **1**:14-25.

Gunther, C.C., Temming, A., Baumann, H., Huwer, B., Mollmann, C., Clemmesen, C., and Herrmann, J.P. 2012. A novel length back-calculation approach accounting for ontogenetic changes in the fish length - otolith size relationship during the early life of sprat (*Sprattus sprattus)*. Canadian Journal of Fisheries and Aquatic Sciences **69**(7): 1214-1229.

Hare, J.A., and Cowen, R.K. 1995. Effect of age, growth-rate, and ontogeny on the otolith size - fish size relationship in bluefish, *Pomatomus saltatrix*, and the implications for back-calculation of size in fish early-life history stages. Canadian Journal of Fisheries and Aquatic Sciences **52**(9): 1909-1922.

Harris, L.N., Bajno, R., Gallagher, C.P., Koizumi, I., Johnson, L.K., Howland, K.L., Taylor, E.B., and Reist, J.D. 2015. Life-history characteristics and landscape attributes as drivers of genetic variation, gene flow, and fine-scale population structure in northern Dolly Varden (*Salvelinus malma malma*) in Canada. Canadian Journal of Fisheries and Aquatic Sciences **72**(10): 1477-1493.

Hendry, A.P., Bohlin, T., Jonsson, B., and Berg, O.K. 2004. To sea or not to sea? Anadromy versus non-anadromy in salmonids. *In* Evolution illuminated: salmon and their relatives. *Edited by* A.P. Hendry and S.C. Stearns. Oxford University Press, pp.92-125.

Hendry, A.P., Day, T., and Cooper, A.B. 2001. Optimal size and number of propagules: Allowance for discrete stages and effects of maternal size on reproductive output and offspring fitness. American Naturalist **157**(4): 387-407.

Hoar, W.S. 1988. The Physiology of Smolting Salmonids. *In* Fish Physiology Volume XI Physiology of Developing Fish, Part B. *Edited by* W.S. Hoar and D.J. Randall. Academic Press, San Diego pp. 275-343.

Hobbs, J.A., Bennett, W.A., Burton, J.E., and Baskerville-Bridges, B. 2007. Modification of the biological intercept model to account for ontogenetic effects in laboratory-reared delta smelt (*Hypomesus transpacificus*). Fishery Bulletin **105**(1): 30-38.

Howland, K.L., Babaluk, J.A., Chiperzak, D., Tallman, R.F., and Low, G. 2009. Variability in diadromous behavior of a northern coregonid based on scanning proton microprobe analysis of otolith strontium. Challenges for Diadromous Fishes in a Dynamic Global Environment **69**: 121-134.

Howland, K., Mochnacz, N., Gallagher, C., Tallman, R., Ghamry, H., Roux, M.J., Sandstrom, S., and Riest, J. 2012. Developing Strategies for Improved Assessment and Ecosystem-Based Management of Canadian Northern Dolly Varden. *In* Global Progress in Ecosystem-Based Fisheries Management. *Edited by* G.H. Kruse, H.I. Browman, K.L. Cochrane, D. Evans, G.S. Jamieson, P.A. Livingston, D. Woodby, and C.I. Zhang. Alaska Sea Grant, University of Alaska Fairbanks, pp. 169-188.

Howland, K.L., Tonn, W.M., Babaluk, J.A., and Tallman, R.F. 2001. Identification of freshwater and anadromous inconnu in the Mackenzie river system by analysis of otolith strontium. Transactions of the American Fisheries Society **130**(5): 725-741.

Hutchings, J.A., and Jones, M.E.B. 1998. Life history variation and growth rate thresholds for maturity in Atlantic salmon, *Salmo salar*. Canadian Journal of Fisheries and Aquatic Sciences **55**: 22-47.

Hutchings, J.A., and Myers, R.A. 1988. Mating success of alternative maturation phenotypes in male Atlantic salmon, *Salmo salar*. Oecologia **75**(2): 169-174.

Huuskonen, H., and Karjalainen, J. 1998. A preliminary study on the relationships between otolith increment width, metabolic rate and growth in juvenile whitefish (*Coregonus lavaretus* L.). Archiv Fur Hydrobiologie **142**(3): 371-383.

