# GROWTH AND ENERGETIC CONDITION OF DOLLY VARDEN CHAR IN COASTAL ARCTIC WATERS

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# GROWTH AND ENERGETIC CONDITION OF DOLLY VARDEN CHAR IN COASTAL ARCTIC WATERS

A

DISSERTATION

Presented to the Faculty

of the University of Alaska Fairbanks

in Partial Fulfillment of the Requirements

for the Degree of

DOCTOR OF PHILOSOPHY

By

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Fairbanks, Alaska

May 2013

# Abstract

Dolly Varden char *Salvelinus malma* are a dominant member of the nearshore Arctic icthyofauna and support one of the largest subsistence fisheries within Arctic coastal communities in Alaska. Despite this importance, numerous aspects of Dolly Varden ecology remain poorly understood, which inhibits efforts to assess the biological consequences of anthropogenic disturbances such as hydrocarbon extraction and climate change within nearshore areas. The goal of this research was to develop and apply new techniques to measure and assess the biological integrity of Dolly Varden populations. To do so, I evaluated the precision of age determination generated from scales, otoliths, and fin rays, developed and validated bioelectrical impedance analysis (BIA) models capable of predicting non-lethal estimates of Dolly Varden proximate content, calculated and correlated retrospective estimates of Dolly Varden growth from archived otolith samples to broad-scale environmental variables, and investigated trends in whole body and tissue proximate content among years and demographics (i.e. reproductive versus non-reproductive individuals). Dolly Varden age determinations can be produced non-lethally using scales for fish up to age 5, while otoliths should be used for fish age 6 and greater. Multi-surface BIA models produced estimates of whole body proximate content with high precision. Retrospective growth analyses indicated growth increased significantly during the early 1980s, and was positively correlated to air temperature, sea surface temperature, and discharge and negatively correlated to ice concentration. Analyses of proximate content suggested that non-reproductive fish contained greater lipid concentrations than reproductive fish. Growth and condition analyses suggest that these metrics vary among years and are a function of reproductive cycles and environmental variability operating at multiple temporal and spatial scales. The adoption of scale-based aging and BIA technology will increase the precision of age-based biological statistics and aid in the detection of change within future Dolly Varden research and monitoring.

## Table of Contents

# List of Tables Page

## List of Figures

# Acknowledgements

I would like to thank my committee members Drs. Joseph Margraf, Anupma Prakash, Amanda Rosenberger, and Trent Sutton for the opportunity to conduct research within the Arctic and for their advice and support throughout my time at the University of Alaska Fairbanks.  Jeff Adams, Randy Brown, and David Daum of the U.S. Fish and Wildlife Service provided technical advice that guided me through the challenges of Arctic research and agency work.  I would also like to thank Dave Sowards for the many hours of flight time he logged transporting me to and from my field sites and for catching the majority of fish used in this research, albeit at the cost of numerous pixies.  Drs. Peter Bechtel, Lara Hortsmann-Dehn, and Matthew Wooller allowed me to borrow laboratory equipment and space.  Funding for this study was provided by the U.S. Fish and Wildlife Service, Arctic National Wildlife Refuge and the Fairbanks Fisheries Resource Office. Finally, I would like to thank my wife, Emily, for following me to Alaska and supporting me through this long process and my parents who first took me fishing. I would have never thought that evenings on the Connecticut River could ever turn into so much, or bring me so far.

## Introduction

The northern-form of Dolly Varden char *Salvelinus malma*, herein referred to as Dolly Varden, are distributed along the Arctic coast of North America from the Mackenzie River in Canada west and south through Alaska to the Seward Peninsula (Reist et al. 1997). Throughout their range, populations are largely organized by major river basin, and may contain both resident and sea-run individuals (Craig 1977a, 1977b, 1989; Everett et al. 1997). Beginning between ages 2 and 4, amphidromous Dolly Varden undertake annual migrations to the marine environment during the short summer open-water period from roughly June to September (McCart et al. 1972; Yoshihara 1973; Fechhelm et al. 1997). While at sea, individuals assemble into mixed-stock aggregates and forage heavily within nearshore lagoonal habitats that have turned brackish due to freshwater input (Craig 1984; Krueger et al. 1999). The brief sojourn at sea is a critical period for Dolly Varden because they must acquire close to 100% of their annual energy budget as little to no forage is consumed during the remainder of the year while in freshwater (Craig 1984; Boivin and Power 1990). Amphidromous fish mature between ages 5 and 8 and are unlikely to reproduce in consecutive years (Armstrong and Morrow 1980; Furniss 1975; Dutil 1986). Migrants return to freshwater spawning and overwintering habitats in coastal rivers during August and September at which time spawning may continue until November (McCart 1980). Following spawning, Dolly Varden move into spring-fed overwintering habitats where they remain, subsisting upon endogenous energy reserves until ice-out the following spring (Dutil 1986; Boivin and Power 1990).

Amphidromous populations of Dolly Varden inhabiting the Arctic coast of Alaska and Canada have received considerable attention since the discovery and development of hydrocarbon deposits in coastal areas during the 1960s (Yoshihara 1973; Glass 1989; Gallaway et al. 1991; Underwood et al. 1995; Brown 2008). Initially, this research focused on taxonomy and distributions, but gradually shifted to address broader ecological topics such as movement patterns and rates, origins, habitat interactions, and the identification of abiotic and biotic mechanisms limiting population structure and abundance (Craig and McCart 1974; Furniss 1975; Craig and Haldorson 1981; Craig 1989; Gallaway et al. 1991; Underwood et al. 1995; Everett et al. 1997; Krueger et al. 1999; Fechhelm et al. 2006). In support of the latter aim, present day research has focused on investigating biotic linkages within nearshore habitats and predicting the potential consequences of climate change and other associated anthropogenic disturbances on Dolly Varden and Arctic anadromous fishes in general (Carmack and MacDonald 2002; Dunton et al. 2006; Reist et al. 2006; Dunton et al. 2012). However, numerous aspects of Dolly Varden ecology and the complexity of nearshore Arctic environments make these investigations difficult.

Assessing the effects of a changing environment or physiological stressor requires the formation of species-habitat relationships (Wiens and Rotenberry 1981). To date, the majority of Dolly Varden research and monitoring activities have taken place during summer within nearshore brackish water habitats (Craig and Haldorson 1981; Gallaway et al. 1991; Underwood et al. 1995; Brown 2008). These sampling activities occur more frequently at this time of year due to warmer temperatures, favorable weather, and because ice cover precludes access to fish in freshwater for the majority of the year. During summer, nearshore lagoon habitats are brackish and exist as a constantly changing mosaic of temperature and salinity patches (Hale 1990; Maughan 1990). Large-scale temperature and salinity variations are driven by the direction and speed of the prevailing winds and freshwater discharge, while local patterns are a function of bathymetric conditions, water inflow, and the presence of barrier islands (Hale 1990; Gallaway et al. 1991). Spatial and temporal variability in local conditions can be high; for example, it is not uncommon to observe alterations in thermal conditions upwards of 5°C over a 2- to 3-day period (Hale 1990). Fish are generally captured using passive gears such as fyke or gill nets, and biological statistics such as length, condition, and catch per unit effort (CPUE) are correlated to environmental variables measured in situ at the net site and used to infer habitat use (Gallaway et al. 1991; Underwood et al. 1995). However, the results of these analyses often lack significant correlation, suggesting that Dolly Varden do not distribute themselves relative to the physical conditions of their environment (Neill and Gallaway 1989; Houghton et al. 1990; Underwood et al. 1995). Such a phenomenon is undoubtedly not the case, and likely reflects individual behavioral selection and the difficulties in characterizing such a dynamic habitat at relevant temporal and spatial scales.

While occupying nearshore areas, Dolly Varden continually seek temperatures optimal to the joint conduct of their physiological processes (Neill 1979). Occupation of a particular habitat will partially depend on the quality of the current habitat relative to adjacent habitats and the juxtaposition of patches in space. Presumably, movement will occur as habitat patches become reorganized and perceived benefits in a new habitat exceed realized benefits in the current habitat (Fretwell and Lucas 1970). If the state of environmental flux is so great as to preclude acclimatization to a particular regime, individuals may exist in a continual state of transit (Neill and Gallaway 1989). Because movement is required for capture using passive gears, selection of these individuals may result in temperature occupancy data that bears little resemblance to an individual's steady state preferences. Estimating other common biological statistics from nearshore catch data presents similar challenges.

Passive gears, such as fyke and gill nets, are used to sample Dolly Varden as they roam nearshore habitats while organized in mixed-stock aggregates (Krueger et al. 1999). Unless nets are set in the immediate vicinity of river mouths, catches will be comprised of varying proportions of individuals from multiple stocks, each with different growth trajectories (Craig 1977a; Fechhelm et al. 1997; Krueger et al. 1999). Furthermore, because larger Dolly Varden tend to occupy habitats further from shore, only small numbers of mature fish are typically captured (Craig and Haldorson 1981; Underwood et al. 1995; Fechhelm et al. 1997). Visual discrimination of sex or demographic (i.e. reproductive versus non-reproductive) attributes are difficult during summer, as reproductive fish have yet to develop secondary sexual characteristics; stock origin is primarily determined using genetic analysis which may not be feasible for moderate to large-scale research and monitoring projects (Everett et al. 1997). Therefore, using nearshore catch data to evaluate temporal and spatial trends in growth, abundance, or population structure or responses in these variables to environmental gradients can be difficult due to net selectivity, variable and unknown movement patterns and rates, environmental stochasticity, and the inability to readily partition variability among populations and demographics.

The inability to control for these additional sources of variability inhibit analyses of length and CPUE and have likely contributed to some findings that suggest few statistical differences exist in these metrics over time or space or in response to environmental gradients (Whitmus et al. 1987; Colonell and Gallaway 1990; Gallaway et al. 1991). Analyses of weight- and length-based condition are often used to supplement the aforementioned analyses (Gallaway et al. 1991; Underwood et al. 1997). Morphometric condition indices assume that changes in morphology are met by proportional alterations to individual energy content, which in fish is primarily in the form of lipid (Shul’man 1974; Pope and Kruse 2007). However, during periods of physiological stress or starvation, such as during overwintering, lipid lost to metabolism may be offset by water uptake (Glass 1989; Shearer 1994; Navarro and Gutiérrez 1995). Such processes maintain individual body mass and morphology despite a potentially substantial loss in whole body energy content. Because morphological condition estimates cannot distinguish lipid from water weight, they are less sensitive to changes in energy content, particularly within species that require the storage and subsequent mobilization of large quantities of lipid such as Dolly Varden (Glass 1989; Sutton et al. 2000). These factors may have contributed to the opinion of some that traditional condition analyses will always be an ineffective means of assessing the effects of environmental variables (Colonell and Gallaway 1990).

As a result of the difficulties in estimating relevant biotic and abiotic variables within nearshore environments with precision, we currently have an incomplete understanding of numerous aspects of Dolly Varden ecology including life-history variation, habitat interactions, movement patterns, and population dynamics (Neill and Gallaway 1989; Houghton et al. 1990; Gallaway et al. 1991; Underwood et al. 1995). To improve our understanding of Dolly Varden ecology, new methods and approaches are warranted. Reproductive Dolly Varden exhibit philopatry to natal drainages; however, some non-spawning and juvenile individuals may overwinter in non-natal drainages (DeCicco 1985; Crane et al. 2005). Thus, sampling adult fish within freshwater habitats may reduce inter-population differences in biological statistics such as growth or condition (Underwood et al. 1995). Furthermore, visual discrimination of demographics may be more likely during this time as the majority of reproductive fish will exhibit coloration and secondary sexual characteristics. Successful identification may permit variability in growth or condition to be partitioned amongst biologically relevant demographic groups more effectively.

Estimates of physiological well-being may be improved by using proximate analysis in lieu of weight- and length-based condition estimates. Proximate analysis may produce more precise estimates of physiological well-being by estimating energy content directly rather than inferring it from individual morphology (Sutton et al. 2000). However, this technique is lethal as well as time- and resource-intensive, two factors that have likely limited its widespread use within fisheries research thus far. Recent research suggests that rapid estimates of proximate composition may be acquired non-lethally in the field using bioelectrical impedance analysis (BIA; Cox and Hartman 2005). Bioelectrical impedance analysis measures the impedance (resistance and reactance) of a current as it is passes through a subject. Resistance measures the opposition by a body to the passage of an electrical current and is related to the amount of lipid-free mass within the subject as lipid is a poor conductor of electricity (Kyle et al. 2004). Alternatively, reactance measures the electrical storage capacity of a tissue and is related to the cellular volume of a subject as the lipid-bilayer of a cell acts as a capacitor when excited by an electrical current (Kyle et al. 2004). Using electrical property equations, BIA data can be converted into numerous predictive variables that can then be used to model proximate composition (Khaled et al. 1988; Cox and Hartman 2005; Hafs and Hartman 2011). Once calibrated, BIA models have produced estimates of condition that rival proximate composition based estimates in terms of quality and traditional estimates in terms of speed and resources required (Cox and Hartman 2005). However, no such model has been created for Dolly Varden.

Research and monitoring activities within the Arctic are logistically challenging and expensive due to the remoteness of field sites, inclement weather, and the short duration of the summer open-water period. These factors likely contribute to the relatively short temporal scales over which the majority of Arctic research and monitoring projects are conducted (Furniss 1974, 1975; Daum et al. 1984; Wiswar and West 1987; Underwood et al. 1995). Given the cost and difficulty of operating within remote Arctic areas, simply extending sampling efforts is often not feasible. Instead, temporal expanse may be lengthened by utilizing archived growth and habitat data that have been collected during past research and monitoring efforts. North Slope aquatic research has been conducted sporadically throughout the past 30 years and a wealth of data exists on several populations of Dolly Varden (Wiswar and West 1987; Underwood et al. 1997; Viavant 2005; Brown 2008). Of particular use may be growth data preserved within the annular increments of calciferous structures such as otoliths. Following sectioning, back-calculation and other techniques can be used to produce retrospective estimates of annual growth (Isely and Grabowski 2007). Combined with archived habitat data collected remotely or on the ground, these data can be used to assess trends in growth over time and space or in response to broad-scale habitat alterations (Woodbury 1999; Rypel 2009; Von Biela et al. 2011)

The goal of this research is to develop and implement new tools and approaches to Dolly Varden research and monitoring in order to obtain a greater understanding of their ecology and dynamics. To do so, I: 1) evaluated the precision of age determinations produced from scales, otoliths, and fin rays, 2) developed and validated BIA models capable of producing non-invasive predictions of Dolly Varden proximate content, 3) used archived otolith samples collected over the past the past 25 years from Arctic Alaska to calculate and then correlate retroactive growth estimates to remotely sensed habitat variables collected over similar time scales, and 4) investigated trends in whole body and tissue proximate composition among demographics and years from Dolly Varden collected within freshwater.

The first two objectives develop new tools with which to efficiently partition variability in biological statistics among cohorts and quantify physiological condition.

The evaluation and/or development of non-lethal aging methods will permit the collection of more aging data which may contribute to more precise age-based biological statistics. Furthermore, the development of Dolly Varden BIA models will permit the production of non-invasive estimates of proximate content (Cox and Hartman 2005). Energy-based condition metrics are superior to traditional weight- and length-based condition metrics as they measure energy content directly rather than inferring it from morphology (Sutton et al. 2000). The latter two objectives apply new approaches to investigating species-habitat relationships and temporal trends in Dolly Varden growth and condition. The temporal extent of retrospective growth analyses may shed new light onto broad-scale abiotic factors limiting Dolly Varden growth while analyzing proximate content of fish captured in freshwater may clarify variability in condition among years and demographics. Together, these analyses will contribute to our understanding of Dolly Varden ecology, develop new tools to better quantify biotic and abiotic statistics, and guide future Dolly Varden research and monitoring activities.

## References

Armstrong, R. H., and J. E. Morrow. 1980. The Dolly Varden char, *Salvelinus malma*. Pages 99-140 *in* U. K. Balon, editor. Charrs: salmonid fishes of the genus *Salvelinus*. Dr. W. Junk bv Publishers, The Hague, The Netherlands.

Boivin, T. G., and G. Power. 1990. Winter condition and proximate composition of anadromous Arctic char (*Salvelinus alpinus*) in eastern Ungava Bay, Quebec. Canadian Journal of Zoology 68:2284-2289.

Brown, R. J. 2008. Life history and demographic characteristics of Arctic cisco, Dolly Varden, and other fish species in the Barter Island region of northern Alaska. U.S. Fish and Wildlife Service, Alaska Fisheries Technical Report No. 101, Fairbanks, Alaska.

Carmack, E. C., and R. W. Macdonald. 2002. Oceanography of the Canadian Shelf of the Beaufort Sea: a setting for marine life. Arctic 55:29-45.

Colonell, J. M., and B. J. Gallaway, editors. 1990. An assessment of marine environmental impacts of West Dock causeway. Report for Prudhoe Bay unit owners represented by ARCO-Alaska, Inc. Prepared by Woodward-Clyde Consultants and LGL Alaska Research Associates, Inc., Anchorage Alaska.

Cox, K. M., and K. J. Hartman. 2005. Nonlethal estimation of proximate composition in fish. Canadian Journal of Fisheries and Aquatic Sciences 62:269-275.

Craig, P. C. 1977a. Ecological studies of anadromous and resident populations of Arctic char in the Canning river drainage and adjacent coastal waters of the Beaufort Sea, Alaska. Pages 1-116 (Chapter 1) *in* P. McCart, editor. Fisheries investigations along the North Slope and Beaufort Sea coast in Alaska with emphasis on Arctic char, Aquatic Environments Limited, Arctic Gas Biological Report Series, Volume 41, Calgary, Alberta.

Craig, P. C. 1977b. Fisheries investigations in the Shaviovik River drainage, Alaska, with emphasis on Arctic char in the Kavik River. Pages 1-28 (Chapter 3) *in* P. McCart, editor. Fisheries Investigations along the North Slope and Beaufort Sea coast in Alaska with emphasis on Arctic char, Aquatic Environments Limited, Arctic Gas Biological Report Series, Volume 41, Calgary, Alberta.

Craig, P. C. 1984. Fish use of the coastal waters of the Alaskan Beaufort Sea: a review. Transactions of the American Fisheries Society 113:265-282.

Craig, P. C. 1989. An introduction to anadromous fishes in the Alaskan Arctic. Biological Papers of the University of Alaska 24:27-54.

Craig, P. C., and L. Haldorson. 1981. Fish. Pages 384-678 *in* S. R. Johnson and W. J. Richardson, editors. Beaufort Sea barrier island-lagoon ecological process studies: final report, Simpson Lagoon, part 4. Environmental assessment of the Alaskan continental shelf, final report of principal investigators vol. 8: Biological Studies. National Oceanic and Atmospheric Administration, Outer Continental Shelf Environment Assessment Program, and Bureau of Land Management, Boulder, Colorado.

Craig, P. C., and P. J. McCart. 1974. Fall spawning and overwintering areas of fish populations along routes of proposed pipeline between Prudhoe Bay and the Mackenzie Delta 1972-1973. Pages 1-37(Chapter 3) *in* P. C. Craig, editor. Fisheries research associated with proposed gas pipeline routes in Alaska, Yukon, and Northwest Territories. Aquatic Environments Limited, Arctic Gas Biological Report Series, Volume 15, Calgary, Alberta

Crane, P., T. Viavant, and J. Wenburg. 2005. Overwintering patterns of Dolly Varden *Salvelinus malma* in the Sagavanirktok River in the Alaskan North Slop inferred using mixed-stock analysis. U.S. Fish and Wildlife Service, Alaska Fisheries Technical Report No. 84, Anchorage, Alaska.

Daum, D., P. Rost, and M. W. Smith. 1984. Fisheries studies on the North Slope of the Arctic National Wildlife Refuge, 1983. Pages 1-57 *in* G. W. Gamer and P. E. Reynolds, editors. Arctic National Wildlife Refuge coastal plain resource assessment, 1983 update report baseline study of the fish, wildlife, and their habitats. U.S. Fish and Wildlife Service, Anchorage, Alaska.