Jensen, A.J., Finstad, B., Fiske, P., Hvidsten, N.A., Rikardsen, A.H., and Saksgard, L. 2012. Timing of smolt migration in sympatric populations of Atlantic salmon (*Salmo salar*), brown trout (*Salmo trutta*), and Arctic char (*Salvelinus alpinus*). Canadian Journal of Fisheries and Aquatic Sciences **69**(4): 711-723.

Jonsson, B. 1985. Life-history patterns of fresh-water resident and sea-run migrant brown trout in Norway. Transactions of the American Fisheries Society **114**(2): 182-194.

Jonsson, B., and L'Abee-Lund, J.H. 1993. Latitudinal clines in life-history variables of anadromous brown trout in Europe. Journal of Fish Biology **43**: 1-16.

Jonsson, B., and Jonsson, N. 1993. Partial migration: niche shift versus sexual maturation in fishes. Reviews in Fish Biology and Fisheries **3**(4): 348-365.

Jonsson, B., Jonsson, N., Brodtkorb, E., and Ingebrigtsen, P.J. 2001. Life-history traits of brown trout vary with the size of small streams. Functional Ecology **15**(3): 310-317.

Jonsson, B., Jonsson, N., and Finstad, A.G. 2013. Effects of temperature and food quality on age and size at maturity in ectotherms: an experimental test with Atlantic salmon. Journal of Animal Ecology **82**(1): 201-210.

Jonsson, N., and Jonsson, B. 2003. Energy allocation among developmental stages, age groups, and types of Atlantic salmon (*Salmo salar*) spawners. Canadian Journal of Fisheries and Aquatic Sciences **60**(5): 506-516.

Jonsson, N., Jonsson, B., and Hansen, L.P. 1998. Long-term study of the ecology of wild Atlantic salmon smolts in a small Norwegian river. Journal of Fish Biology **52**(3): 638-650.

Kalish, J.M. 1991. C-13 and O-18 isotopic disequilibria in fish otoliths: metabolic and kinetic effects. Marine Ecology Progress Series **75**(2-3): 191-203.

Klemetsen, A., Amundsen, P.A., Dempson, J.B., Jonsson, B., Jonsson, N., O'Connell, M.F., and Mortensen, E. 2003. Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories. Ecology of Freshwater Fish **12**(1): 1-59.

Kowalchuk, M.W., Sawatzky, C.D., and Reist, J.D. 2010. A Review of the Taxonomic Structure within Dolly Varden, *Salvelinus malma* (Walbaum 1792), of North America. Canadian Science Advisory Secretariat Research Document 013: i-vi, 1-16.

Lahti, K., Huuskonen, H., Laurila, A., and Piironen, J. 2002. Metabolic rate and aggressiveness between Brown Trout populations. Functional Ecology **16**(2): 167-174.

Laidig, T.E., Ralston, S., and Bence, J.R. 1991. Dynamics of growth in the early life-history of shortbelly rockfish *Sebastes jordani*. Fishery Bulletin **89**(4): 611-621.

Lea, E. 1910. On the methods used in the herring investigations. Publications de Circconstance Conseil Permanent Interational pour L'Exploration de la Mer **53**:7-25.

Lee, R.M. 1920. A review of the methods of age and growth determination in fishes by means of scales. Fishery Investigations London Series **4**(2): 1-34.

Loewen, T.N., Carriere, B., Reist, J.D., Halden, N.M., and Anderson, W.G. 2016. Linking physiology and biomineralization processes to ecological inferences on the life history of fishes. Comparative Biochemistry and Physiology A **202**: 123-140.

Loewen, T.N., Gillis, D., and Tallman, R.F. 2010. Maturation, growth and fecundity of Arctic charr, *Salvelinus alpinus* (L.), life-history variants co-existing in lake systems of Southern Baffin Island, Nunavut, Canada. Hydrobiologia **650**(1): 193-202.

Loewen, T.N., Reist, J.D., Yang, P., Koleszar, A., Babaluk, J.A., Mochnacz, N., and Halden, N.M. 2015. Discrimination of northern form Dolly Varden Char (*Salvelinus malma malma*)

stocks of the North Slope, Yukon and Northwest Territories, Canada via otolith trace elements and Sr-87/Sr-86 isotopes. Fisheries Research **170**: 116-124.

McCart, P.J. 1980. A review of the systematics and ecology of Arctic char, *Salvelinus alpinus*, in the Western Arctic. Can. Tech. Rep. Fish. Aquat. Sci. 935: vii + 89p.

McCormick, S.D., and Saunders, R.L. 1987. Preparatory physiological adaptations for marine life of salmonids: osmoregulation, growth, and metabolism. American Fisheries Symposium **1**:211-229.

Metcalfe, N.B. 1998. The interaction between behavior and physiology in determining life history patterns in Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences **55**: 93-103.

Metcalfe, N.B., Huntingford, F.A., Graham, W.D., and Thorpe, J.E. 1989. Early social status and the development of life-history strategies in Atlantic salmon. Proceedings of the Royal Society Series B-Biological Sciences **236**(1282): 7-19.

Metcalfe, N.B., Huntingford, F.A., and Thorpe, J.E. 1988. Feeding intensity, growth rates, and the establishment of life-history patterns in juvenile Atlantic salmon *Salmo salar*. Journal of Animal Ecology **57**(2): 463-474.

Metcalfe, N.B., Huntingford, F.A., Thorpe, J.E., and Adams, C.E. 1990. The effetcs of social status on life history variation in juvenile salmon. Canadian Journal of Zoology **68**(12): 2630-2636.

Metcalfe, N.B., Taylor, A.C., and Thorpe, J.E. 1995. Metabolic rate, social status and life history strategies in Atlantic salmon. Animal Behaviour **49**(2): 431-436.

Metcalfe, N.B., and Thorpe, J.E. 1992. Early predictors of life-history events: the link between 1st feeding date, dominance and seaward migration in Atlantic salmon *Salmo salar* L.. Journal of Fish Biology **41**: 93-99.

Mochnacz, N.J., Schroeder, B.S., Sawatzky, C.D., and Reist, J.D. 2010. Assessment of northern Dolly Varden, *Salvelinus malma malma* (Walbaum, 1792), habitat in Canada. Canadian Manuscript Report of Fisheries and Aquatic Sciences 2926: i-vi, 1-48.

Molony, B.W., and Choat, J.H. 1990. Otolith increment widths and somatic growth-rate: the presence of a time-lag. Journal of Fish Biology **37**(4): 541-551.

Morales-Nin, B. 2000. Review of the growth regulation processes of otolith daily increment formation. Fisheries Research **46**(1-3): 53-67.

Morinville, G.R., and Rasmussen, J.B. 2003. Early juvenile bioenergetic differences between anadromous and resident brook trout (*Salvelinus fontinalis*). Canadian Journal of Fisheries and Aquatic Sciences **60**(4): 401-410.

Morita, K., and Matsuishi, T. 2001. A new model of growth back-calculation incorporating age effect based on otoliths. Canadian Journal of Fisheries and Aquatic Sciences **58**(9): 1805-1811.

Morris, J.A., Rulifson, R.A., Babaluk, J.A., May, P.G., and Campbell, J.L. 2005. Use of micro-PIXE to investigate otolith Sr distributions of the anadromous striped bass, *Morone saxatilis*. X-Ray Spectrometry **34**(4): 301-305.

Mosegaard, H., Svedang, H., and Taberman, K. 1988. Uncoupling of somatic and otolith growth-rates in Arctic char (*Salvelinus alpinus*) as an effect of differences in temperature response. Canadian Journal of Fisheries and Aquatic Sciences **45**(9): 1514-1524.

Neat, F.C., Wright, P.J., and Fryer, R.J. 2008. Temperature effects on otolith pattern formation in Atlantic cod *Gadus morhua*. Journal of Fish Biology **73**(10): 2527-2541.

Nielsen, C., Holdensaard, G., Petersen, H.C., Bjornsson, B.T., and Madsen, S.S. 2001. Genetic differences in physiology, growth hormone levels and migratory behaviour of Atlantic salmon smolts. Journal of Fish Biology **59**(1): 28-44.

Nordeng, H. 1983. Solution to the char problem based on Arctic char (*Salvelinus alpinus*) in Norway. Canadian Journal of Fisheries and Aquatic Sciences **40**(9): 1372-1387.

Okland, F., Jonsson, B., Jensen, A.J., and Hansen, L.P. 1993. Is there a threshold size regulating seaward migration of brown trout and Atlantic salmon. Journal of Fish Biology **42**(4): 541-550.