DeCicco, A. L. 1985. Inventory and cataloging of sport fish and sport fish waters of western Alaska with emphasis on Arctic char life history studies. Alaska Department of Fish Game, Federal Aid in Fish Restoration, Project F-9-17, Annual Report 1984-1985, Fairbanks.

Dunton, K. H., S. V. Schonberg, and L. W. Cooper. 2012. Food web structure of the Alaskan nearshore shelf and estuarine lagoons of the Beaufort Sea. Estuaries and Coasts 35:416-435.

Dunton, K. H., T. Weingartner, and E. C. Carmack. 2006. The nearshore western Beaufort Sea ecosystem: circulation and importance of terrestrial carbon in Arctic coastal food webs. Progress in Oceanography 71:362-378.

Dutil, J. D. 1986. Energetic constraints and spawning interval in the anadromous Arctic charr (*Salvelinus alpinus*). Copeia 4:945-955.

Everett, R. J., R. L. Wilmot, and C. C. Krueger. 1997. Population genetic structure of Dolly Varden from Beaufort Sea drainages of Northern Alaska and Canada. American Fisheries Society Symposium 19:240-249.

Fechhelm, R. G., J. D. Bryan, W. B. Griffiths, and L. R. Martin. 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 54:1103-1110.

Fechhelm, R. G., G. B. Buck, and M. R. Link. 2006. Year 24 of the long-term monitoring of nearshore Beaufort Sea fishes in the Prudhoe Bay region, 2006. Report for BP Exploration (Alaska) Inc. by LGL Alaska Research Associates, Inc., Anchorage.

Fretwell, S. D., and H. L. Lucas. 1970. On territorial behavior and other factors influencing habitat distribution in birds. I. theoretical development. Acta Biotheoretica 19:16-36.

Furniss, R. A. 1974. Inventory and cataloging of Arctic area waters. Alaska Department of Fish and Game, Federal Aid in Fish Restoration, Project F-9-6, Annual Report of Progress, Anchorage.

Furniss, R. A. 1975. Inventory and cataloging of Arctic area waters. Alaska Department of Fish and Game, Federal Aid in Fish Restoration, Project F-9-7, Annual Report of Progress, Anchorage.

Gallaway, B. J., W. J. Gazey, J. M. Colonell, A. W. Niedoroda, and C. J. Herlugson. 1991. The Endicott Development Project - preliminary assessment of impacts from the first major offshore oil development in the Alaskan Arctic. American Fisheries Society Symposium 11:42-80.

Glass, D. R. 1989. Changes in the condition and physiological parameters of anadromous fish species in the central Beaufort Sea during the overwintering period. Part I, Chapter II *in* Endicott Environmental Monitoring Program - 1987. Report by Envirosphere Company for the U.S. Army Corps of Engineers, Anchorage, Alaska.

Hafs, A. W., and K. J. Hartman. 2011. Influence of electrode type and location upon bioelectrical Impedance analysis measurements of brook trout. Transactions of the American Fisheries Society 140:1290-1297.

Hale, D. A. 1990. A description of the physical characteristics of nearshore and lagoonal waters in the eastern Beaufort Sea. National Oceanic and Atmospheric Administration, Office of Oceanography and Marine Assessment. Report to U.S. Fish and Wildlife Service, Anchorage, Alaska.

Houghton, J. P., C. J. Whitmus, and A. W. Maki. 1990. Habitat relationships of Beaufort Sea anadromous fish: integration of oceanographic information and fish-catch data. Pages 73-88 *in* R. M. Meyer and T. M. Johnson, editors. Fisheries oceanography-a comprehensive formulation of technical objectives for offshore application in the Arctic. United States Department of the Interior, Minerals Management Service, OCS Study MMS 88-0042.

Isely, J. J., and T. B. Grabowski. 2007. Age and growth. Pages 187-228 *in* C. S. Guy and M. L. Brown, editors. Analysis and interpretation of freshwater fisheries data. American Fisheries Society, Bethesda, Maryland.

Khaled, M., M. J. McCutcheon, S. Reddy, P .L. Pearman, G. R. Hunter, and R. L. Weinsier. 1988. Electrical impedance in assessing human body composition: the BIA method. The American Journal of Clinical Nutrition 47:789-792.

Krueger, C. C., R. L. Wilmot, and R. J. Everett. 1999. Stock origins of Dolly Varden collected from Beaufort Sea coastal sites of Arctic Alaska and Canada. Transactions of the American Fisheries Society 128:49-57.

Kyle, U. G., I. Bosaeus, A. D. De Lorenzo, P. Deurenberg, M. Elia, and J. M. Gomez. 2004. Bioelectrical impedance analysis - part 1: review of principles and methods. Clinical Nutrition 23:1226-1243.

Maughan, O. E. 1990. Habitat. Pages 85-96 *in* MBC Applied Environmental Sciences, editors. A synthesis of environmental information on causeways in the nearshore Beaufort Sea. United States Department of the Interior, Minerals Management Service, OCS Study MMS 89-0038, Anchorage, Alaska

McCart, P. J. 1980. A review of the systematic and ecology of Arctic char, *Salvelinus alpinus*, in the western Arctic. Canadian Technical Report of Fisheries and Aquatic Sciences No. 935, Winnipeg, Manitoba.

McCart, P., P. Craig, and H. Bain. 1972. Report on fisheries investigations in the Sagavanirktok River and neighboring drainages. Alyeska Pipeline Service Company, Bellevue,Washington.

Navarro, I., and J. Gutiérrez. 1995. Fasting and starvation. Pages 393-434 *in* P. W. Hochachika and T. P. Mommsen, editors. Biochemistry and molecular biology of fishes, volume 4, metabolic biochemistry. Elsevier, Amsterdam.

Neill, W. H. 1979. Mechanisms of fish distribution in heterothermal environments. American Zoologist 19:305-315.

Neill, W. H., and B. J. Gallaway. 1989. "Noise" in the distributional responses of fish to environment: an exercise in deterministic modeling motivated by the Beaufort Sea experience. Biological Papers of the University of Alaska 24:123-130.

Pope, K. L., and C. G. Kruse. 2007. Age and growth. Pages 187-228 *in* C. S. Guy and M. L. Brown, editors. Analysis and interpretation of freshwater fisheries data. American Fisheries Society, Bethesda, Maryland.

Reist, J. D., J. D. Johnson, and T. J. Carmichael. 1997. Variation and specific identity of char from Northwestern Arctic Canada and Alaska. American Fisheries Society Symposium 19:250-261.

Reist, J. D., F. J. Wrona, T. D. Prowse, M. Power, J. B. Dempson, R. J. Beamish, J. R. King, T. J. Carmichael, C. D. and Sawatzky. 2006. General effects of climate change on Arctic fishes and fish populations. Ambio 35:370-380.

Rypel, A. L. 2009. Climate-growth relationships for largemouth bass (*Micropterus salmoides*) across three southeastern USA states. Ecology of Freshwater Fish 18:620-628.

Shearer, K. D. 1994. Factors affecting the proximate composition of cultured fishes with emphasis on salmonids. Aquaculture 119:63-88.

Shul'man, G. E. 1974. Life cycles of fish, physiology and biochemistry. Wiley, New York.

Sutton, S. G., T. P. Bult, and R. L. Haedrich. 2000. Relationships among fat weight, body weight, water weight, and condition factors in wild Atlantic salmon parr. Transactions of the American Fisheries Society 129:527-538.

Underwood, T. J., J. A. Gordon, M. J. Millard, L. A. Thorpe, and B. M. Osborne. 1995. Characteristics of selected fish populations of Arctic Wildlife Refuge coastal waters, final report, 1988-1991. U.S. Fish and Wildlife Service, Alaska Fisheries Technical Report No. 28, Fairbanks, Alaska.

Underwood, T. J., D. E. Palmer, and L. A. Thorpe. 1997. Weight-length relationships and condition of Dolly Varden in coastal waters of the Arctic National Wildlife Refuge, Alaska. American Fisheries Society Symposium 19:295-309.

Viavant, T. 2005. Eastern North Slope Dolly Varden stock assessment. Alaska Department of Fish and Game. Fishery Data Series Number 05-07, Anchorage.

Von Biela, V. R., C. E. Zimmerman, and L. L. Moulton. 2011. Long-term increases in young-of-the-year growth of Arctic cisco *Coregonus autumnalis* and environmental influences. Journal of Fish Biology 78:39-56.

Whitmus, C. J., T. C. Cannon, and S. S. Parker. 1987. Age, growth, and condition of anadromous fish. Pages 1-34 *in* 1985 Final report for the Endicott Environmental Monitoring Program, volume 7. Report of Envirosphere Company to United States Army Corps of Engineers, Anchorage, Alaska.

Wiens, J. A., and J. T. Rotenberry. 1981. Habitat associations and community structure of birds in shrubsteppe environments. Ecological Monographs 51:21-42.

Wiswar, D. W., and R. L. West. 1987. Fisheries investigations in Beaufort Lagoon, Arctic National Wildlife Refuge, Alaska, 1985. Pages 778-800 *in* G. W. Garner and P. E. Reynolds, editors. Arctic National Wildlife Refuge coastal plain resource assessment, 1985 update report, baseline study of the fish, wildlife, and their habitats. U.S. Fish and Wildlife Service, Anchorage, Alaska.

Woodbury, D. 1999. Reduction of growth in otoliths of widow and yellow rockfish (*Sebastes entomelas* and *S. flavidus*) during the 1983 El Nińo. Fisheries Bulletin 97:680-689.

Yoshihara, H. T. 1973. Monitoring and evaluation of Arctic waters with emphasis on the North Slope drainages. Alaska Department of Fish and Game, Division of Sport Fish, Federal Aid in Fish Restoration, Project F-9-5, Annual Progress Report 1972-1973, Juneau

# Chapter 1: Precision analysis of three aging structures for amphidromous DollyVarden Char from Alaskan Arctic rivers[1]

## Abstract

The accuracy of population statistics, and the validity of management actions they motivate, are in part dependent on the acquisition of quality age determinations. Such data for northern-form Dolly Varden char *Salvelinus malma* have been traditionally garnered using otoliths, despite little research investigating the consistency of this, or alternative non-lethal techniques. To address these data gaps, the precision of age determinations generated from scales, otoliths, and fin rays was examined for 126 amphidromous Dolly Varden collected from two Arctic rivers. We used three independent readers, age-bias plots, coefficient of variation (CV), and percent agreement (PA) to estimate bias and precision for within-reader, among-structure and among-reader, within-structure comparisons. Among-reader, within-structure tests of CV suggested that otoliths produced more precise age determinations than fin rays, while scale and otolith aging precision were similar. Age-bias plots suggested scales consistently underestimated age relative to otoliths beginning at age 6. Underestimation was also apparent, but less distinct, within fin ray-otolith and scale-fin ray comparisons. Potential sources of error and management implications are discussed. Because scale and otolith ages exhibited little bias within cohorts younger than age 6, age may be determined non-lethally in these cohorts using scales; otoliths should be used otherwise.

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[1] Stolarski, J. T., and T. M. Sutton. North American Journal of Fisheries Management (submitted).

## Introduction

Northern-form Dolly Varden char *Salvelinus malma*, herein referred to as Dolly Varden, are distributed along the Arctic coast of North America from the Mackenzie River in Canada, west and south through Alaska to the Seward Peninsula (Reist et al. 1997). Throughout their range, populations are largely organized by major river basin, and may contain both resident and sea-run individuals (McCart 1980; Everett et al. 1997). Amphidromous fish are generally larger and more abundant than residents and support one of largest and most important traditional subsistence fisheries within Arctic coastal communities of Alaska (McCart 1980; Pedersen and Linn 2005). Concerns regarding the potential ecological impacts of oil and gas exploration and climate change in the Arctic have strengthened the need for sound management and monitoring practices (Hachmeister et al. 1991; Reist et al. 2006). The validity of such practices are, in part, dependent upon the acquisition of quality age determinations as they are often developed using age-specific biological data.

Northern fish species, such as Dolly Varden, are typically aged using calcified structures due to their longevity and slow rates of growth (McCart 1980; Howland et al. 2004). For a structure to be useful for age determination purposes, it must produce ages that are both accurate (not addressed herein) and precise. Dolly Varden age is almost exclusively estimated using otoliths, either viewed whole or broken through the nucleus (Heiser 1966; Yoshihara 1973; Armstrong 1974; McCart 1980; Underwood 1995). Scale techniques have been largely disregarded due to research within Arctic char *Salvelinus alpinus* suggesting scale circuli patterns are unreliable predictors of fish age (Barber and

McFarlane 1987; Baker and Timmons 1991); fin ray techniques have rarely been used (Heiser 1966; Barber and McFarlane 1987). Non-lethal techniques using scales and fin rays conserve fish and allow age data to be collected from a greater proportion of individuals within a population. This may be particularly advantageous when aging Dolly Varden, as the length ranges of successive cohorts typically display considerable overlap (Underwood et al. 1995). Such overlap can contribute to error in age-specific biological statistics when extrapolating age data from a sub-sample to a larger population as is often the case when using age-length keys. However, before nonlethal techniques can be employed, the precision of scale, otolith, and fin ray techniques must be compared.

In the only study that could be found investigating the reproducibility of age determinations for Dolly Varden, Barber and McFarlane (1987) concluded that otoliths generally produced older age determinations relative to pectoral and anal fin rays. However, this research did not determine age using scales, used a single reader which limited analyses to comparisons among structures, and was conducted on pooled samples containing both Dolly Varden and Arctic char (Reist et al. 1997). As a result, the precision of Dolly Varden aging techniques both within and among structures remains poorly defined. To address this data gap, the objective of this study was to estimate the precision of scale, otolith, and fin ray age determinations for within- and among-structure comparisons.

## Methods

### Study site

This study was conducted at spawning and overwintering habitats of amphidromous Dolly Varden on the Ivishak and Hulahula rivers, located on the coastal plain of the Alaskan Arctic (Figure 1.1; Daum et al. 1984; Viavant 2005). The Ivishak River is a north-flowing tributary of the Sagavanirktok River, the second largest river on the North Slope of Alaska. Both rivers originate in the Brooks Mountain range and drain into the Beaufort Sea, the Sagavanirktok River at Prudhoe Bay and the Hulahula River near the coastal community of Kaktovik. Both rivers contain resident and amphidromous populations of Dolly Varden.

### Fish sampling

Post-smolt Dolly Varden were captured via angling from the Ivishak River during sampling events in early September 2009, 2010, and 2011. Pre-smolt fish were collected using minnow traps from the Hulahula River during August 2011. Sampling exclusively within habitats known to be frequented by large numbers of amphidromous fish minimized the likelihood of capture and inclusion of resident fish into the study. Upon capture, individuals were sacrificed, weighed to the nearest 1 g, and measured to the nearest 1 mm in fork length. Each fish was individually labeled, wrapped in plastic, and transported to the University of Alaska Fairbanks where they were frozen. In the laboratory, scales were sampled from an area posterior to the dorsal fin and above the lateral line using a scalpel, then stored on waterproof paper (DeVries and Frie 1996).

The right pectoral fin was removed from each fish, rinsed in water, and stored in a similar fashion in a well-ventilated area to facilitate drying. Sagittal otoliths were removed using the “open the hatch” method of Secor et al. (1992), rinsed in water, dried, and stored dry in individually labeled plastic vials.

## Structure preparation

Fifteen to 20 scales from each fish were wet mounted on a glass slide and viewed with a compound microscope under transmitted light at 40X magnification. After screening the sub-sample for the presence of regenerated scales, an image of a representative scale was captured using a 3.3 megapixel microscope-mounted digital camera (Quantitative Imaging Co., Burnaby, Canada).

Fin rays were embedded in Epoxycure® epoxy resin (Buehler, Lake Bluff, Illinois) following methods outlined in Koch and Quist (2007). Multiple transverse sections, each 0.5 to 0.75 mm in thickness, were cut using an Isomet® low speed saw (Buehler, Lake Bluff, Illinois), equipped with a 102 mm diameter diamond wafering blade rotating at 240 revolutions per minute. Care was taken to assure the first thin section encompassed or was slightly posterior to the inflection point of the ray (Beamish 1981). Sections were affixed to a glass slide using Crystalbond® thermoplastic cement (Structure Probe Inc., West Chester, Pennsylvania) and viewed with a compound microscope. A digital image was captured of a representative fin ray at 20X and 40X magnifications under transmitted light.

The right sagittal otolith of each fish was affixed to a glass slide using Crystalbond® thermoplastic cement perpendicular to the long axis of the otolith. Each otolith was ground to the core in the transverse plane using a thin section machine (Hillquist Inc., Denver, Colarado) and remounted to the slide flat side down before being ground to a final thickness of approximately 0.3 mm. The otolith was hand polished with a 1-µm diamond abrasive and viewed with a compound microscope under transmitted light. Digital images were captured at 20X and 40X magnifications. If the mounted otolith section was deemed inadequate for age determination, the left sagitta was processed in the same fashion.

### Age determination

Age determinations were produced by three independent readers trained in annulus identification. Each reader estimated fish age from scales, otoliths, and fin rays. Readers were provided with the capture date of the fish, but had no knowledge of fish length. Scale annuli were identified as areas of greater circuli density or when successive circuli cut over each other. Annuli in fin ray and otolith sections were identified as alternating opaque and hyaline zones (DeVries and Frie 1996). Fin ray age estimates were derived from the first or second ray. Images were organized into separate libraries by structure and no reader was allowed to determine age from multiple libraries within a single day. To our knowledge, scale, otolith, and fin ray age determinations for Dolly Varden have yet to be validated.

### Statistical analysis

Age-bias plots were used to assess among-reader, within-structure and within-reader, among-structure bias (Campana et al. 1995). Age-bias plots depict the mean age of fish determined by one reader that are assigned a given age by a second reader. Cohorts displaying complete agreement among ages assigned by each reader will fall on the 1:1 line of equivalence. Thus, bias is detected visually as persistent (> 2 successive years) deviations of the 95% confidence intervals surrounding each mean from the line of equivalence. Detection of among-reader, within-structure bias is important as it indicates if readers are using unified criteria to identify and count annuli. If one or multiple readers consistently over- or under-estimates age relative to others, precision within that structure will reflect variability in aging methods rather than the reproducibility of age determinations. If bias is detected, the criteria by which annuli are identified and counted must be revisited and agreed upon by readers and ages must be redetermined. Alternatively, within-reader, among-structure bias can be used to evaluate the relative strength of any under- or overestimation of ages between the techniques. Precision of among-reader, within-structure and within-reader, among-structure comparisons was estimated using percent agreement (PA), percent agreement to within one year (PA1), and coefficient of variation (CV). Percent agreement statistics were calculated as the number of pairwise comparisons in which age was in total agreement (in the case of PA) or the number of pairwise comparisons in which age was in agreement to within one year (in the case of PA1) divided by the total number of comparisons made. Percent agreement statistics, once the predominant means of assessing the precision of aging structures, are slowly being replaced with statistics such as CV as the latter measures do not account for age structure variation among species (Beamish and Fournier 1981). As such, these statistics are only mentioned briefly and included primarily as a means of comparison to past research. The coefficient of variation was calculated as:

$$CV_j = 100 \bullet \frac{\sqrt{\sum_{i=1}^{R} \frac{(X_{ij} - X_j)^2}{R-1}}}{X_j}, \qquad (1.1)$$

where $X_{ij}$ is the *i*th age determination for the *j*th fish, $X_j$ is the mean age of the jth fish, and R is the number of times the age of the fish is estimated (Chang 1982). The coefficient of variation was averaged across all fish for each structure in the case of among-reader, within structure comparisons and across specific comparisons (i.e., scales versus fin rays) for within-reader, among-structure comparisons. Potential differences among structures and comparisons were tested using analysis of variance with a post-hoc Tukey’s honest significance test when significant differences were detected. All statistical analyses were conducted using the statistical software package R (R development Core Team 2012) and evaluated at an $\alpha = 0.05$.