Olsson, I.C., Greenberg, L.A., Bergman, E., and Wysujack, K. 2006. Environmentally induced migration: the importance of food. Ecology Letters **9**(6): 645-651.

Otterlei, E., Folkvord, A., and Nyhammer, G. 2002. Temperature dependent otolith growth of larval and early juvenile Atlantic cod (*Gadus morhua*). Ices Journal of Marine Science **59**(2): 401-410.

Phillips, R.B., Gudex, L.I., Westrich, K.M., and DeCicco, A.L. 1999. Combined phylogenetic analysis of ribosomal ITS1 sequences and new chromosome data supports three subgroups of Dolly Varden char (*Salvelinus malma*). Canadian Journal of Fisheries and Aquatic Sciences **56**(8): 1504-1511.

Radtke, R.L., Fey, D.P., DeCicco, A.F., and Montgomery, A. 1996. Otolith microstructure in young-of-the-year Dolly Varden, *Salvelinus malma*, from American and Asian populations: Resolution of comparative life history characteristics. Arctic **49**(2): 162-169.

Reist, J.D. 1989. Genetic structuring of allopatric populations and sympatric life history types of charr, Salvelinus alpinus/malma, in the western Arctic, Canada. *In* Biology of Charrs and Masu Salmon, special volume 1. *Edited by* K. Hiroya, Y. Fumio and L.G.N. David. Physiology and Ecology Japan Editorial Office, Kyoto, Japan, pp.405-420.

Reist, J.D., and Sawatzky, C.D. 2010. Diversity and Distribution of Chars, genus Salvelinus, in northwestern North America in the context of northern Dolly Varden (*Salvelinus malma malma* (Walbaum 1792)). Canadian Science Advisory Secretariat Research Document 014: i-vi, 1-18.

Ricker, W.E. 1938. "Residual" and kokanee salmon in Cultus Lake. Journal of the Fisheries Research Board of Canada **4a**(3): 192-218.

Rikardsen, A.H., and Elliott, J.M. 2000. Variations in juvenile growth, energy allocation and life-history strategies of two populations of Arctic charr in North Norway. Journal of Fish Biology **56**(2): 328-346.

Rikardsen, A.H., Svenning, M.A., and Klemetsen, A. 1997. The relationships between anadromy, sex ratio and parr growth of Arctic charr in a lake in North Norway. Journal of Fish Biology **51**(3): 447-461.

Roff, D.A. 1988. The evolution of migration and some life-history parameters in marine fishes. Environmental Biology of Fishes **22**(2): 133-146.

Roff, D.A. 1992. The evolution of life histories: theory and analysis. Chapman & Hall, New York.

Roff, D.A. 1996. The evolution of threshold traits in animals. Quarterly Review of Biology **71**(1): 3-35.

Rounsfell, G.A. 1958. Anadromy in North American Salmonidae. Fish. Bull. Wildl. Serv. pp. 171-185.

Roux, M.J., Howland, K., Gallagher, C.P., and Tallman, R.F. 2012. Synthesis of biological and harvest information used to assess populations of northern form Dolly Varden (*Salvelinus malma malma*) in Canada. Part I: Rat River. DFO Can. Sci. Advis. Sec. Res. Doc. 2011/132. viii + 77p.

Rowe, D.K., Thorpe, J.E., and Shanks, A.M. 1991. Role of fat stores in the maturation of male atlantic salmon (*Salmo salar*) parr. Canadian Journal of Fisheries and Aquatic Sciences **48**(3): 405-413.

Sandstrom, S.J. 1995. The effect of overwintering site temperature on energy allocation and life history characteristics of anadromous female Dolly Varden char (*Salvelinus malma*), from the Yukon and Northwest Territory North Slope, Canada. M.Sc. Thesis, University of Manitoba, Winnipeg, MB.

Sandstrom, S.J., Chetkiewicz, C.B., and Harwood, L.A. 2001. Overwintering habitat of juvenile Dolly Varden (*Salvelinus malma*) (W.) in the Rat River, NT, as determined by radio telemetry. Canadian Science Advisory Secretariat 2001/092.

Sandstrom, S., Harwood, L., and Howland, K. 2009. Status of anadromous Dolly Varden char (*Salvelinus malma*) of the Rat River, Northwest Territories, as assessed through mark-recapture and live-sampling at the spawning and over-wintering site (1995-2007). Can. Tech. Rep. Fish. Aqua. Sci. p.75.

Sandstrom, S.J., and Harwood, L.A. 2002. Studies of anadromous Dolly Varden (*Salvelinus malma*) (W.), of the Big Fish River, NT, Canada 1972-1994. Canadian Manuscript Report of Fisheries and Aquatic Sciences 2603: i-vi, 1-31p.

Sandstrom, S.J., Chetkiewicz, C.B., and Harwood, L.A. 2001. Overwintering habitat of juvenile Dolly Varden (*Salvelinus malma*) (W.) in the Rat River, NT, as determined by radio telemetry. Canadian Science Advisory Secretariat Res.Doc. 2001/092, p.16.

Sandstrom, S.J., Lemieux, P.J., and Reist, J.D. 1997. Enumeration and biological data from the upstream migration of Dolly Varden charr (*Salvelinus malma*) (W.), from the Babbage River, Yukon north slope, 1990 to 1992. Canadian Data Report of Fisheries and Aquatic Sciences 1018: iv + 132p.

Secor, D.H., and Dean, J.M. 1992. Comparison of otolith-based back-calculation methods to determine individual growth histories of larval striped bass, *Morone saxatilis*. Canadian Journal of Fisheries and Aquatic Sciences **49**(7): 1439-1454.

Sirois, P., Lecomte, F., and Dodson, J.J. 1998. An otolith-based back-calculation method to account for time-varying growth rate in rainbow smelt (*Osmerus mordax*) larvae. Canadian Journal of Fisheries and Aquatic Sciences **55**(12): 2662-2671.

Solomon, C.T., Weber, P.K., Cech, J.J., Ingram, B.L., Conrad, M.E., Machavaram, M.V., Pogodina, A.R., and Franklin, R.L. 2006. Experimental determination of the sources of otolith carbon and associated isotopic fractionation. Canadian Journal of Fisheries and Aquatic Sciences **63**(1): 79-89.

Stearns, S.C. 1976. Life history tactics: review of ideas. Quarterly Review of Biology **51**(1): 3-47.

Stearns, S.C. 1992. The evolution of life histories. Oxford University Press, New York.

Stearns, S.C. 2000. Life history evolution: successes, limitations, and prospects. Naturwissenschaften **87**(11): 476-486.

Stefansson, S.O., Björnsson, B.T., Ebbesson, L.O.E., and McCormick, S.D. 2008. Smoltification. *In* Fish Larval Physiology. *Edited by* R.N. Finn and B.G. Kapoor, B.G. Science Publishers, Enfield, NH, pp. 639-681.

Stewart, D.B., Mochnacz, N.J., Reist, J.D., Carmichael, T.J., and Sawatzky, C.D. 2010. Fish life history and habitat use in the Northwest Territories: Dolly Varden (*Salvelinus malma*). Can. Manuscr. Rep. Fish. Aquat. Sci. 2915: vi + 63p.

Stewart, D.C., Middlemas, S.J., and Youngson, A.F. 2006. Population structuring in Atlantic salmon (*Salmo salar*): evidence of genetic influence on the timing of smolt migration in sub-catchment stocks. Ecology of Freshwater Fish **15**(4): 552-558.

Svenning, M.A., Smith-Nilsen, N., and M., J. 1992. Sea water migration of Arctic charr (*Salvelinus alpinus* L.): correlation between freshwater growth and seawater migration, based on back-calculation from otoliths. Nordic Journal of Freshwater Research **67**:18-26.

Swanson, H.K., Kidd, K.A., Babaluk, J.A., Wastle, R.J., Yang, P.P., Halden, N.M., and Reist, J.D. 2010. Anadromy in Arctic populations of lake trout (*Salvelinus namaycush*): otolith microchemistry, stable isotopes, and comparisons with Arctic char (*Salvelinus alpinus*). Canadian Journal of Fisheries and Aquatic Sciences **67**(5): 842-853.

Theriault, V., Bernatchez, L., and Dodson, J.J. 2007. Mating system and individual reproductive success of sympatric anadromous and resident brook charr, *Salvelinus fontinalis*, under natural conditions. Behavioral Ecology and Sociobiology **62**(1): 51-65.

Theriault, V., and Dodson, J.J. 2003. Body size and the adoption of a migratory tactic in brook charr. Journal of Fish Biology **63**(5): 1144-1159.