## Results

Of the total 143 pre- and post-smolt Dolly Varden that were collected over the three years of sampling, 126 of these fish were included into the final analyses. Individuals ranged in fork length from 63 to 680 mm and encompassed ages 0 to 14 (Figure 1.2). Annuli were identified from digital images for all three structures (Figure 1.3). Scale circuli patterns varied substantially between the freshwater and marine periods of growth, with the marine phase exhibiting far greater spacing between successive circuli. Visual examination of among-reader, within-structure age-bias plots showed little persistent (> 2 consecutive years) deviation from the 1:1 equivalence line, indicating readers used similar standards in identifying and counting annuli (Figure 1.4). Mean PA and PA1 of among-reader, within-structure comparisons were similar among structures (Table 1.1). However, mean PA did not exceed 55% for any structure while mean PA1 exceeded 90% for all structures (Table 1.1). Age-bias plots of within-reader, among-structure comparisons indicated that scales began to underestimate fish age relative to otoliths beginning at age 6 (Figure 1.5), with errors increasing with age. These plots also indicated that fin rays tended to underestimate age relative to otoliths and that scales tended to underestimate age relative to fin rays also beginning at age 6, with errors generally remaining constant with increasing age (Figure 1.5). However, these trends are less pronounced relative to scale-otolith comparisons. Mean PA and PA1 of within-reader, among-structure comparisons were similar among comparisons but were generally lower than among-reader, within-structure estimates (Table 1.1). No differences in CV were detected for within-reader, among-structure comparisons (Table 1.1: $F_{2, 373} = 0.347$, $p = 0.707$). The coefficient of variation of among-reader, within-structure comparisons differed among structures (Table 1.1; $F_{2, 373} = 3.143$, $p = 0.044$). A post-hoc Tukey test indicated that otoliths were more precise predictors of Dolly Varden age than fin rays.

## Discussion

This research contributes to a growing body of literature indicating that scales typically underestimate fish age relative to otoliths (Silkstrom 1983; Hubert et al. 1987; Sharpe and Bernard 1988; Graynoth 1996; Kruse et al. 1997; DeCicco and Brown 2006; Stolarski and Hartman 2008). The onset of scale underestimation corresponded well with estimates of the age at first reproduction for Dolly Varden, suggesting underestimation was a result of ontogenetic reductions in growth and the formation of a "dense edge" on the scale margins (Nordeng 1961; Yoshihara 1973; Craig and Haldorson 1981). A similar artifact was often present in the interior of the scale and was most likely a result of slow pre-smolt growth while in freshwater (McCart 1980). These features highlight the importance of training readers in both freshwater and marine annulus identification as scale morphology and annuli appearance will change depending upon the growth rate of the fish (Carlander 1974).

Within-reader comparisons of fin ray and otolith age determinations suggested that fin rays underestimated age relative to otoliths beginning at age 6. Barber and McFarlane (1987) noted similar results studying age determinations from a mixed sample of Dolly Varden and Arctic char. Fin ray underestimation has also been reported in Arctic grayling *Thymallus arcticus* (Silkstrom 1983), rainbow trout *Oncorhynchus mykiss* and brown trout *Salmo trutta* (Graynoth 1996), cutthroat trout *Salmo clarki* (Hubert et al. 1987), and brook trout *Salvelinus fontinalis* (Stolarski and Hartman 2008). However, Zymonas and McMahon (2009) reported no bias among comparisons of ages derived from pelvic fin rays and otoliths of bull trout *Salvelinus confluentus*. Chronic misidentification of the first few annuli in fin ray sections is commonly cited as a potential cause of underestimation (Silkstrom 1983; Hubert et al. 1987). Working with a population of slow-growing white suckers *Catostomus commersoni*, Beamish (1973) noted that the first fin ray annulus was often too closely associated with the ray center to be consistently identified, particularly within older fish. For Dolly Varden, interior annuli clarity was often diminished within older fish and also declined as the location where the fin ray section was cut moved further from the inflection point of the ray. The effect of the latter phenomenon was minimized by deriving ages from one of the first three fin ray sections of the series. However, evidence of more constant errors within older fish suggests that misidentification of freshwater annuli could be occurring within these cohorts.

Within-reader comparisons of scale and fin ray age determinations suggested that scales often underestimated fish age, again beginning at age 6. However, this relationship was less pronounced relative to scale-otolith and fin ray-otolith comparisons. Previous research involving similar comparisons has been generally inconsistent, with some studies confirming (Silkstrom 1983; Stolarski and Hartman 2008), and others refuting (Hubert et al. 1987; Copeland et al. 2007) our results. Given suspected sources of error within each of the two structures (see above), the lack of a consistent trend could be a function of the proportion of instances in which reader errors are isolated within a single structure versus when errors occur simultaneously in both.

Percent agreement of among-reader, within-structure comparisons were generally low compared to previous research (Graynoth 1996; Zymonas and McMahon 2009).

However, such inter-species comparisons are made difficult by the fact that PA varies as a function of the age structure of the species in question (Beamish and Fournier 1981). The low percent agreement seen here could be a result of the age structure of the sample (Beamish and Fournier 1981; Zymonas and McMahon 2009), the use of multiple readers instead of multiple reads by the same reader (Ihde and Chittenden 2011), the relatively slow growth rates of high latitude fishes (Silkstrom 1983), or a combination of the three factors. Percent agreement of among-reader, within-structure comparisons of scales, otoliths, and fin rays for species with similar age structures such as Arctic grayling and bull trout have been found to range between 50 and 67% and are more comparable to PA observed in Dolly Varden (Silkstrom 1983; Zymonas and McMahon 2009). Despite these contentions, PA1 was greater than 90% for all structures, suggesting that gross disagreements in Dolly Varden age were infrequent.

Tests of among-reader, within-structure CV suggested that otoliths were more precise estimators of Dolly Varden age than fin rays. Similar results have been reported in other species and are likely a result of misidentification of interior fin ray annuli as previously discussed (Graynoth 1996; Stolarski and Hartman 2008; Zymonas and McMahon 2009). However, the precision of age determinations garnered from scales and otoliths were found to be similar, which is contrary to the findings of numerous studies indicating that scale-based age determinations are often less precise than otolith determinations (Silkstrom 1983; Kruse et al. 1997; DeCicco and Brown 2006; Zymonas and McMahon 2009; Schill et al. 2010). This finding may be a direct result of the intensity and duration of Dolly Varden grow throughout the year. Dolly Varden acquire nearly 100% of their annual energy budget during the short Arctic summers, while the remainder of the year is spent overwintering in freshwater where little to no food is consumed (Craig 1984; Boivin and Power 1990). Prior to reproductive age, the intensity of growth within these periods and the consistency of their occurrence likely contribute to the distinctiveness of scale annuli. The annulus formed following a fish's first migration to sea is particularly distinguishable due to the contrast between it and the adjacent freshwater annuli. The consistency of annulus formation in scales stemming from this seasonal pattern likely rivals that of otoliths over the same time interval, and contributes to the similarity in precision observed between the two structures. However, if our sample had contained a larger proportion of older fish our results might have differed.

This research suggests that Dolly Varden age may be determined non-lethally using scales within individuals age 5 and younger. Our assertion is a result of data indicating that bias of within-reader, among-structure comparisons of scales and otoliths is minimal within cohorts less than age 6. Furthermore, no statistical differences in CV calculated from among-reader, within-structure comparisons of scale and otolith age determinations were detected. However, beyond age 5, otoliths should be used to generate age determinations for Dolly Varden. The majority of Dolly Varden research and monitoring projects have been conducted within nearshore coastal areas using fyke nets. These catch data suggest Dolly Varden distribute themselves along shore in relation to size, with smaller individuals occupying shallower habitats closer to shore (Craig and Haldorson 1981; Hachmeister et al. 1991; Underwood 1995; Fechhelm et al. 1997; Brown 2008). Age data collected from random subsets of this catch indicate that up to

70% of the individuals are less than age 6 (Underwood et al. 1995). While age composition likely varies over time and space, it is reasonable to assume that many Dolly Varden captured in nearshore fyke nets can be aged non-lethally using scales. Scale-based age determination may be particularly valuable for identifying first year smolts. This demographic is often pooled for analysis purposes and can be easily and quickly identified using scales due to the contrast between freshwater and marine circuli patterns (Fechhelm et al. 1997). Smolt identification has been previously accomplished using graphical methods; however, these techniques are not as successful when sampling locations are distant from river mouths (Fechhelm et al. 1997; Brown 2008). Non-lethal age determination will also allow age data to be collected from a greater proportion of the population, which may increase the precision of age-specific statistics. Additional research may be required to assess potential side affects resulting from fin ray excision within Dolly Varden (Zymonas and McMahon 2006). As always, it is important to independently verify the consistency of scale, otolith, or fin ray based age determinations in the field within a subset of fish prior to implementation of a particular technique.

## Acknowledgements

We thank William Carter, David Daum, and Dave Sowards for field and logistical help and assisting with the age determinations. Scientific sampling was conducted under the authority of Alaska Department of Fish and Game Fishery Resource Permit SF2011-208 and SF2011-046. Funding for this study was provided by the U.S. Fish and Wildlife Service, Arctic National Wildlife Refuge and the Fairbanks Fisheries Resource office.

The use of trade names of commercial products in this report does not constitute endorsement or recommendation for use. Care and handling of all fish included in this study was in accordance with approved protocols of the University of Alaska Fairbanks Institutional Animal Care and Use Committee assurance 175440-3.

## References

Armstrong, R. H. 1974. Migration of anadromous Dolly Varden (*Salvelinus malma*) in Southeastern Alaska. Journal of the Fisheries Research Board of Canada 31:435-444.

Baker, T. T., and S. L. Timmons. 1991. Precision of ages estimated from five bony structures of Arctic char (*Salvelinus alpinus*) from the Wood River System, Alaska. Canadian Journal of Fisheries and Aquatic Sciences 48:1007-1014.

Barber, W. E., and G.A. McFarlane. 1987. Evaluation of three techniques to age Arctic char from Alaska and Canada. Transactions of the American Fisheries Society 116:874-881.

Beamish, R. J. 1973. Determination of age and growth of populations of the white sucker (*Catastomus commersoni*) exhibiting a wide range in size at maturity. Journal of the Fisheries Research Board of Canada 30:607-616.

Beamish, R. J. 1981. Use of fin ray sections to age walleye pollock, Pacific cod, and albacore, and the importance of this method. Transactions of the American Fisheries Society 11:287-299.

Beamish, R. J., and D. A. Fournier. 1981. A method for comparing the precision of a set of age determinations. Canadian Journal of Fisheries and Aquatic Sciences 38:982-983.

Boivin, T. G., and G. Power. 1990. Winter condition and proximate composition of anadromous Arctic charr (*Salvelinus alpinus*) in eastern Ungava Bay, Quebec. Canadian Journal of Zoology 68:2284-2289.

Brown, R. J. 2008. Life history and demographic characteristics of Arctic cisco, Dolly Varden, and other fish species in the Barter Island region of northern Alaska. U.S. Fish and Wildlife Service, Alaska Fisheries Technical Report No. 101, Fairbanks, Alaska.

Campana, S. E., M. Christina Annand, and J. McMillan. 1995. Graphical and statistical methods for determining the consistency of age determinations. Transactions of the American Fisheries Society 124:131-138.

Carlander, K. D. 1974. Difficulties in aging fish in relation to inland fishery management. Pages 200-205 *in* T.B Bagenal, editor. Proceedings of an international symposium on the aging of fish. Unwin Brothers, Surrey, England.

Chang, W. Y. B. 1982. A statistical method for evaluating the reproducibility of age determination. Canadian Journal of Fisheries and Aquatic Sciences 39:1208-1210.

Copeland, T., M. W. Hyatt, and J. Johnson. 2007. Comparison of methods used to age spring-summer Chinook salmon in Idaho: validation and simulated effects on estimated age composition. North American Journal of Fisheries Management 27:1393-1401.

Craig, P. C. 1984. Fish use of the coastal waters of the Alaskan Beaufort Sea: a review. Transactions of the American Fisheries Society 113:265-282.

Craig, P. C., and L. Haldorson. 1981. Fish. Pages 384-678 *in* S. R. Johnson and W. J. Richardson, editors. Beaufort Sea barrier island-lagoon ecological process studies: final report, Simpson Lagoon, part 4. Environmental assessment of the Alaskan continental shelf, final report of principal investigators vol. 8: Biological Studies. National Oceanic and Atmospheric Administration, Outer Continental Shelf Environment Assessment Program, and Bureau of Land Management, Boulder, Colorado.

Daum, D., P. Rost, and M. W. Smith. 1984. Fisheries studies on the North Slope of the Arctic National Wildlife Refuge, 1983. Pages 1-57 *in* G. W. Gamer and P. E. Reynolds, editors. Arctic National Wildlife Refuge coastal plain resource assessment, 1983 update report baseline study of the fish, wildlife, and their habitats. U.S. Fish and Wildlife Service, Anchorage, Alaska.

DeCicco, A. L., and R. J. Brown. 2006. Direct validation of annual growth increments on sectioned otoliths from adult Arctic grayling and a comparison of otolith and scale ages. North American Journal of Fisheries Management 26:580-586.

DeVries, D. R., and R. V. Frie. 1996. Determination of age and growth. Pages 483-508 *in* B. R. Murphy and D. W. Willis, editors. Fisheries techniques, second edition. American Fisheries Society, Bethesda, Maryland.

Everett, R. J., R. L. Wilmot, and C. C. Krueger. 1997. Population genetic structure of Dolly Varden from Beaufort Sea drainages of Northern Alaska and Canada. American Fisheries Society Symposium 19:240-249.

Fechhelm, R. G., J. D. Bryan, W. B. Griffiths, and L. R. Martin. 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 54:1103-1110.

Graynoth, E. 1996. Determination of the age of brown and rainbow trout in a range of New Zealand lakes. Marine & Freshwater Research 47:749-756.

Hachmeister, L. E., D. R. Glass, and T. C. Cannon. 1991. Effects of solid-gravel causeways on the coastal central Beaufort Sea environment. American Fisheries Society Symposium 11:81-96.

Heiser, D. W. 1966. Age and growth of anadromous Dolly Varden, *Salvelinus malma* (Walbaum) in Eva Creek, Baranof Island, Southeastern Alaska. Alaska Department of Fish and Game, Federal Aid in Fish Restoration, Project F-5-R-4, -5, Research Report No. 5, Juneau.

Howland, K. L., M. Gendron, W. M. Tonn, and R. F. Tallman. 2004. Age determination of a long-lived coregonid from the Canadian North: comparison of otoliths, fin rays and scales in inconnu (*Stenodus leucichthys*). Annales Zoologici Fennici 41:205-214.

Hubert, W. A., G. T. Baxter, and M. Harrington. 1987. Comparison of age determinations based on scales, otoliths and fin rays for cutthroat trout from Yellowstone Lake. Northwest Science 61:32-36.

Ihde, T. F., and M. E. Chittenden. 2002. Comparison of calcified structures for aging spotted seatrout. Transactions of the American Fisheries Society 131:634-642.

Koch, J. D., and M. C. Quist. 2007. A technique for preparing fin rays and spines for age and growth analysis. North American Journal of Fisheries Management 27:782-784.

Kruse, C. G., W. A. Hubert, and F. J. Rahel. 1997. Using otoliths and scales to describe age and growth of Yellowstone cutthroat trout in a high-elevation stream system, Wyoming. Northwest Science 71:30-38.

McCart, P. J. 1980. A review of the systematic and ecology of Arctic char, *Salvelinus alpinus*, in the western Arctic. Canadian Technical Report of Fisheries and Aquatic Sciences No. 935, Winnipeg, Manitoba.

Nordeng, H. 1961. On the biology of char (*Salmo alpinus* L.) in Salangen, North Norway. I. age and spawning frequency determined from scales and otoliths. Nytt Magasin For Zoologi (Oslo) 10:67-123.

Pedersen, S., and A. Linn, Jr. 2005. Kaktovik 2000-2001 subsistence fishery harvest assessment. U.S. Fish and Wildlife Service, Office of Subsistence Management, Fishery Information Services Division, Federal Subsistence Fishery Monitoring Program, Final Project Report No. FIS 01-101, Anchorage, Alaska.

R Development Core Team. 2012. R: a language and environment for statistical computing. R foundation for Statistical Computing, Vienna. Availaible: www.R-project.org.

Reist, J. D., J. D. Johnson, and T. J. Carmichael. 1997. Variation and specific identity of char from northwestern Arctic Canada and Alaska. American Fisheries Society Symposium 19:250-261.

Reist, J. D., F. J. Wrona, T. D. Prowse, M. Power, J. B. Dempson, R. J. Beamish, J. R. King, T. J. Carmichael, C. D. and Sawatzky. 2006. General effects of climate change on Arctic fishes and fish populations. Ambio 35:370-380.

Schill, D. J., E. M. Mamer, and G. W. LaBar. 2010. Validation of scales and otoliths for estimating age of redband trout in high desert streams of Idaho. Environmental Biology of Fishes 89:319-332.

Secor, D. H., J. M. Dean, and E. H. Laban. 1992. Otolith removal and preparation for microstructural examination. Special Publication of the Canadian Journal of Fisheries and Aquatic Sciences 117:19-57.

Sharpe, D., and D. R. Bernard. 1988. Precision of estimated ages of lake trout from five calcified structures. North American Journal of Fisheries Management 8:367-372.

Silkstrom, C. B. 1983. Otolith, pectoral fin ray, and scale age determinations for Arctic grayling. Progressive Fish Culturist 45:220-223.

Stolarski, J. T., and K. J. Hartman. 2008. An evaluation of the precision of fin ray, otolith, and scale age determinations for brook trout. North American Journal of Fisheries Management 28:1790-1795.

Underwood, T. J., J. A. Gordon, M. J. Millard, L. A. Thorpe, and B. M. Osborne. 1995. Characteristics of selected fish populations of Arctic Wildlife Refuge coastal waters, final report, 1988-1991. U.S. Fish and Wildlife Service, Alaska Fisheries Technical Report No. 28, Fairbanks, Alaska.

Viavant, T. 2005. Eastern North Slope Dolly Varden stock assessment. Alaska Department of Fish and Game. Fishery Data Series Number 05-07, Anchorage.

Yoshihara, H. T. 1973. Monitoring and evaluation of Arctic waters with emphasis on the North Slope drainages. Alaska Department of Fish and Game, Division of Sport Fish, Federal Aid in Fish Restoration, Project F-9-5, Annual Progress Report 1972-1973, Juneau.

Zymonas, N. D., and T. E. McMahon. 2006. Effect of pelvic fin ray removal on survival and growth of bull trout. North American Journal of Fisheries Management 26:953-959.

Zymonas, N. D., and T. E. McMahon. 2009. Comparison of pelvic fin rays, scales and otoliths for estimating age and growth of bull trout *Salvelinus confluentus*. Fisheries Management and Ecology 16:155-164.

**Table 1.1**: Coefficient of variation (CV), mean percent agreement (PA), and mean percent agreement to within 1 year (PA1) of among-reader, within-structure and within-reader, among-structure comparisons of age determinations based on scales, otoliths, and fin rays for Dolly Varden sampled from the Ivishak and Hulahula rivers.

| Comparison type | Structures | CV* | Mean PA | Mean PA1 |
|---|---|---|---|---|
| Among-reader, within-structure | Scales | $9.08^{AB}$ | 55.91 | 94.35 |
| Among-reader, within-structure | Otoliths | $7.91^{A}$ | 55.02 | 94.18 |
| Among-reader, within-structure | Fin rays | $11.91^{B}$ | 52.38 | 94.18 |
| Within-reader, among-structure | Scale-otolith | $14.28^{Z}$ | 33.87 | 81.18 |
| Within-reader, among-structure | Scale-fin ray | $14.11^{Z}$ | 40.05 | 81.74 |
| Within-reader, among-structure | Otolith-fin ray | $13.59^{Z}$ | 33.07 | 83.33 |

*Within each comparison type, CV estimates with different alphabetical superscripts are significantly different ($P < 0.05$).

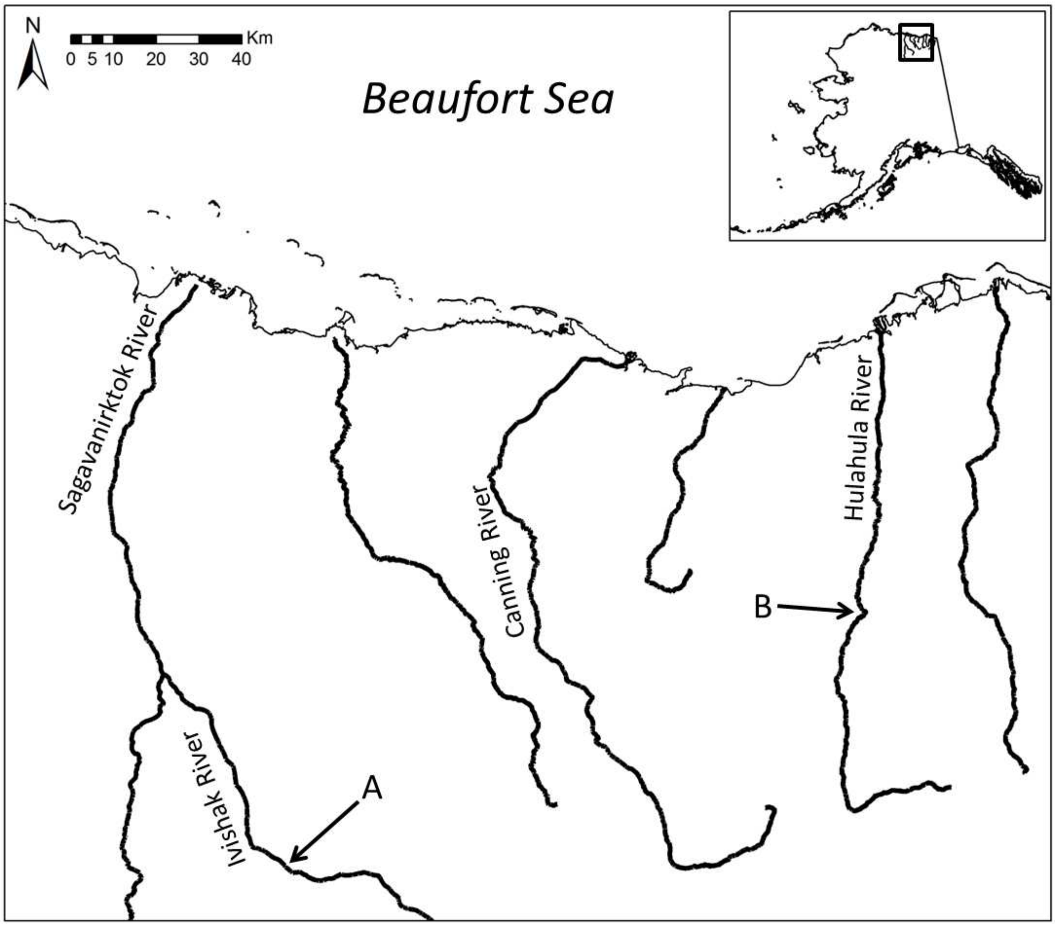

**Figure 1.1**: Map of the Eastern North Slope of Alaska with arrows indicating the general locations where post-smolt (A) and pre-smolt (B) Dolly Varden were sampled from the Ivishak and Hulahula rivers, respectively.

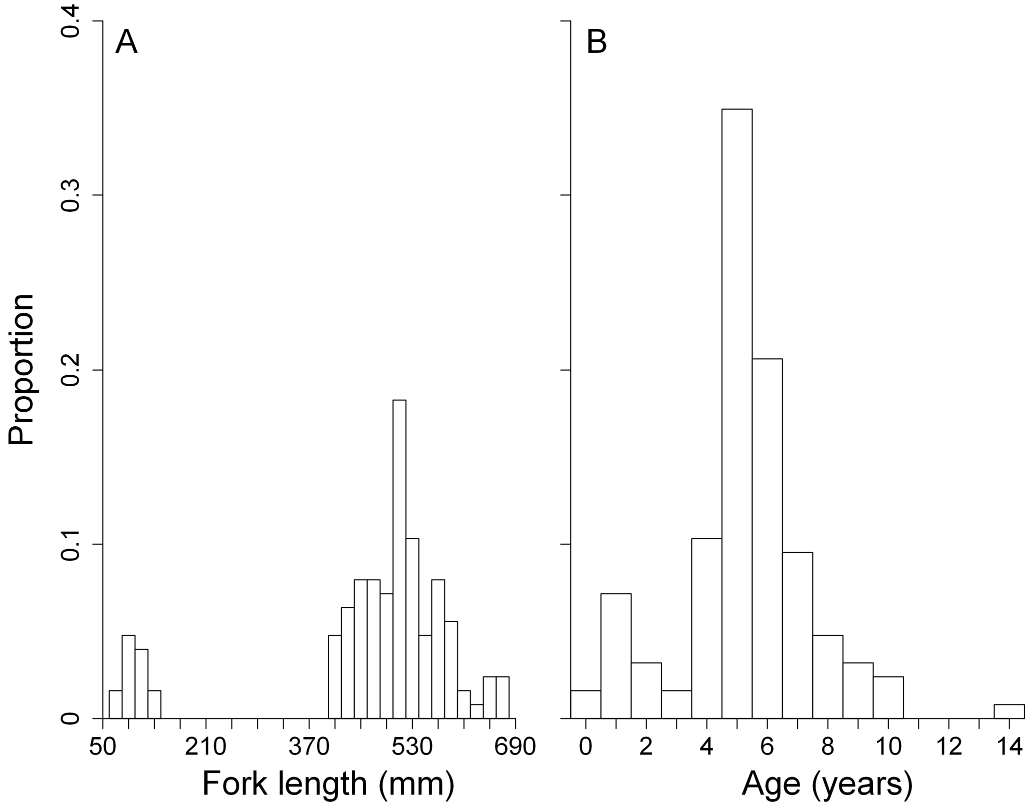

**Figure 1.2**: Composite length (A) and age (B) data plotted against sample proportion for Dolly Varden collected from the Ivishak and Hulahula rivers between 2009 and 2011. Age data in panel B were derived from otoliths.

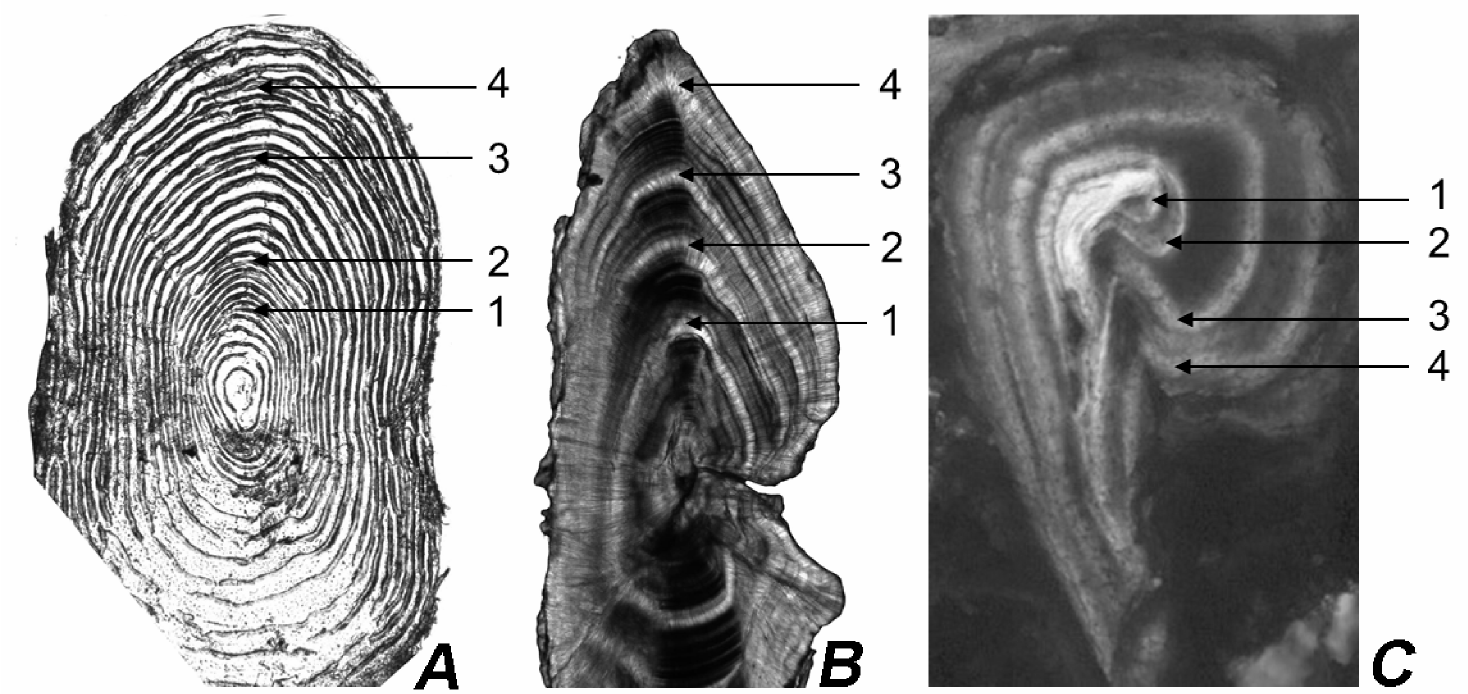

**Figure 1.3**: Digital image of a northern-form, amphidromous, Dolly Varden scale (A), otolith (B), and fin ray (C) collected from the Ivishak River, Alaska. Each structure depicts 4 annuli. Note the "cutting over" of scale circuli at labeled annuli and the proximity of the first and second annulus on the fin ray.

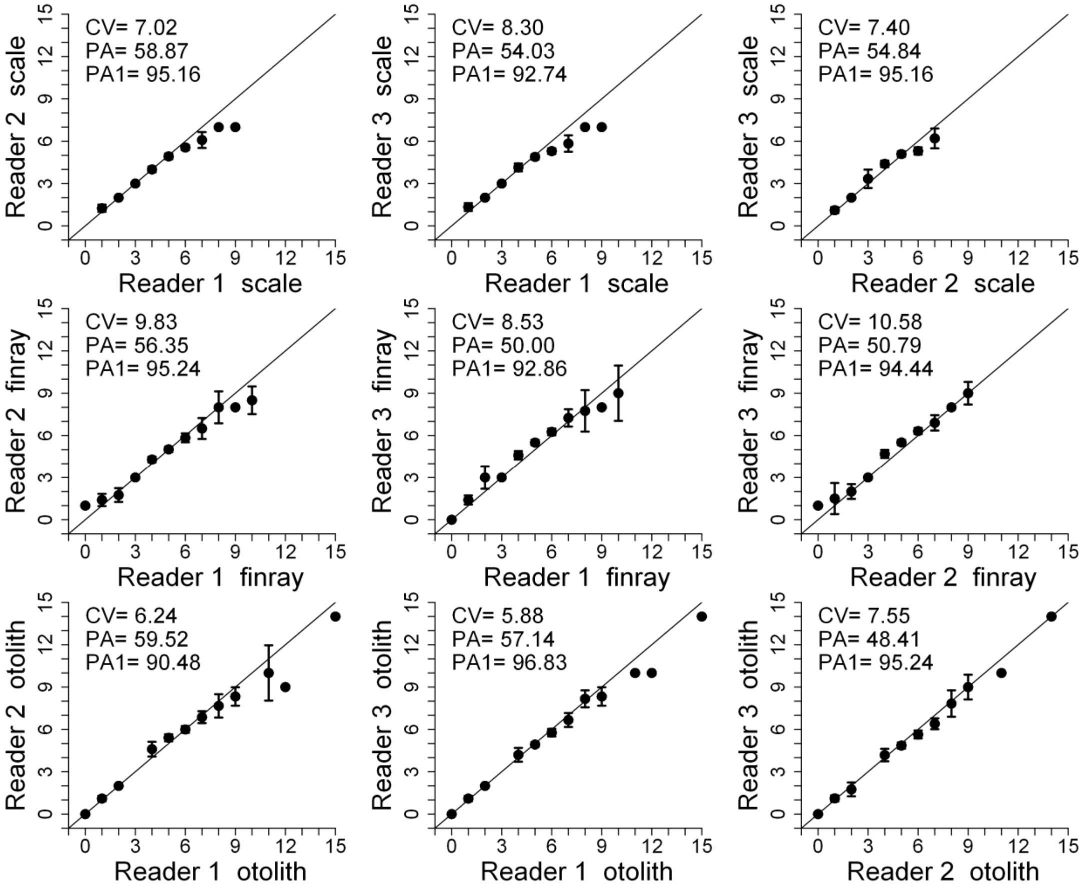

**Figure 1.4**: Age-bias plots with pair-wise estimates of coefficient of variation (CV), percent agreement (PA), and percent agreement to within 1 year (PA1) for among-reader, within-structure comparisons of scale, otolith, and fin ray age determinations for Dolly Varden collected from the Ivishak and Hulahula rivers. Error bars represent 95% confidence intervals (for points with multiple observations) around the mean age assigned by one reader relative to all fish assigned a given age by a second reader.

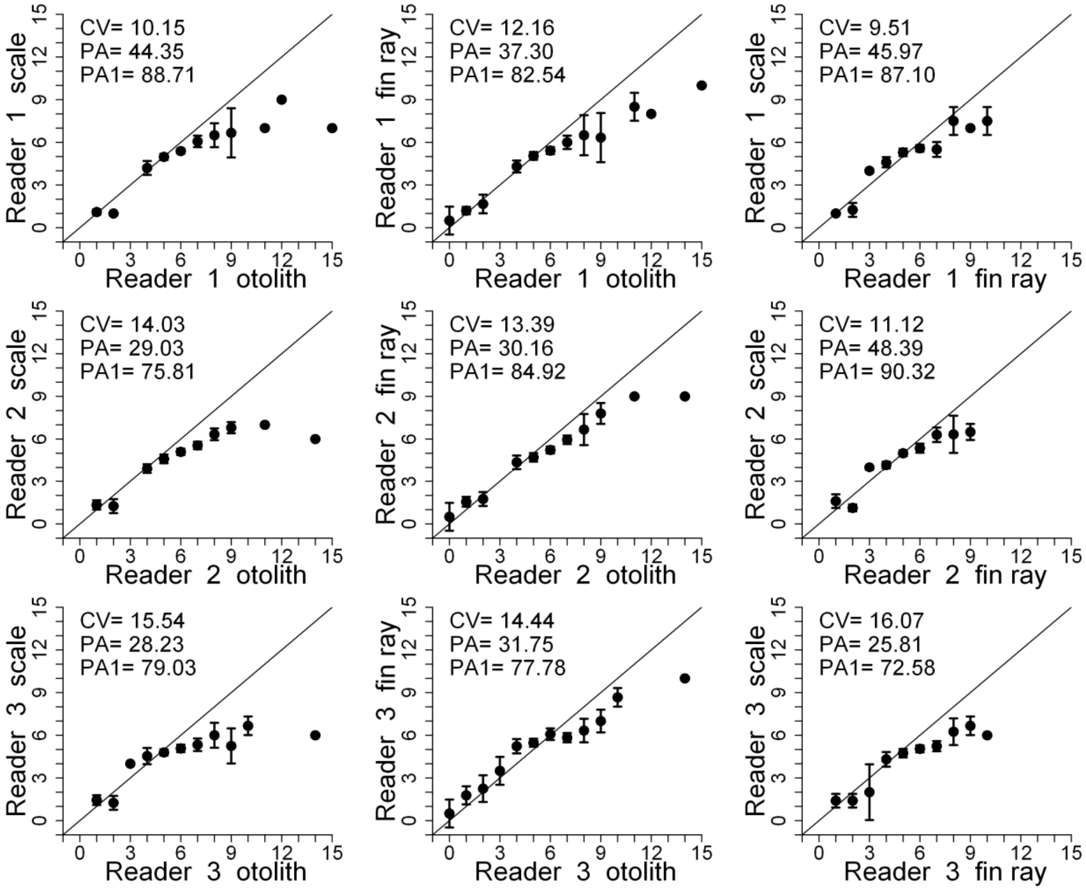

**Figure 1.5**: Age-bias plots with pair-wise estimates of coefficient of variation (CV), percent agreement (PA), and percent agreement to within 1 year (PA1) for within-reader, among-structure comparisons of scale, otolith, and fin ray age determinations for Dolly Varden collected from the Ivishak and Hulahula rivers. Error bars represent 95% confidence intervals (for points with multiple observations) around the mean age assigned by one reader relative to all fish assigned a given age by a second reader.

# Chapter 2: Bioelectrical impedance modeling of amphidromous Dolly Varden char[1]

## Abstract

The physiological well-being, or condition, of fish is most commonly estimated from aspects of individual morphology. However, these metrics may only be weakly correlated to nutritional reserves stored as lipid, the primary form of accumulated energy in fish. We constructed and evaluated bioelectrical impedance analysis (BIA) models as an alternative method for assessing condition in amphidromous Dolly Varden char *Salvelinus malma* collected from nearshore estuarine and lotic habitats of the Alaskan Arctic. Electrical resistance and reactance were measured on the lateral and ventral surfaces of 192 fish and tissue lipid, water, protein, and ash content was determined using standardized laboratory methods. Prior to analysis, resistance and reactance were standardized to a constant temperature using laboratory derived correction equations developed from a subset of fish. Resistance and reactance were not affected by reproductive status (i.e., spawner versus non-spawner) or by differences in water ion concentration between estuarine and freshwater habitats. Bioelectrical impedance analysis models incorporating electrical variables calculated from multiple surfaces displayed the strongest association ($R^2$ = 0.73 to 0.81) between observed and model predicted estimates of proximate content. These models explained between 7 and 20%

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[1] Stolarski, J. T., F. J. Margraf, J. G, Carlson, and T. M. Sutton. North American Journal of Fisheries Management (in preparation).

more of the variability in laboratory-derived estimates of proximate content relative to models developed from single-surface BIA data only. This research provides further evidence of the validity of the BIA technique, in that models developed here are capable of generating high quality predictions of percent-based proximate constituents for Dolly Varden.

## Introduction

Estimating the physiological well-being, or condition, of an individual fish or a population is a common goal of fisheries research (Pope and Kruse 2007). Traditionally, condition has been estimated from aspects of an individual's morphology such as length or weight, with the assumption that changes in condition are reflected by changes in morphology (Gallaway et al. 1991; Brown 2008). Morphological approaches, including Fulton's condition factor (K), and relativistic measures, such as residuals from a linear regression of log-transformed weight and length data, are often preferred as they are non-lethal and can be easily calculated from commonly collected field data (Brown 2008). Although these data are easy to collect, the assumption of a proportional link between physiological well-being and morphology may not always be appropriate (Novinger and Martinez Del Rio 1999; Sutton et al. 2000; Hartman and Margraf 2006).

Lipid is the primary form of accumulated energy and respiratory substrate in fish, and on a percentage basis, is inversely related to the amount of water (energetically inert) contained within an individual (Shul'man 1974; Shearer 1994; Hartman and Margraf

2008). During periods of physiological stress or starvation, such as overwintering and migration, lipid may be metabolized at rates faster than water is lost (Sutton et al. 2000; Breck 2008). Other research suggests further that metabolized lipid may actually be replaced with water (Shearer 1994; Novinger and Martinez Del Rio 1999). These physiological processes may aid in the maintenance of individual body weight and morphology despite potentially large changes in body composition and energy content (Glass 1989). Because morphological condition estimates cannot distinguish lipid from water weight, they may be insensitive to changes in energy content, particularly within species or life stages that require the storage and subsequent mobilization of large quantities of lipid.