Thorpe, J.E. 1994. An alternative view of smolting in salmonids. Aquaculture **121**(1-3): 105-113.

Thorpe, J.E., Mangel, M., Metcalfe, N.B., and Huntingford, F.A. 1998. Modelling the proximate basis of salmonid life-history variation, with application to Atlantic salmon, *Salmo salar* L. Evolutionary Ecology **12**(5): 581-599.

Thorpe, J.E., Metcalfe, N.B., and Huntingford, F.A. 1992. Behavioural influences on life-history variation in juvenile Atlantic salmon, *Salmo salar*. Environmental biology of fishes **33**(4): 331-340.

Thorpe, J.E., and Morgan, R.I.G. 1980. Growth-rate and smolting-rate of progeny of male Atlantic salmon parr, *Salmo salar* L. Journal of Fish Biology **17**(4): 451-459.

Thorstad, E.B., Whoriskey, F., Uglem, I., Moore, A., Rikardsen, A.H., and Finstad, B. 2012. A critical life stage of the Atlantic salmon *Salmo salar*: behaviour and survival during the smolt and initial post-smolt migration. Journal of Fish Biology **81**(2): 500-542.

Underwood, T.J., Millard, M.J., and Thorpe, L.A. 1996. Relative abundance, length frequency, age, and maturity of Dolly Varden in nearshore waters of the Arctic National Wildlife Refuge, Alaska. Transactions of the American Fisheries Society **125**(5): 719-728.

Vigliola, L., Harmelin-Vivien, M., and Meekan, M.G. 2000. Comparison of techniques of back-calculation of growth and settlement marks from the otoliths of three species of *Diplodus* from the Mediterranean Sea. Canadian Journal of Fisheries and Aquatic Sciences **57**(6): 1291-1299.

Vigliola, L., and Meekan, M.G. 2009. The back-calculation of fish growth from otoliths. *In* Tropical Fish Otoliths: Information for Assessment, Management and Ecology. *Edited by* B.S. Green, B.D. Mapstone, G. Carlos and G.A. Begg. Springer, Dordrecht pp. 174-211.

Weisberg, S., Spangler, G., and Richmond, L.S. 2010. Mixed effects models for fish growth. Canadian Journal of Fisheries & Aquatic Sciences **67**(2): 269-277.

Wilson, J.A., Vigliola, L., and Meekan, M.G. 2009. The back-calculation of size and growth from otoliths: validation and comparison of models at an individual level. Journal of Experimental Marine Biology and Ecology **368**(1): 9-21.

Wright, P.J. 1991. The influence of metabolic rate on otolith increment width in Atlantic salmon parr, *Salmo salar* L. Journal of Fish Biology **38**(6): 929-933.

Wright, P.J., Fallon-Cousins, P., and Armstrong, J.D. 2001. The relationship between otolith accretion and resting metabolic rate in juvenile Atlantic salmon during a change in temperature. Journal of Fish Biology **59**(3): 657-666.

Wright, P.J., Metcalfe, N.B., and Thorpe, J.E. 1990. Otolith and somatic growth-rates in Atlantic salmon parr, *Salmo salar* L.: evidence against coupling. Journal of Fish Biology **36**(2): 241-249.

Wysujack, K., Greenberg, L.A., Bergman, E., and Olsson, I.C. 2009. The role of the environment in partial migration: food availability affects the adoption of a migratory tactic in brown trout *Salmo trutta*. Ecology of Freshwater Fish **18**(1): 52-59.

Yamamoto, T., Ueda, H., and Higashi, S. 1998. Correlation among dominance status, metabolic rate and otolith size in masu salmon. Journal of Fish Biology **52**(2): 281-290.

Yoshihara, H.T. 1973. Annual Progress Report for Monitoring and evaluation of Arctic waters with emphasis on the North Slope drainages. Alaska Dep. Fish Game, G-III-A, v.13, pp. 1-83.

Zimmerman, C.E. 2005. Relationship of otolith strontium-to-calcium ratios and salinity: experimental validation for juvenile salmonids. Canadian Journal of Fisheries and Aquatic Sciences **62**(1): 88-97.

Zuur, A.F., Ieno, E.N., N., W., Saveliev, A.A., and Smith, G.M. 2009. Mixed effects models and extensions in ecology with R. Springer, New York.