Amphidromous northern-form Dolly Varden char *Salvelinus malma*, herein referred to as Dolly Varden, inhabit spring-fed coastal rivers and nearshore areas of the Beaufort Sea in Alaska and Canada (Reist et al. 1997). Individuals aquire close to 100% of their annual energy budget during the short three-month sojourn at sea, as the remainder of the year is spent overwintering in freshwater where little to no forage is consumed (Craig 1989). Such asynchrous peaks in energy availability and expenditure require adult fish to store, and eventually mobilize, vast quantities of lipid (Dutil 1986). For example, Dutil (1986) found that non-spawning Arctic char *S. alpinus* lost on average 30% of their energy stores during winter, and that these stores were replenished and even bolstered following a single summer foraging at sea. Because these processes have the potential to disrupt the relationship between lipid and water content, relativistic condition metrics may not adequately characterize physiological well-being within these and other capital breeding Arctic fishes (Glass 1989). While proximate analysis may permit the estimation of proximate constituents such as lipid and water directly, it is time consuming, expensive, and requires sacrificing the subject. What is needed is a link between simple and economical field-based approaches and costly, more complicated but sensitive lab-based methods. Recent research using bioelectrical impedance analysis (BIA) suggests that this technique may provide that link (Cox and Hartman 2005; Willis and Hobday 2008; Hafs and Hartman 2011).

Bioelectrical impedance analysis (BIA) has been used in the assessment of human body condition since the 1970s, but has only recently been applied to fish (Cox and Hartman 2005; Duncan et al. 2007; Pothoven et al. 2008; Willis and Hobday 2008; Hanson et al. 2010; Rasmussen et al. 2012). Bioelectrical impedance analysis measures the resistance and reactance of an electrical current of known frequency and amperage as it is passed through a subject. Resistance measures the opposition by a body to the passage of an electrical current and is related to the amount of lipid-free mass within the subject as lipid is a poor conductor of electricity (Kyle et al. 2004). Alternatively, reactance measures the electrical storage capacity of a tissue and is related to the cellular volume of a subject, as the lipid bilayer of a cell acts as a capacitor when excited by an electrical current (Kyle et al. 2004). Using electrical property equations, BIA data can be converted into numerous predictive variables that can then be used to model proximate composition (Khaled et al. 1988; Cox and Hartman 2005; Hafs and Hartman 2011).

To date, the majority of BIA research has focused on predicting mass-based proximate constituents (Cox and Hartman 2005). However, as pointed out by Pothoven et al. (2008), this may be less desirable than predicting percent-based constituents, as prediction of the former may be largely driven by the underlying weight-length relationship (Lukaski et al. 1985; Cox and Hartman 2005; Hartman et al. 2011). Bioelectrical impedance analysis models predicting percent-based constituents are rare; however, the majority of these studies suggest that BIA is capable of predicting percent-based proximate constituents with relatively high coefficient of determination scores (0.72 to 0.86; Hafs and Hartman 2011; Hartman et al. 2011; Rasmussen et al. 2012; but see Pothoven et al. 2008). Additionally, there is a lack of research investigating the potential effects of confounding variables such as sex, ontogeny, species, reproductive status (i.e., spawner versus non-spawner) and others on BIA measures (Hafs and Hartman 2011; Rasmussen et al. 2012). The objectives of this research were to: (1) determine if reproductive status or differences in the ionic character of the habitat in which an individual was sampled affects BIA measures of resistance and reactance; and (2) build and validate statistical models relating BIA data to laboratory-derived estimates of Dolly Varden proximate composition. These analyses will further our understanding of potential drawbacks to the BIA method and provide statistical models that will permit non-lethal estimation of Dolly Varden proximate content in the future.

## Methods

### Sample collection

Dolly Varden were captured from nearshore brackish water (10-25‰) and lotic habitats of the Alaskan Arctic (Craig 1989; Figure 2.1). Nearshore sampling was conducted using fyke nets set in Kaktovik and Jago lagoons located near the coastal community of Kaktovik. Fyke nets consisted of a 60-m lead line set perpendicular to shore leading to a mesh trap anchored in shallow (< 1.5 m) water equipped with two 15-m mesh wings emanating from each side. Nets were checked daily (weather permitting), and fish were sampled throughout the summer open-water period from mid-July to early-September 2005. Dolly Varden were also sampled using hook and line from overwintering habitats in the Ivishak River during September sampling events from 2009 to 2011.

### Field methods

Upon capture, fish were sacrificed via cranial concussion, measured to the nearest 1-mm fork length (FL), weighed to the nearest 1 g, and internal body temperature measured to the nearest 0.1°C through the vent. Dolly Varden were then immediately blotted dry and placed on a nonconductive surface in the left-lateral recumbent position in preparation for BIA measurements. Electrical resistance and reactance were measured at consistent locations on both the lateral and ventral surfaces of the fish using a BIA analyzer (RJL Systems, Detroit, Michigan; Figure 2.2). The analyzer consisted of two sets of needle electrodes (stainless, 28 gauge, 5 mm in length), each containing a signalemitting and -detecting electrode spaced 10 mm apart. For lateral measurements, one set of electrodes was set in the anterior dorsal region and the second set in the caudal peduncle (Cox and Hartman 2005; Figure 2.2). Ventral measurements were obtained by inserting one set of electrodes posterior to the gill isthmus and the other anterior to the vent, both on the ventral midline (Figure 2.2). Once in place, the BIA analyzer sent a current (800 μA, AC, and 50 kHz) through the signal electrodes with the proximal detecting electrodes measuring the voltage drop. Resistance and reactance in Ohms (Ω) and the distance between anterior and posterior electrodes, or detector length (DL), was recorded to the nearest 1 mm. Fish were then individually labeled, placed on ice or frozen, and returned to the laboratory for storage and analysis of proximate composition.

### Laboratory methods

In the laboratory, fish were thawed and stomachs were excised, flushed, and then replaced to minimize potential among-fish differences in energy content due to the quantity and quality of stomach contents. Fish were cut into sections to increase surface area, then desiccated in a freeze drier until they achieved a constant weight, which typically took between 7 and 10 days, depending on fish size. Percent water was calculated as the quotient of wet weight and the difference between wet weight and dry weight for each fish. Each fish was homogenized using an industrial blender, and subsamples (~0.5 to 1.5 g) were then taken for analysis of proximate composition following standardized methods (AOAC 1990). Lipid was extracted using the Soxhlet method and protein content was estimated from nitrogen analysis following the application of a nitrogen:protein conversion factor of 6.25. Ash content was determined from weight differences following the combustion of a subsample in a muffle furnace operating at 550°C for 24 hours. All samples were run in triplicate, averaged, and expressed as a percentage of the dry weight of the subsample.

Temperature correction equations were developed from a subsample of 10 Dolly Varden collected via angling from the Ivishak River during fall 2012. Biological data were collected (as described above) and fish were immediately placed on ice and transported back to University of Alaska Fairbanks laboratories. In the laboratory, multiple measures of resistance and reactance were collected on the lateral and ventral surfaces of each fish (as described above) at four degree temperature increments spanning 3 to 19 °C. To speed tissue warming, fish were temporarily placed in water baths at the next temperature increment, then blotted dry prior to measurement. Tissue temperature was monitored using a digital meat thermometer inserted 5 mm into the musculature on the lateral line, proximal to the gills, and was removed prior to each electrical measurement. Total experiment time, beginning at time of capture, did not exceed 6 hours for any fish (Cox et al. 2011).

### Statistical methods

To promote the adoption of standardized methods for the statistical treatment of BIA data, analyses followed those of Hafs and Hartman (2011) and references contained therein wherever possible. All statistical procedures were conducted using the statistical software program R version 2.15 (R Development Core Team 2012) and were evaluated at an alpha = 0.05. Lateral and ventral resistance and reactance were modeled as a function of temperature using ordinary least squares regression (OLS). Temperature correction equations were developed following Hafs (2011), and lateral and ventral resistance and reactance were standardized to 10°C. Prior to modeling procedures, analysis of covariance (ANCOVA) was used to test for differences in raw measures of resistance and reactance among fish captured in freshwater and estuarine habitats. While Dolly Varden maintain osmo- and ionoregulatory homeostasis when exposed to salt water (Finstad et al. 1989; Arnesen et al. 1993), it is unknown if differences in the ionic character of a habitat affect BIA measures. Analysis of covariance was also used to test for differences in raw resistance and reactance due to the presence (or absence) of ripe ova (i.e., spawner versus non-spawner) within mature (FL > 400 mm) females (Underwood et al. 1996). Differences in males were not tested due to the low numbers of spawning males within the sample. Because resistance and reactance are sensitive to among-fish variability in lipid content and circuit length (DL), these variables were included as covariates into the aforementioned analyses (Kyle et al. 2004; Cox and Hartman 2005; Hartman et al. 2011).

Electrical resistance, reactance, and detector length were used to calculate a suite of electrical parameters for ventral and lateral data independently (Khaled et al. 1988; Cox and Hartman 2005; Hafs and Hartman 2011; Table 2.1). With the exception of phase angle and raw measures of resistance and reactance, each parameter was standardized to electrical volume by dividing it by $DL^2$. Standardized phase angle was computed by multiplying phase angle by detector length. In addition to these electrical variables, biological data such as fork length, weight, and a body mass index (BMI; Khaled et al. 1988) were also included into the candidate variable set (Gudivaka et al. 1996; Cox and Heintz 2009; Hartman et al. 2011).

To evaluate the predictive ability of BIA data collected on the lateral, ventral, and combined surfaces of the fish, three independent variable sets were formed. Each of these sets, herein referred to as lateral, ventral, and combined, contained the aforementioned BIA data and biological variables. Proximate components were modeled separately as a function of each of the three independent variable sets using multivariate OLS regression in the R software package rms (R Development Core Team 2012). Mallows' $C_p$ was calculated for all subsets of the global model using the R software package leaps (R Development Core Team 2012). Models were organized by length, and models with the lowest Mallows' $C_p$ score for each unique length were retained for further analysis. These models were validated using the procedure validate, located within the R software package rms (R Development Core Team 2012). Over a predefined number of iterations (set at 10,000), the validate procedure selected random training subsets of the data, fit a user defined model, then applied the model to the entire data set. Cross-validated coefficient of determination ($R^2_{validate}$) and root mean square error (RMSE) were calculated and averaged among iterations to measure the performance of the model. Akaike's information criterion with the small sample correction ($AIC_c$)

was used to determine the final model from the subset of models previously selected by Mallows' $C_p$ (Akaike 1974; Hurvich and Tsai 1989).

## Results

A total of 192 Dolly Varden, ranging from 131 to 680 mm in fork length, were included in the study (Figure 2.3). This sample was comprised of 95 females, 67 males, and 30 fish of unknown sex, and included multiple reproductive classes (i.e. spawners versus non-spawners), and juveniles. Resistance and reactance measurements taken in the field were collected at temperatures ranging from 3 to 18°C, with a mean temperature of 11°C. As a result of temporally-stratified sampling and the inclusion of multiple demographics, proximate-composition data exhibited a high degree of contrast (Figure 2.4). Lateral and ventral measures of resistance and reactance displayed a significant negative relationship to temperature (Table 2.2: Figure 2.5). Furthermore, regression slopes of both the resistance and reactance relationships with temperature were quite similar among data collected laterally and ventrally. Following standardization to a constant 10°C (Table 2.2), analysis of covariance suggested that both lateral and ventral measures of resistance ($F_{1, 190} = 0.76$, $p = 0.385$; $F_{1, 190} = 3.03$, $p = 0.083$) and reactance ($F_{1, 190} = 0.07$, $p = 0.786$; $F_{1, 190} = 0.93$, $p = 0.333$) were not affected by differences in water chemistry among capture locations. Similar results were found for reproductive status in that lateral estimates of resistance ($F_{1, 55} = 0.77$, $p = 0.385$) and reactance ($F_{1, 55} =$

0.68, p = 0.411) and ventral estimates of resistance ($F_{1, 55}$ = 1.75, p = 0.191) and reactance ($F_{1, 55}$ = 0.22, p = 0.639) were not affected by the presence of ripe ova.

The predictive ability of single-surface BIA models varied slightly depending upon the proximate constituent modeled and the type of data included (Table 2.3). In general, best-fit protein and lipid models developed using ventral BIA data displayed better fit (lower AICc and RMSE and greater $R^2$ and $R^2_{validate}$) relative to models developed using lateral data. The opposite was true for water, with models developed using lateral BIA data exhibiting better fit. There was little difference between ash models developed using lateral or ventral BIA data. Among all proximate constituents, BIA models containing both lateral and ventral BIA data (the combined data set) displayed lower AICc and RMSE and greater $R^2$ and $R^2_{validate}$ relative to models incorporating either lateral or ventral data alone (Table 2.3; Figure 2.6). In general, models containing combined BIA data explained between 7% and 20% more of the variability in laboratory-derived estimates of proximate content than models using either lateral or ventral data alone. Regression coefficients for best-fit single-surface BIA models can be found in Table 2.4, while multi-surface BIA model coefficients are located in Table 2.5.

## Discussion

Bioelectrical impedance analysis assumes the biological tissues of a subject are organized into cylinders of uniform conductivity (Kyle et al. 2004). Clearly, fish are not homogenous in composition, nor are they cylindrical, but may be more similar to biological cylinders relative to most terrestrial organisms (Hundertmark and Schwartz 2002). Statistical analyses permit empirical relationships between BIA measures and body condition by matching these metrics through appropriate coefficients, assuming individual deviations in body geometry and internal composition from theoretical norms are constant. Among-fish variability in morphology or conductivity may be introduced by sampling spawning and non-spawning fish from different habitats (i.e. estuarine versus freshwater). However, the affect of this variation on resistance and reactance has yet to be quantified in BIA research.

Analysis of covariance results suggested that both lateral and ventral measures of resistance and reactance were not affected by differences in the ionic character of the water in which fish were captured. Dolly Varden possess a highly advanced hypoosmoregulatory ability that permits successful osmoregulation and occupation within waters exhibiting a wide range of salinities (Finstad et al. 1989; Arnesen et al. 1993). While the transfer to salt water may elicit acute short-term changes in blood ion concentration (Arnesen et al. 1993), the first Dolly Varden sampled from estuarine environments were not captured until the second week of July. Considering Dolly Varden typically migrate to sea during the latter half of June (McCart 1980; Fechhelm et al. 1997), it is unlikely that individuals used in our study were not acclimated to estuarine conditions. Additionally, Cox et al. (2011) found that pouring a cup of salt water under the subject prior to measurement resulted in significant changes to resistance and reactance. When numerous electrical pathways are available, as is the case when the subject is in contact with salt water or placed on a conductive surface, ohms law dictates that current will tend to follow the least resistant course, which may not include the internal surfaces of the fish. However, because fish in our study were thoroughly blotted dry prior to the collection of BIA measurements, this type of error was likely minimized.

Analysis of covariance results also suggested that both lateral and ventral measures of resistance and reactance were not affected by the presence of ripe ova. The electrical pathway of lateral measurements is likely dominated by muscle tissue and bone. While the amount of bone does not change among reproductive classes, spawning fish may mobilize lipid from muscle tissue and other storage areas to facilitate gamete production and migration to spawning areas (Aksnes et al. 1991; Jørgensen et al. 1997). In fact, the carcasses of spawning Dolly Varden contained significantly greater proportions of water (inversely related to percent lipid; Hartman and Margraf 2008) relative to the carcasses of non-spawners (J. Stolarski, University of Alaska Fairbanks [UAF], unpublished data). However, this difference was small and similar to the RMSE of the best predictive water BIA models, which could account for the lack of significance in the model. Alternatively, the electrical pathway of ventral measurements most likely includes peritoneal tissue and possibly organs such as gonads. The gonads of spawning fish were on average 30 times larger by weight and contained 14% less water relative to non-spawning fish (J. Stolarski, UAF, unpublished data). However, no differences in ventral measures of resistance or reactance were detected among reproductive groups.

These results are difficult to interpret, as the specific current pathway of the ventral measurements is less defined. If the current remained within the peritoneal tissue, these results mirror what was observed in the lateral measures of resistance and reactance. However, if the current traveled through gonad tissue, resistance and reactance might be expected to decrease as lipid-rich tissues offer greater resistance to the passage of current (Liedtke 1997). The fact that this did not occur suggests that the current pathway did not intersect gonad tissue and that BIA measures are not affected by the presence of ripe gonads.

Coefficient of determination scores of the best-fit BIA models developed using both lateral and ventral (combined data set) BIA data ranged between 0.73 and 0.81. These models are generally consistent with the predictive ability of other BIA models predicting percent-based proximate content of brook trout *Salvelinus fontinalis* and blue fish *Pomatomus saltatrix*, which displayed $R^2$ values ranging between 0.72 and 0.86 (Hafs and Hartman 2011; Hartman et al. 2011; Rasmussen et al. 2012). However, our results conflict with those of Pothoven et al. (2008) who reported coefficient of determination scores of 0.18, 0.31, and 0.53 for BIA models predicting percent lipid content for yellow perch *Perca flavescens*, walleye *Sander vitreus*, and lake whitefish *Coregonus clupeaformis*, respectfully. These differences could be a result of species-specific differences in BIA performance and/or methodological differences as well.

Recent research has demonstrated that factors such as electrode needle location, needle type, procedure deviation, time after death, experience, and most notably, temperature, can effect BIA measurements (Cox et al. 2011; Hafs and Hartman 2011). Temperature may be controlled for by maintaining the subject at a constant temperature, a task made difficult in field applications of BIA, particularly when sampling is temporally stratified (Hafs and Hartman 2011). Alternatively, BIA measures can be standardized to constant temperature post hoc, provided adequate corrective equations are available (Cox et al. 2011). Pothoven et al. (2008) did not control for fish temperature, collected a relatively small sample exhibiting low contrast in proximate constituents, and used hollow hypodermic needles as electrodes, all of which could, at least, partially explain poor model performance. However, BIA research in general is fraught with procedural variations in the collection and statistical treatment of BIA data. For example, considerable variation exists in the number, types, and combinations of electrical variables used to model proximate constituents. The majority of research uses volumetric-based calculations of electrical variables; however, confusion exists as to the relationship between these parameters and total impedance. The electrical circuit formed when a current is applied to biological tissue can be thought to be arranged in series ($Z^2 = R^2+X_c^2$) or in parallel ($Z^{-2} = R_p^{-2}+X_{cp}^{-2}$; Liedtke 1997). Some researchers choose to model proximate content as a function of series- (Rasmussen et al. 2012) or parallel-based (Pothoven et al. 2008) calculations in isolation while others use both (Cox and Hartman 2005; Duncan 2007; Hafs and Hartman 2011; Hartman et al. 2011). Furthermore, phase angle, which is the ratio of the two vector components R and $X_c$ (see Table 2.1), has shown to be a good predictor of body condition but is often left out of analyses (Pothoven et al. 2008; Cox and Heintz 2009; Hanson et al. 2010). Considering the variability in methods used by researchers, it is not surprising that there is some contention regarding the utility of the BIA technique (Pothoven et al. 2008; Hanson et al. 2010). Comparative research investigating various modeling and measurement techniques is required.

Among all proximate constituents, BIA models developed using lateral and ventral data (combined data set) were more precise estimators of Dolly Varden proximate content than models developed from either lateral or ventral data alone. Hafs and Hartman (2011) also noted that brook trout models developed using BIA data collected on multiple surfaces were superior to models developed using single-surface data. Multisurface models incorporate greater amounts of information about the internal composition of a subject, which likely improves predictive ability. However, single-surface BIA models developed by Rasmussen et al. (2012) were capable of predicting proximate content with a relatively high degree of precision ($R^2 = 0.72$). Decisions regarding the number of surfaces on which to collect BIA data should be made only after research goals and data quality requirements are determined.

These results suggest that BIA is capable of producing high quality predictions of Dolly Varden proximate content. However, the validity of these BIA models should be confirmed on a subset of fish using the methods and equipment outlined here prior to implementation in field studies. Additional research is required to gain a greater understanding of how variability in equipment such as electrode type (needle gauge, separation, and depth), and other potentially confounding factors such as ontogeny, gut fullness, and size affect BIA measurements and the generality of models. Furthermore, research investigating BIA model output among different formulations and combinations of independent electrical variables using parametric and nonparametric techniques would aid in the development of standardized modeling practices for BIA data. These efforts would standardize practices for the collection and statistical treatment of BIA data, improve the quality of model predictions, and facilitate BIA model comparisons among species.

## Acknowledgements

We thank Mark Nelson, John Richard, and Dave Sowards for assistance in capturing fish in the field, and Peter Bechtel, Lara Hortsmann-Dehn, and Matthew Wooller for the use of their laboratory facilities. Technical and statistical assistance were provided by Dr. Andrew Hafs and Dr. Keith Cox. Scientific sampling was conducted under the authority of Alaska Department of Fish and Game Fishery Resource Permit SF2010-088, SF2011-046, and SF2012-265. Funding for this study was provided by the U.S. Fish and Wildlife Service, Arctic National Wildlife Refuge and the Fairbanks Fisheries Resource Office. Care and handling of all fish included in this study was in accordance with approved protocols of the University of Alaska Fairbanks Institutional Animal Care and Use Committee assurance 175440-3. The use of trade names of

commercial products in this report does not constitute endorsement or recommendation for use.

## References

Akaike, H. 1974. A new look at the statistical model identification. IEEE Transactions on Automatic Control 19:716-723.

Aksnes, A., B. Gjerde, and S. Roald. 1991. Biological, chemical, and organoleptic changes during maturation of farmed Atlantic salmon, *Salmo salar*. Aquaculture 53:7-20.

Arnesen, A. M., E. H. Jørgensen, and M. J. Jobling. 1993. Feed intake, growth and osmoregulation in Arctic charr, *Salvelinus alpinus* (L.), following abrupt transfer from freshwater to more saline water. Aquaculture 114:327-338.

Association of Official Analytical Chemists (AOAC). 1990. Official methods of analysis. Association of Official Analytical Chemists, Washington, D.C.

Breck, J. E. 2008. Enhancing bioenergetics models to account for dynamic changes in fish body composition and energy density. Transactions of the American Fisheries Society 137:340-356.

Brown, R. J. 2008. Life history and demographic characteristics of Arctic cisco, Dolly Varden, and other fish species in the Barter Island region of northern Alaska. U.S. Fish and Wildlife Service, Alaska Fisheries Technical Report No. 101, Fairbanks, Alaska.

Cox, K. M., and K. J. Hartman. 2005. Nonlethal estimation of proximate composition in fish. Canadian Journal of Fisheries and Aquatic Sciences 62:269-275.

Cox, M. K., and R. Heintz. 2009. Electrical phase angle as a new method to measure fish condition. U.S. National Marine Fisheries Service Fishery Bulletin 107:477–487.

Cox, M. K., R. Heintz, and K. J. Hartman. 2011. Measurements of resistance and reactance in fish with the use of bioelectrical impedance analysis: sources of error. Fishery Bulletin 109:34-47.

Craig, P. C. 1989. An introduction to anadromous fishes in the Alaskan Arctic. Biological Papers of the University of Alaska 24:27-54.

Duncan, M., S. R. Craig, A. N. Lunger, D. D. Kunn, G. Salze, and E. McLean. 2007. Bioimpedance assessment of body composition in cobia *Rachycentron canadum*. Aquaculture 271:432-438.

Dutil, J. D. 1986. Energetic constraints and spawning interval in the anadromous Arctic charr (*Salvelinus alpinus*). Copeia 4:945-955.

Fechhelm, R. G., J. D. Bryan, W. B. Griffiths, and L. R. Martin. 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 54:1103-1110.

Finstad, B., K. J. Nilssen, and A. M. Arnesen. 1989. Seasonal changes in sea-water tolerance of Arctic charr *(Salvelinus alpinus).* Journal of Comparative Physiology B 159:37 l-378.

Gallaway, B. J., W. J. Gazey, J. M. Colonell, A. W. Niedoroda, and C. J. Herlugson. 1991. The Endicott Development Project - preliminary assessment of impacts from the first major offshore oil development in the Alaskan Arctic. American Fisheries Society Symposium 11:42-80.

Glass, D. R. 1989. Changes in the condition and physiological parameters of anadromous fish species in the central Beaufort Sea during the overwintering period. Part I, Chapter II *in* Endicott Environmental Monitoring Program-1987. Report by Envirosphere Company for the U.S. Army Corps of Engineers, Anchorage, Alaska.

Gudivaka, R., D. Schoeller, and R. F. Kushner. 1996. Effect of skin temperature on multifrequency bioelectrical impedance analysis. Journal of Applied Physiology 81:838-845.

Hafs, A. W. 2011. Bioelectrical impedance analysis methods for prediction of brook trout *Salvelinus fontinalis* percent dry weight. Doctoral dissertation. West Virginia University, Morgantown.

Hafs, A. W., and K. J. Hartman. 2011. Influence of electrode type and location upon bioelectrical impedance analysis measurements of brook trout. Transactions of the American Fisheries Society 140:1290-1297.

Hanson, K. C., K. C. Ostrand, A. L. Gannam, and S. L. Ostrand. 2010. Comparison and validation of nonlethal techniques for estimating condition in juvenile salmonids. Transactions of the American Fisheries Society 139:1733-1741.

Hartman, K. J., and F. J. Margraf. 2006. Relationships among condition indices, feeding, and growth of walleye in Lake Erie. Fisheries Management and Ecology 13:121-130.

Hartman, K. J., and F. J. Margraf. 2008. Common relationships among proximate composition components in fishes. Journal of Fish Biology 73:2352-2360.

Hartman, K. J., B. A. Phelan, and J. E. Rosendale. 2011. Temperature effects on bioelectrical impedance analysis (BIA) used to estimate dry weight as a condition proxy in coastal bluefish. Marine and Coastal Fisheries 3:307-316.

Hundertmark, K. J., and S. C. Schwartz. 2002. Evaluation of bioelectrical impedance analysis as an estimator of moose body composition. Wildlife Society Bulletin 30:915-921.

Hurvich, C. M., and C. L. Tsai. 1989. Regression and time series model selection in small samples. Biometrika 76:297-307.

Jørgensen, E. H., S. J. S. Johansen, and M. Jobling. 1997. Seasonal patterns of growth, lipid deposition and lipid depletion in anadromous Arctic charr. Journal of Fish Biology 51:312-326.

Khaled, M., M. J. McCutcheon, S. Reddy, P .L. Pearman, G. R. Hunter, and R. L. Weinsier. 1988. Electrical impedance in assessing human body composition: the BIA method. The American Journal of Clinical Nutrition 47:789-792.

Kyle, U. G., I. Bosaeus, A. D. De Lorenzo, P. Deurenberg, M. Elia, and J. M. Gomez. 2004. Bioelectrical impedance analysis - part 1: review of principles and methods. Clinical Nutrition 23**:**1226-1243.

Liedtke, R. J. 1997. Principles of bioelectrical impedance analysis. RJL Systems Inc., Clinton, Michigan.

Lukaski, H. C., P. E. Johnson, W. W. Bolonchuk, and G. I. Lykken. 1985. Assessment of fat-free mass using bioelectrical impedance measurements of the human body. American Journal of Clinical Nutrition 41:81-817.

McCart, P. J. 1980. A review of the systematics and ecology of Arctic char, *Salvelinus alpinus*, in the western Arctic. Canadian Technical Report of Fisheries and Aquatic Sciences. No. 935, Winnipeg, Manitoba.

Novinger, D. C., and C. Martinez Del Rio. 1999. Failure of total body electrical conductivity to predict lipid content of Brook trout. North American Journal of Fisheries Management 19:942-947.

Pope, K. L., and C. G. Kruse. 2007. Condition. Pages 423-471 *in* C. S. Guy and M. L. Brown, editors. Analysis and interpretation of freshwater fisheries data. American Fisheries Society, Bethesda, Maryland.

Pothoven, S. A., S. A. Ludsin, T. O. Hook, D. L. Fanslow, D. M. Mason, P. D. Collingsworth, and J. J. Van Tassell. 2008. Reliability of bioelectrical impedance analysis for estimating whole-fish energy density and percent lipids. Transactions of the American Fisheries Society 137:1519-1529.

R Development Core Team. 2012. R: a language and environment for statistical computing. R foundation for Statistical Computing, Vienna. Availaible: www.R-project.org.

Rasmussen, J. B., A. N. Krimmer, A. J. Paul, and A. Hontela. 2012. Empirical relationships between body tissue composition and bioelectrical impedance of brook trout *Salvelinus fontinalis* from a Rocky Mountain Stream. Journal of Fish Biology 80:2317-2327.

Reist, J. D., J. D. Johnson, and T. J. Carmichael. 1997. Variation and specific identity of char from northwestern Arctic Canada and Alaska. American Fisheries Society Symposium 19:250-261.

Shearer, K. D. 1994. Factors affecting the proximate composition of cultured fishes with emphasis on salmonids. Aquaculture 119:63-88.

Shul'man, G. E. 1974. Life cycles of fish, physiology and biochemistry. Wiley, New York.

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

Sutton, S. G., T. P. Bult, and R. L. Haedrich. 2000. Relationships among fat weight, body weight, water weight, and condition factors in wild Atlantic salmon parr. Transactions of the American Fisheries Society 129:527-538.

Willis, J., and A. Hobday. 2008. Application of bioelectrical impedance analysis as a method for estimating composition and metabolic condition of southern bluefin tuna (*Thunnus maccoyii*) during conventional tagging. Fisheries Research 93:64-71.

**Table 2.1**: Electrical parameters, their units, and associated equations used in the calculation of BIA electrical variables.

| Electrical parameter | Symbol | Units | Equation |
|---|---|---|---|
| Reactance | $x$ | Ohms | Measured by Quantum II analyzer |
| Resistance | $r$ | Ohms | Measured by Quantum II analyzer |
| Reactance in parallel | $X_{cp}$ | Ohms | $DL^2/(x + (r^2/x))$ |
| Resistance in parallel | $R_p$ | Ohms | $DL^2/(r + (x^2/r))$ |
| Impedance in parallel | $Z_p$ | Ohms | $DL^2/(r\cdot x/(r^2 + x^2)^{0.5})$ |
| Reactance in series | $X_c$ | Ohms | $DL^2/x$ |
| Resistance in series | $R_s$ | Ohms | $DL^2/r$ |
| Impedance in series | $Z_s$ | Ohms | $DL^2/(r^2 + x^2)^{0.5}$ |
| Phase angle | PA | Degrees | $\text{Arctan}(x/r)\cdot 180/\pi$ |
| Standardized phase angle | DLPA | Degrees | $DL\cdot(\arctan(x/r)\cdot 180/\pi)$ |
| Capacitance | $C_{pf}$ | Picofarads | $DL^2/((1/(2\cdot\pi\cdot 50{,}000\cdot r))\cdot(1\cdot 10^{12}))$ |
| Body mass index | BMI | Ohms | $(((r^2 + x^2)\hat{}^{0.5})\text{weight})/DL^2$ |

**Table 2.2**: Regression slopes, t values, and associated P values from ordinary least squares regressions of lateral and ventral measurements of electrical resistance and reactance and temperature (°C) developed from ten Dolly Varden collected from the Ivishak River. In the temperature correction equations developed from the regressions, T = the temperature (°C) in at which the electrical measurement was taken and $T_s$ = the standardized temperature (°C) that is being corrected to.

| Variable | Slope | t | p value | Correction equation |
|---|---|---|---|---|
| Lateral | | | | |
| Resistance (r) | -7.8025 | -11.1585 | < 0.001 | $-7.8025*(T_s-T) + r$ |
| Reactance (x) | -1.7600 | -8.2461 | < 0.001 | $-1.7600*(T_s-T) + x$ |
| Ventral | | | | |
| Resistance (r) | -7.3175 | -6.7609 | < 0.001 | $-7.3175*(T_s-T) + r$ |
| Reactance (x) | -1.0750 | -3.3333 | 0.002 | $-1.0750*(T_s-T) + x$ |

**Table 2.3**: Model fit and cross-validation statistics of BIA models for all proximate constituent and independent variable set combinations. Model fit statistics include number of parameters (K), Akaike's information criterion with the small sample correction ($AIC_c$) and coefficient of determination ($R^2$); cross-validation statistics include root mean squared error (RMSE) and mean $R^2$ of observed and cross-validated predicted values ($R^2_{validate}$).

| Proximate component and data set | K | $AIC_c$ | $R^2$ | RMSE | $R^2_{validate}$ |
|---|---|---|---|---|---|
| Lipid | | | | | |
| Lateral | 9 | 1325.78 | 0.57 | 7.40 | 0.55 |
| Ventral | 5 | 1310.76 | 0.59 | 7.21 | 0.57 |
| Combined | 16 | 1220.65 | 0.77 | 5.57 | 0.74 |
| Water | | | | | |
| Lateral | 10 | 917.78 | 0.66 | 2.56 | 0.64 |
| Ventral | 6 | 972.50 | 0.53 | 2.99 | 0.51 |
| Combined | 15 | 883.04 | 0.73 | 2.32 | 0.70 |
| Protein | | | | | |
| Lateral | 10 | 1238.42 | 0.57 | 5.90 | 0.54 |
| Ventral | 6 | 1206.27 | 0.62 | 5.47 | 0.61 |

**Table 2.3 continued:**

| | | | | | |
|---|---|---|---|---|---|
| Combined | 14 | 1152.18 | 0.74 | 4.69 | 0.71 |
| Ash | | | | | |
| Lateral | 7 | 549.68 | 0.70 | 0.99 | 0.68 |
| Ventral | 6 | 550.56 | 0.69 | 1.00 | 0.68 |
| Combined | 12 | 472.03 | 0.81 | 0.80 | 0.79 |

**Table 2.4**: Single-surface BIA model coefficients for best-fit models developed using either lateral or ventral BIA data organized by proximate constituent. Electrical or biological variables not included are indicated by a series of dots.

| | Proximate component | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Lateral data | | | | Ventral data | | | |
| Parameter | Lipid | Water | Protein | Ash | Lipid | Water | Protein | Ash |
| Intercept | 65.9535 | 45.1752 | 20.2392 | 1.4602 | 52.4281 | 52.4943 | 42.7139 | 7.8730 |
| Biological variables | | | | | | | | |
| FL | -0.3909 | 0.1310 | 0.2608 | 0.0290 | .... | 0.0173 | .... | -0.0143 |
| Weight | .... | .... | .... | .... | 0.0095 | -0.0044 | -0.0089 | .... |
| Body mass index (BMI) | 9.9899 | -3.6379 | -5.9804 | -0.6048 | .... | .... | .... | .... |
| Electrical variables | | | | | | | | |
| Reactance (x) | -0.3739 | 0.1721 | 0.2443 | 0.0265 | -0.2185 | 0.1250 | 0.1842 | 0.0189 |
| Reactance in parallel ($X_{cp}$) | -53.8870 | 24.0874 | 65.1811 | 0.0992 | -0.3968 | .... | -2.0111 | -0.0473 |
| Resistance in parallel ($R_p$) | -448.0030 | 187.1088 | 499.0031 | .... | .... | .... | .... | .... |
| Impedance in parallel ($Z_p$) | .... | .... | .... | -346.6878 | .... | .... | .... | 328.0952 |
| Reactance in series ($X_c$) | -0.8248 | 0.4117 | 1.2242 | .... | -0.0282 | 0.0100 | .... | 0.0014 |
| Resistance in series ($R_s$) | -285.3004 | 116.4487 | 310.0435 | .... | .... | 0.0278 | 6.4655 | .... |
| Impedance in series ($Z_s$) | 745.4179 | -309.1565 | -824.6681 | .... | .... | .... | -6.0060 | .... |
| Phase angle (PA) | .... | 0.7446 | 1.5762 | 0.5067 | .... | .... | .... | .... |
| Standardized phase angle (DLPA) | 0.0273 | -0.0114 | -0.0227 | -0.0044 | .... | .... | .... | 0.0010 |
| Capacitance ($C_{pf}$) | .... | .... | .... | .... | 2.7499 | -1.3539 | -2.0905 | .... |

**Table 2.5**: Bioelectrical impedance analysis model coefficients for best-fit models developed using combined BIA data organized by proximate constituent. Electrical or biological variables not included are indicated by a series of dots.

| | Proximate component | | | |
|---|---|---|---|---|
| Parameter | Lipid | Water | Protein | Ash |
| Intercept | 56.9367 | 57.9891 | 41.3514 | 0.5354 |
| Biological variables | | | | |
| Fork length | -0.1976 | 0.0956 | 0.1481 | 0.0154 |
| Body mass index (BMI) | 6.1901 | -2.8534 | -4.8834 | -0.6168 |
| Lateral BIA variables | | | | |
| Reactance (x) | -0.2187 | 0.1801 | 0.2289 | 0.0301 |
| Resistance (r) | -0.0723 | …. | …. | …. |
| Reactance in parallel ($X_{cp}$) | -53.9209 | 22.8374 | 50.9030 | 0.1233 |
| Resistance in parallel ($R_p$) | -417.8390 | 176.4037 | 385.8771 | …. |
| Impedance in parallel ($Z_p$) | …. | …. | …. | -579.9346 |
| Reactance in series ($X_c$) | -0.9154 | 0.3735 | 0.9295 | …. |
| Resistance in series ($R_s$) | -260.1150 | 109.3261 | 238.5641 | …. |
| Impedance in series ($Z_s$) | 690.5391 | -290.9841 | -636.5997 | …. |
| Phase angle (PA) | …. | …. | …. | 0.4406 |
| Standardized phase angle (DLPA) | 0.0184 | -0.0090 | -0.0138 | -0.0042 |

**Table 2.5 continued:**

| | | | | |
|---|---|---|---|---|
| Ventral BIA variables | | | | |
| Reactance (x) | …. | …. | …. | -0.0335 |
| Resistance (r) | 0.0606 | -0.0123 | …. | 0.0078 |
| Reactance in parallel ($X_{cp}$) | 2.2431 | …. | …. | -0.1322 |
| Resistance in parallel ($R_p$) | …. | 21.9520 | 46.6852 | …. |
| Impedance in parallel ($Z_p$) | -1086.9941 | 484.1092 | 1152.4623 | 413.8573 |
| Resistance in series ($R_s$) | -4.8567 | 19.6177 | 42.4412 | …. |
| Impedance in series ($Z_s$) | 4.5407 | -41.5593 | -89.0604 | …. |
| Standardized phase angle (DLPA) | -0.0116 | 0.0032 | 0.0059 | 0.0030 |

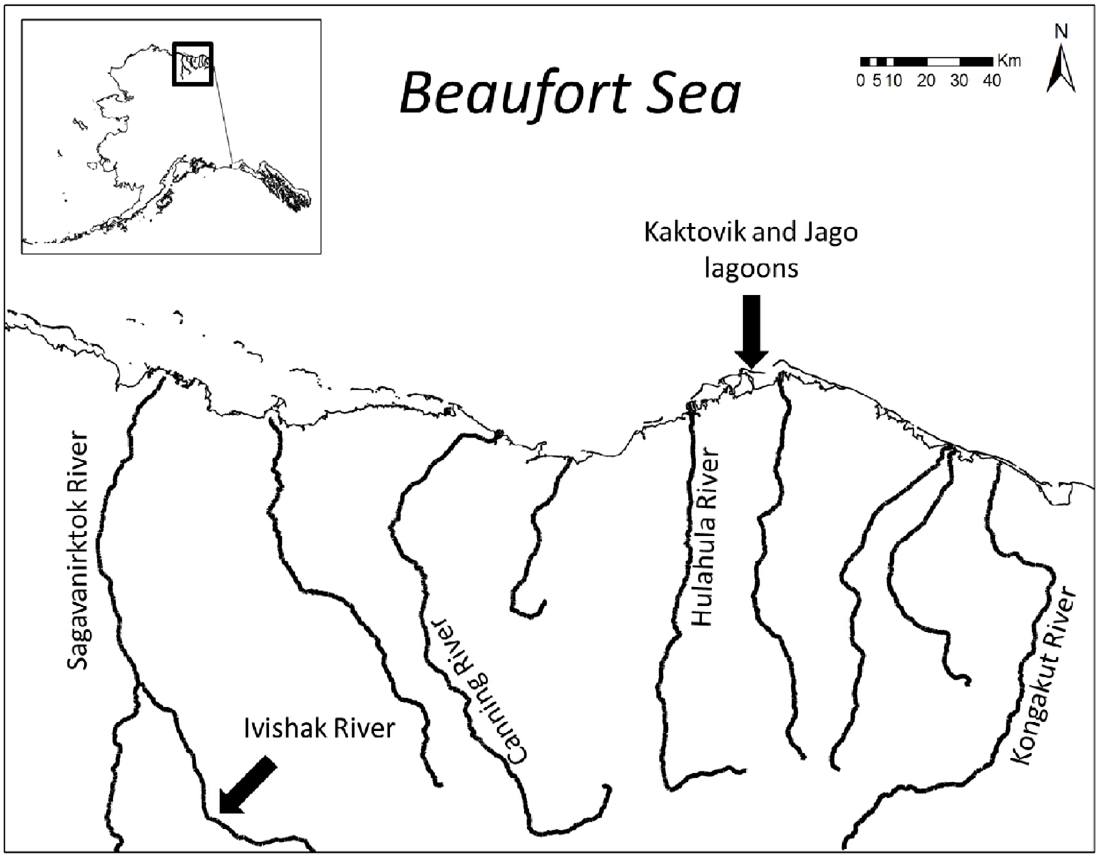

**Figure 2.1**: Map of the Eastern North Slope of Alaska with arrows indicating the general locations where Dolly Varden were collected. Nearshore sampling occurred in summer 2005, while freshwater habitats were sampled in fall of 2009, 2010, and 2011.

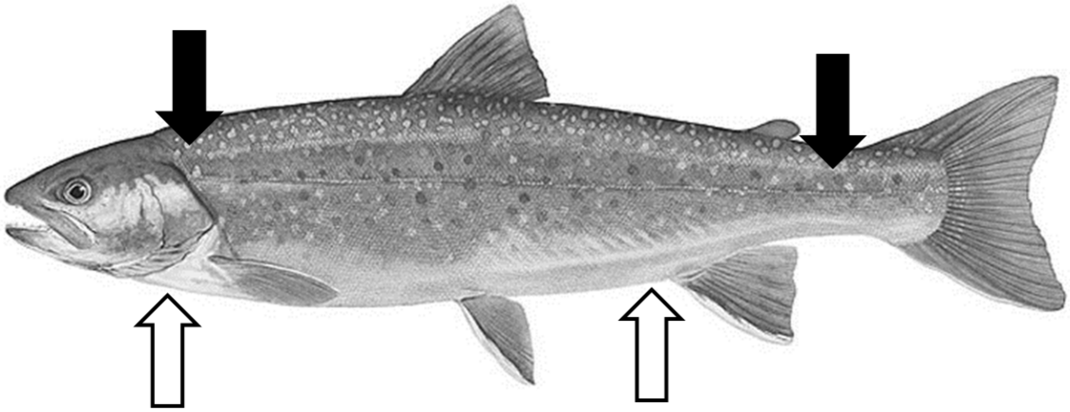

**Figure 2.2**: Electrode placement schemes of BIA electrodes for the collection of lateral (solid arrows) and ventral (hollow arrows) measurements of resistance, reactance, and detector length on Dolly Varden.

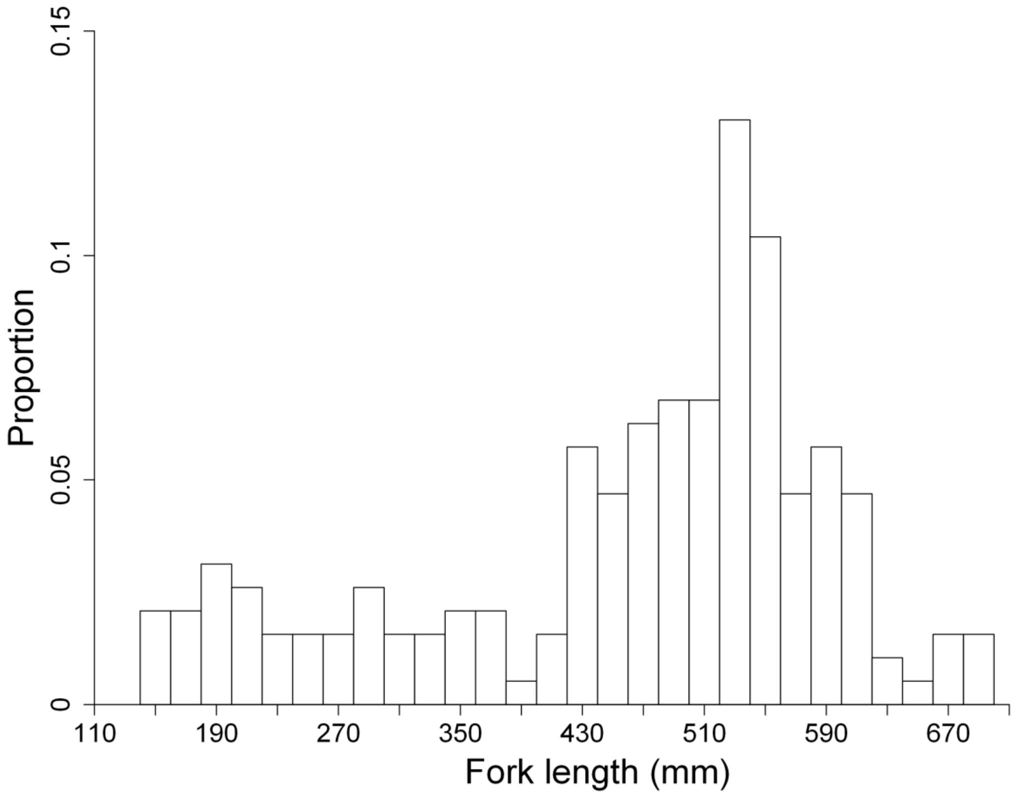

**Figure 2.3**: Sample proportion plotted as a function of composite length data for Dolly Varden collected from Kaktovik and Jago lagoons during 2005, and the Ivishak River between 2009 and 2011.

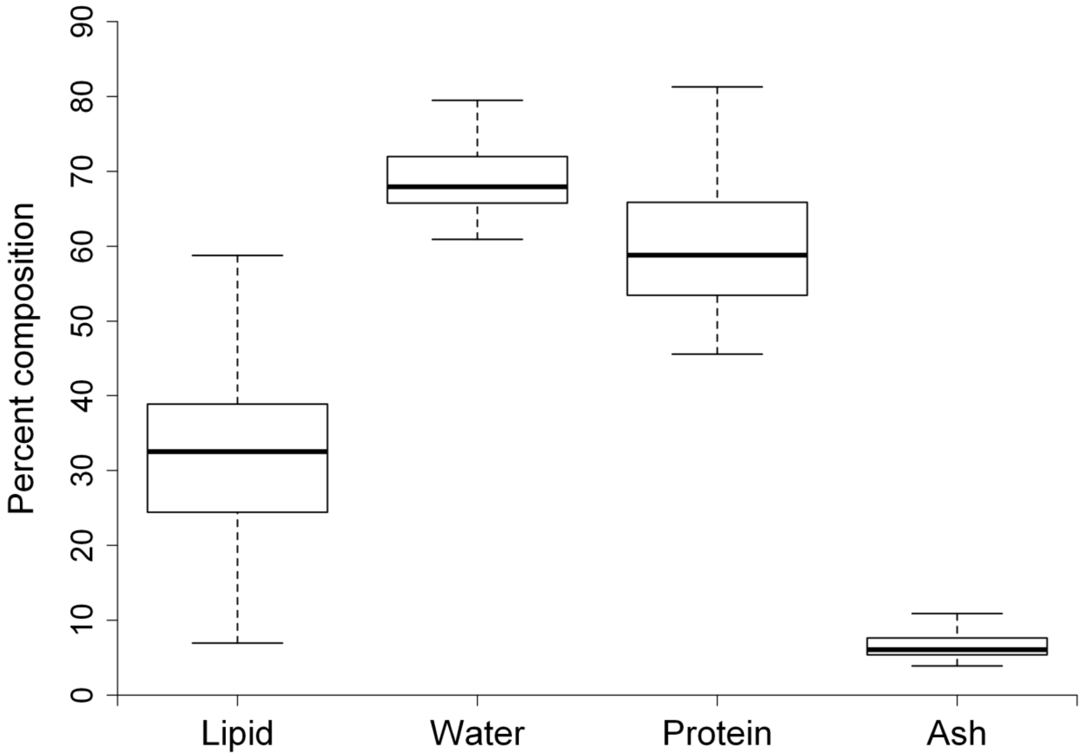

**Figure 2.4**: Percent composition of proximate constituents for Dolly Varden collected from Kaktovik and Jago lagoons and the Ivishak River. Boxplot whiskers encompass 1.5X the interquartile range.

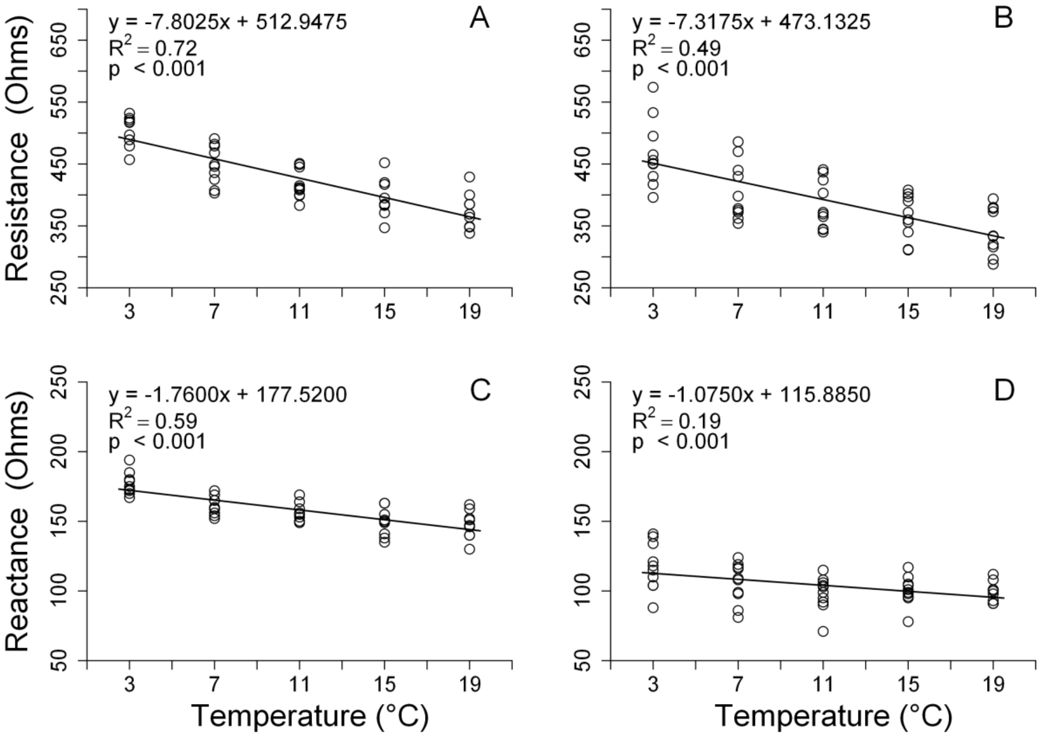

**Figure 2.5**: Trends in electrical resistance and reactance collected laterally (A and C) and ventrally (B and D) across a 16°C temperature range for 10 Dolly Varden collected from the Ivishak River.

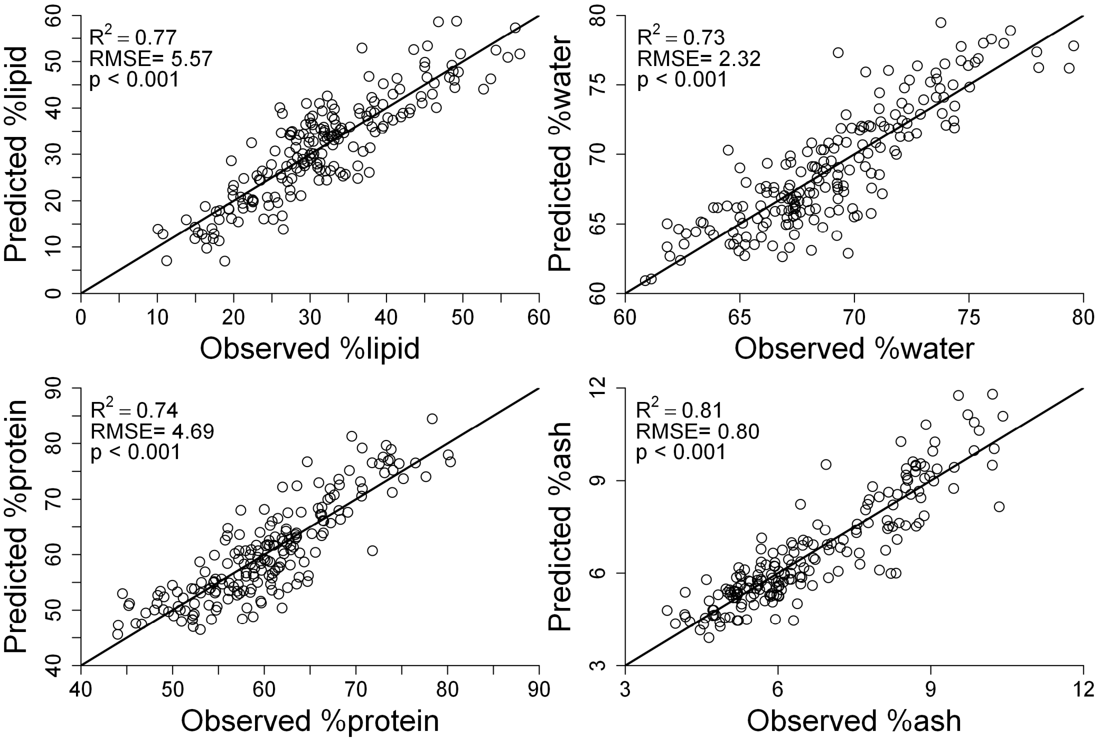

**Figure 2.6**: Bioelectrical impedance analysis model predicted versus observed percent proximate constituent with associated coefficient of determination ($R^2$) and root mean squared error (RMSE) statistics for BIA models developed using combined (lateral and ventral) BIA data.

# Chapter 3: Temporal trends and environmental correlates of amphidromous Dolly Varden growth inferred from otoliths.

## Abstract

The Arctic is warming at rates that exceed global averages; however, little is known regarding how altered thermal regimes or other associated environmental changes will affect fish. Recent research using long-term growth data derived from otoliths has shown promise in clarifying relationships between broad-scale environmental characteristics and fish populations. Using otolith growth as a proxy for fish growth, temporal trends and environmental correlates of Dolly Varden *Salvelinus malma* growth were examined from 202 otoliths collected from the Alaskan Arctic over the past 25 years. Annual estimates of Dolly Varden growth increased significantly from 1980 to 1989, which coincided with similar increases experienced by other Arctic fishes. Significant positive correlations were found between Dolly Varden growth and air and sea surface temperature and river discharge; in contrast, ice concentration was negatively associated with growth. Temporal patterns in the strength of correlations between Dolly Varden growth and sea surface temperature and discharge suggest these environmental characteristics become increasingly important during late summer and early fall. Growth implications of nearshore estuarine habitat quantity, quality, and persistence and methodological and study design limitations are discussed. Future research should determine if, or the degree to which, Dolly Varden behaviorally thermoregulate as this

information will greatly improve our understanding of how Dolly Varden may respond to future climate warming.

## Introduction

Amphidromous northern-form Dolly Varden char *Salvelinus malma*, herein referred to as Dolly Varden, inhabit spring-fed coastal rivers and nearshore areas of the Beaufort Sea in Alaska and Canada (Reist et al. 1997). Individuals spawn and overwinter in freshwater and undergo annual migrations to coastal brackish waters to forage during the short, three month Arctic summer (Craig 1989). During this brief period, Dolly Varden must consume close to 100% of their annual energy budget, as little to no forage is consumed in freshwater (Craig 1989; Boivin and Power 1990). Energy consumed fuels growth and daily metabolic demands, but is also sequestered for subsequent mobilization during spawning and the lengthy overwintering period. Because Dolly Varden forage exclusively in nearshore areas and access to this habitat is temporally limited, it is likely that nearshore habitat quality and quantity imposes substantial consequences on every aspect of the annual life cycle of adult fish, including growth, fecundity, and overwinter survival (Craig 1989).

Recent observations and climate-model predictions suggest that the Arctic is warming at rates that exceed global averages (Serreze et al. 2000; Solomon et al. 2007). Elevated atmospheric temperature has the potential to alter ocean and terrestrial ice dynamics, hydrology, water temperature and salinity, primary and secondary production, and food-web interactions, which will, in turn, directly and indirectly alter the biotic and abiotic structure of nearshore coastal environments, ultimately affecting fish (Magnuson et al. 2000; Carmack and Macdonald 2002; Prowse et al. 2006; Reist et al. 2006; Wagner and Benndorf 2007). While it has been suggested that changes in thermal regimes and associated losses in sea ice may ultimately result in a more productive Arctic, species specifically adapted to Arctic conditions may be negatively affected (Reist et al. 2006; Pabi et al. 2008). For example, Arctic-dwelling Dolly Varden inhabit the northern fringes of their geographic distribution and may be adapted to operate most efficiently within narrow temperature tolerances (Jarvela and Thorsteinson 1997; Reist et al. 2006; Mortensen et al. 2007). Considering the importance of temperature to ectothermic organisms and the short length of the growing season, even small increases in nearshore water temperature have the potential to elicit large biological responses (Brett 1976; Craig 1989).

Assessment and prediction of the population-level effects of an environmental stressor require knowledge of species-habitat relationships (Wiens and Rotenberry 1981). Currently, these relationships are poorly understood for Dolly Varden. While this is partly a result of the complexity of Dolly Varden ecology and the highly dynamic nature of their habitats, logistical challenges associated with operating within remote and often extreme environments have impeded the collection of long-term data (Neill and Gallaway 1989; Hale 1990; Krueger et al. 1999). Recent research using otoliths to derive long-term growth histories has shown promise in elucidating relationships between fish populations and environmental regimes (Guyette and Rabeni 1995; Black et al. 2005). These methods assume otolith growth represents a running average of fish growth, with individual growth chronologies reflecting the integrated outcome of age-specific physiological, behavioral, and environmental characteristics experienced by an individual. Using otolith growth as a proxy for fish growth, long-term chronologies have been applied to evaluate the effects of broad environmental phenomenon such as El Nino events, as well as the effects of individual environmental characteristics such as water and air temperature, precipitation, and ice conditions on fish growth (Guyette and Rabeni 1995; Woodbury 1999; Lebrenton and Beamish 2000; Rypel 2009; Von Biela et al. 2011).

Due to the absence of detailed field or laboratory data regarding Dolly Varden habitat relationships, there is a poor understanding of how Dolly Varden may be affected by anthropogenic stressors such as climate change (Reist et al. 2006). Recent research extracting long-term growth histories from otoliths has shown promise in describing relationships between fish growth and broad scale environmental characteristics (Guyette and Rabeni 1995; Woodbury 1999; LeBrenton and Beamish 2000; Rypel 2009; Von Biela et al. 2011). Such relationships for Dolly Varden would provide an initial first step toward a greater understanding of the potential consequences of anthropogenic stressors such as climate change for these fish. Thus, the overall goal of this work is to explore growth data extracted from both archived and contemporary Dolly Varden otoliths within the Alaskan Arctic over the past 25 years. The specific objectives are to: 1) examine temporal trends in growth and compare these data to growth of other Arctic fishes during similar time intervals, and 2) correlate growth data to broad-scale environmental characteristics to gain a greater understanding of Dolly Varden-habitat relationships. It is important to emphasize the exploratory nature of these analyses given the reliance on samples collected during previous work which, at the time of collection, were not intended to be applied to a retrospective analysis of growth. However, while tenuous in nature, these analyses are unrivaled in the literature, and may guide future research investigating the effects of anthropogenic stressors such as climate change on Dolly Varden.

## Methods

### Sample collection

Archived Dolly Varden otoliths were gathered from six research projects and surveys conducted within nearshore and freshwater habitats of the Alaskan Arctic during the past 25 years (West 1987; Thorsteinson et al. 1991; Underwood et al. 1995; Wiswar and Fruge 2006; J. Carlson, University of Alaska Fairbanks, UAF, unpublished data; J. Stolarski, UAF, unpublished data; Figure 3.1). Nearshore habitats were primarily sampled using fyke nets supplemented by variable-mesh gill nets set within 50 to 60 m from shore, typically in depths less than 1.5 m (Underwood et al. 1995). While sampling occurred throughout the open-water season (June - September), the majority of fish were captured in July and August. Freshwater sampling was conducted during September using hook and line at overwintering habitats in the Ivishak River, a tributary of the Sagavanirktok River. While the objectives and methods of each study varied, in general individuals were measured to the nearest 1-mm fork length and weighed to the nearest 1 g following capture. Otoliths were removed and the sex of mature fish was recorded after examination of external characteristics or following dissection. While date of capture was known for every fish, accompanying information on length, weight, or sex was occasionally incomplete. However, fish length was known for more than 85% of samples.

### Structure preparation

In preparation for sectioning, otoliths were affixed to glass slides using Crystalbond thermoplastic cement (Structure Probe Inc., West Chester, Pennsylvania) perpendicular to the long axis of the otolith. Otoliths were ground to the core in the transverse plane using a thin section machine (Hillquist Inc., Denver, Colorado), remounted to the slide flat side down, and ground to a final thickness of approximately 0.3 mm. In preparation for viewing with a compound microscope, otoliths were hand polished using a 1-µm diamond abrasive. Mounts were viewed and digital images captured at 10X and 40X magnifications using a Micropublisher 3.3 mega pixel microscope mounted digital camera (Quantitative Imaging Co., Burnaby, Canada) under transmitted light. If, after inspection, the mounted otolith section was deemed inadequate for age determination, it was discarded and the other sagitta was processed in the same fashion if available.

### Annuli identification and measurement

Annuli were identified as alternating opaque and hyaline zones (Devries and Frie 1996). Annuli were counted on two separate occasions by a single reader trained in annulus identification. When age estimates were in disagreement, the sample was revisited with the aid of a second trained reader. If age remained in contention, the sample was discarded. The birth year of each fish was determined by subtracting fish age from the year in which it was captured. All otolith measurements were taken using Qcapture pro image processing software (Quantitative Imaging Co., Burnaby, Canada) to the nearest 0.0001 mm. Otolith diameter was measured at 10X magnification as the longest axis that bisected the focus. Annular increments each consisted of one opaque summer growth zone and one translucent winter growth zone, and were measured along a standard transect at 40X magnification (Figure 3.2). The transect on which measurements were collected was chosen based on preliminary data suggesting greater measurement precision relative to other transects tested (Figure 3.2). Annular measurements were only collected from otoliths with clear annular delineations.

Following annuli measurement and the assembly of individual increment width chronologies, ontogenetic growth effects were isolated from environmental effects and removed from each chronology. Typically, ontogenetic growth effects are removed by fitting a negative exponential or similar but more complex function to each chronology (Black et al. 2005; Rypel 2009). Detrended annual adjusted increment widths are then calculated as the observed increment width minus the expected increment width predicted by the function (Black et al. 2005; Rypel 2009). However, these methods were inappropriate for Dolly Varden for two reasons. First, because Dolly Varden are a relatively short-lived species, the temporal scope of each individual chronology was limited, spanning on average only 6 years. As a result, we lacked sufficient degrees of freedom to fit moderately complex or even simple functions to the majority of chronologies. Second, Dolly Varden experience a significant habitat shift when they migrate to sea for the first time, and as a result individual growth chronologies may not conform to the simple negative exponential model used by some researchers when applying these methods to short-lived species (Rypel 2009). Seaward migration is initiated between ages 1 and 5; however, the majority of fish enter the sea for the first time between the ages of 2 and 3, with 95% of all fish having migrated at least once by age 4 (Yoshihara 1973; Underwood et al. 1995; Fechhelm et al. 1997). Upon the onset of amphidromy, somatic and thus otolith growth may increase substantially as a result of productivity differences between marine and freshwater environments (Craig 1977). The magnitude of this anomalous otolith increment and its effect on the fit of the function applied to each growth chronology will likely differ depending on the age at which fish first migrate to sea. Because these dates are both unknown and variable among individuals, their effect cannot be accounted for. As a result, applying a function to remove the effects of size at age from Dolly Varden increment width chronologies may be inappropriate.

In lieu of applying a mathematical function to control for ontogenetic growth effects, a single index of growth for each individual was calculated by dividing the sum of increment widths of the age-0 to -3 cohorts by the width of the age-4 increment. This method attempts to control for age and size affects in two ways. First, by examining only a single year of growth, ontogenetic affects may be minimized as they are more likely to be similar among individuals of the same age. Second, by standardizing the width of the age-4 increment by the summed width of the otolith at the beginning of the fourth year, age-4 growth differences resulting from variability in size at the beginning of the growing season may be minimized. For example, fish that are smaller at the beginning of their fourth year may be less efficient swimmers and possess smaller gapes, two characteristics that could impede piscivory and growth as fish are generally a higher quality forage (Mittelbach and Persson 1998). The age-4 increment was chosen as the basis for the index because previous research indicated that 95% of individuals had migrated to the sea at least once by this age and assessment of marine-growing conditions was desired (Yoshihara 1973; Underwood et al. 1995; Fechhelm et al. 1997).

These methods represent a conservative approach to standardizing growth among individuals as they ignore growth data contained in otolith increments beyond age 4. Cross-dating techniques used to validate age estimates were also not possible due to the collection of only one year of growth information from each individual (Black et al. 2005). However, the removal of samples with contentious age estimates and indistinct annular boundaries may help to prevent aging errors. Furthermore, because measurement of the entire age-4 increment is required to calculate the growth index, fish must be at least age 5 to be included in the study. While these constraints will likely reduce the number of individuals included in the study, we feel they are the most suitable for standardizing increment widths and growth estimates within a relatively short-lived species that undergoes a substantial habitat shift.

### Collection of environmental data

Broad-scale environmental data from the Alaskan Arctic were collected from a variety of sources and expressed at time lags of 0 to 2 years to attempt to account for the multi-year life cycles of common prey items such as mysid shrimp, amphipods, and fish (Craig et al. 1982; Boudrias and Carey 1988; Weslawski 1989; Von Biela et al. 2011). The growth and abundance of such prey species in a particular year is potentially a function of environmental conditions experienced in previous years. Thus, correlations between Dolly Varden growth and environmental conditions can be out of phase. To account for potential delays in the biological expression of environmental conditions resulting from the storage of biological production among years, lags were incorporated. Unless otherwise specified, environmental data were gathered exclusively from the portion of the year encompassing the open water period and monthly and seasonal (open-water period) means were used to summarize each environmental characteristic. The open-water period lasts from June to September and corresponds with annual peaks in Dolly Varden growth (McCart 1980). Thus, environmental data collected during this time should explain the greatest amount of variation in Dolly Varden growth.

Air temperature (ºC), wind speed (km/hr), and wind direction (degrees; Table 3.1), collected at the airport in Deadhorse, Alaska, were assessed from the on-line database of the National Climate Data Center (2012). Typically, measurements were collected hourly; however, during periods of inclement weather, multiple observations per hour may have been recorded. To equalize sampling effort within hours, only the observation recorded at or closest to the beginning of each hour was retained for analysis. Wind speed and direction were converted to linear coordinates (x and y), with the x axis representing the east-west component and the y axis representing the north-south component (Fechhelm et al. 2007). Only the east-west wind component was retained for analysis due to its effect on nearshore productivity during the open-water period (Gallaway et al. 1991; Fechhelm et al. 2007).

Discharge data ($m^3$/sec) from the Sagavanirktok and Mackenzie rivers were gathered due to their influence on the quantity and quality of nearshore estuarine habitat during summer (Table 3.1; Carmack and Macdonald 2002). Sagavanirktok River discharge was measured at USGS gauging station number 15908000 and accessed from the on-line National Water Information System database (2012). Mackenzie River discharge was measured at station 10GC001and accessed from the online database of the Water Survey of Canada (2012). Analysis of discharge data from both rivers was conducted on monthly averages during the open water period but also on an annual average. The Mackenzie River flows year round which, during winter, results in the formation of a large freshwater lake within coastal areas proximate to the river's mouth (Carmack and Macdonald 2002). The water is released following breakup in spring, and may move west along the Beaufort Sea coast altering the temperature and salinity of nearshore habitats (Carmack and Macdonald 2002). Thus, because winter flow may affect summer habitat conditions and ultimately Dolly Varden growth, it must be accounted for.

Arctic Oscillation Index data were accessed via the NOAA National Weather Service Climate Prediction Center (2012) from their on-line database (Table 3.1). The Arctic Oscillation Index is a broad-scale statistical summary of air pressure anomalies over the Arctic Ocean. The index displays negative and positive phases associated with high and low pressure anomalies that reflect the major mode of climate variability in the Arctic, affecting conditions such as air temperature, wind speed and direction, sea ice, and ocean currents (Thompson and Wallace 1998). Optimum interpolation sea surface temperature (SST) and ice concentration version 2 data were provided by the NOAA/OAR/ESRL PSD, Boulder, Colorado, and accessed from the online database of the NOAA Earth Systems Research Laboratory (2012; Table 3.1). These data incorporate in-situ and remote measurements of SST (ºC) and ice concentration (% area covered) that are optimally interpolated over a 1 x 1 degree grid (Reynolds and Smith 1994). Data were obtained from the coordinates 69.5 to 71.5°N by 134.5 to 152.5°W, which encompassed a broad swath of some nearshore, but primarily marine habitat between Barrow, Alaska, and the mouth of the Mackenzie River, Canada, excluding land.

### Statistical analyses

To confirm the relationship between otolith and somatic growth, otolith diameter was modeled as a function of capture length using ordinary least-squares linear regression. The potential effect of capture age on growth estimates was evaluated using one-way Analysis of Variance (Von Biela et al. 2011). Based on the findings of Lee (1912), the selective removal of the largest and fastest-growing individuals of a population by fishing may restructure populations such that the oldest and largest members display the smallest rates of growth. While the amount of fishing pressure exerted on these populations is unknown, the identification of capture age effects is warranted because they may bias growth estimates if the age distribution of samples varies among years. Data were standardized by subtracting the mean and dividing by the standard deviation and ordinary least squares linear regression, weighted by sample size within years, was used to evaluate change Dolly Varden growth over time. Pearson's product-moment correlations were used to measure and test the strength of associations between standardized growth and environmental data. Nonlinear associations among pairwise comparisons were evaluated visually using scatter plots fitted with Loess smooth functions. Statistical procedures were performed using the statistical software package R (R Development Core Team 2012) and all statistical tests, including sequential tests of Pearson's correlation coefficients, were evaluated at alpha = 0.05 (Cabin and Mitchell 2000). However, when evaluating the significance of multiple comparisons using an unadjusted alpha, the probability of type I error increases as the number of comparisons increase.

## Results

A total of 349 otoliths collected from six general locations within freshwater and nearshore estuarine habitats of the Alaskan Arctic were included in the study (Figure 3.1). These fish ranged in length from 91 to 672 mm and encompassed ages 1 through 14 (Figure 3.3). Retrospective growth data were calculated for 202 fish following the exclusion of samples younger than age 5 and individuals whose age-4 growth increment was assigned to a calendar year with fewer than four observations. These fish ranged in length from 285 to 672 mm, encompassed ages 5 to 11, and were collected from the aforementioned locations, minus Pokok Bay (Table 3.2; Figure 3.3). Capture length and otolith diameter data were not available for all samples due the absence of length data, poorly mounted otoliths, or both. Following exclusion of samples with incomplete records, a significant positive relationship was found between otolith diameter and capture length ($F_{1,\ 286} = 2988$, $R^2 = 0.91$, $p < 0.001$; Figure 3.4). Analysis of variance results suggested capture age had no effect on growth estimates ($F_{6,\ 195} = 1.49$, $p = 0.184$). Sex data were not collected or reported for the majority of samples, thus it was not included as a covariate in any analyses.

The reliance on otoliths collected during previous research and surveys resulted in several research design difficulties as once these data sources were exhausted, it was not possible to procure additional samples. In general, the spatio-temporal distribution of samples mirrored the discrete nature in which research projects and surveys are designed and implemented. Due to limited sample sizes, data were pooled among locations within years to extend the temporal record of the data. As a result, growth data were available for two general periods, the first spanning from 1980 to 1989 and the second from 2003 to 2009, with the exception of 2005 (Table 3.2). Due to the large gap in growth data between the years 1990 and 2002, separate weighted linear models were fit to each general period. Linear model results suggested that Dolly Varden growth increased significantly from 1980 to 1989 ($F_{1, 101} = 19.48$, $R^2 = 0.16$, $p < 0.001$). A decreasing trend is noted from 2006 to 2009, but was not significantly different from zero ($F_{1, 81} = 2.52$, $R^2 = 0.03$, $p = 0.116$; Figure 3.5). Pearson's correlation coefficients were computed for a total of a total 86 pairwise comparisons between Dolly Varden growth and environmental characteristics expressed at various time lags. Sequential tests of Pearson's correlation coefficients indicated significant correlations between Dolly Varden growth and SST and air temperature, ice concentration, and discharge (Table 3.3; Figure 3.6). While sample size was limited, visual examination of scatter plots fitted with Loess smooth functions did not reveal evidence of the presence of non-linear relationships among pairwise comparisons of growth and non-significant or significant environmental characteristics (Figure 3.7).

## Discussion

Our results suggest that Dolly Varden growth increased significantly from 1980 to 1989. Unfortunately, there are few data available to compare to our results. Fechhelm et al. (2004) noted that Dolly Varden smolt growth increased from 1985 to a peak in 1989, then declined to 2003. Our results also suggest that Dolly Varden growth increased to a peak in 1989, but data limitations prevent assessment in subsequent years. Growth of age-0 Arctic cisco *Coregonus autumnalis* collected from the Colville River delta also increased during the 1980s (Von Biela et al. 2011). While the authors did not investigate the presence of non-linear trends, Arctic cisco growth appears to asymptote beginning around 1990. Although the causes of growth shifts in Dolly Varden smolts and Arctic cisco around 1990 are unknown, they do correspond to when a major climatic regime shift was reported in the North Pacific Ocean and Bering Sea (Hare and Mantua 2000; Minobe 2002). Unfortunately, assessment of similar trends in adult Dolly Varden growth post 1989 is not possible here due to data limitations.

Analyses of correlations between Dolly Varden growth and environmental characteristics tested 86 multiple comparisons of which eight were found to be significant. Based upon number of tests that were evaluated, four significant results would be expected by chance alone. However, if a Bonferroni correction was applied there would be no significant results. Given the exploratory nature of these analyses and the general lack of information regarding long-term trends in Dolly Vaden growth we feel our methods are appropriate. However, caution should be used when applying the results of these analyses to similar species or locations.

Correlations of Dolly Varden growth and environmental characteristics suggest the importance of three broad types of environmental characteristics: air and water temperature, ice concentration, and freshwater discharge. These analyses incorporated 86 multiple comparisons of which eight were found to be significant. However, based on the number of tests, 4 comparisons would be expected to exhibit significant correlations by chance alone. Dolly Varden are ectothermic organisms whose physiological processes are largely dictated by the temperature of the surrounding environment (Jobling 1994). As such, significant positive correlations between growth and air temperature, through its influence on water temperature, and SST may seem intuitive, provided unlimited forage (Murphy et al. 2007). Additionally, the strength of association between SST and growth increases from June to August, suggesting that thermal environments become increasingly important as summer progresses. Summer Dolly Varden growth may be sigmoidal in shape, with early and late season lulls potentially resulting from an ecological strategy favoring migration over foraging (Fechhelm et al. 1997). Beginning in August, nearshore areas are marked by decreasing temperatures and increasing salinities as declines in freshwater input lead to fragmentation of estuarine habitats and the slow dissolution of the estuarine band. Late season variability in thermal conditions, coupled with the energetic consequences of this variability on migration costs and the efficiency in which forage is captured and assimilated may magnify the effect of temperature on growth, potentially resulting in a tighter temperature-growth relationship during this period (Brett 1976; Beamish 1980; Jobling 1994).

Increased temperature of nearshore areas is one mechanism by which growth of Arctic amphidromous fishes may be affected by climate change (Reist et al. 2006). Dolly Varden and other stenothermic Arctic fishes may be physiologically adapted to operate most efficiently at relatively cold temperatures (Larsson 2005; Reist et al. 2006; Mortensen et al. 2007). The general relationship between salmonid growth and temperature is nonlinear in form with growth increasing from zero at the lower thermal threshold to the thermal optima, then declining back to zero again as temperature approaches the upper thermal threshold; growth is negative outside threshold values (Brett 1976; Jobling 1994). The specific temperatures of the upper and lower thresholds vary by fish size and ration and are unknown for Dolly Varden; however, it is believed these fish are capable of growing at temperatures close to zero (Larsson and Berglund 1998; Reist et al. 2006). While our data are limited, visual examination of growth and temperature plots do not convincingly indicate the presence of non-linear relationships that would suggest nearshore thermal conditions have exceeded upper threshold values. However, the relationship between growth and temperature may be far more complex if individuals behaviorally select for, or avoid subsets of, available thermal habitat (Neill and Gallaway 1989; Bevelhimer and Adams 1993; Neverman and Wurtsbaugh 1994).

Dolly Varden are highly mobile and, within heterogeneous thermal landscapes, capable of selecting conditions most beneficial to the joint conduct of their physiological processes (Neill 1979; Krueger et al. 1999). If Dolly Varden disproportionally select for a subset of available thermal habitats, estimates of mean SST may have little relationship to growth. This is further exacerbated by the inability of SST estimates to capture the thermal profile of the water column. Because nearshore areas may thermally stratify during parts of the summer, SST estimates may not reflect the true diversity and abundance of thermal conditions available to fish (Hale 1990). However, despite these difficulties, the presence of significant linear associations between growth and SST suggest that Dolly Varden are at least, in part, responding to changes in SST or other correlated, but unmeasured, variables. Without knowledge of the degree to which Dolly

Varden behaviorally thermoregulate, and given the potential error associated with SST measurements, assessment of the quality of nearshore thermal habitats for Dolly Varden growth is not possible.

Significant positive correlations between freshwater discharge and Dolly Varden growth highlight the importance of coastal rivers, particularly the Mackenzie River, to nearshore ecosystems. Mackenzie River discharge, supplemented by additional freshwater contributions from smaller systems such as the Sagavanirktok River, largely influences the abundance of estuarine habitat along the Beaufort Sea coast during summer (Gallaway et. al 1991; Carmack and Macdonald 2002). These waters are generally warmer and less saline (5-10°C, 10-25‰) than adjacent marine waters (-1-3°C, 27-32‰), which afford Dolly Varden occupying these habitats several physiological advantages that may allow them to grow more efficiently (Craig 1989; Jobling 1994; Larrson 2005). Furthermore, freshwater runoff contains substantial quantities of dissolved organic carbon and other nutrients which may be important drivers of production within nearshore food webs (Dunton et al. 2006, 2012). Thus, Dolly Varden growth may be inherently linked to freshwater discharge of the Mackenzie River and other rivers through their effect on the quantity and quality of estuarine habitat. In addition, as evidenced by significant correlations between Dolly Varden growth and late summer discharge, freshwater inputs may become increasingly important as the open water season comes to a close. Increased late summer discharge may contribute to the persistence of estuarine habitats into fall and afford Dolly Varden access to favorable foraging and growing conditions for longer periods of time. As a result, predicted changes in Arctic precipitation, air temperature, and the amplitude and timing of annual discharge events have the potential to affect Dolly Varden growth through alterations in the quantity, quality, and persistence of estuarine habitat along the Beaufort Sea coast during summer (Maxwell and Barrie 1989; Miller and Russell 1992; Solomon et al. 2007).

Sea ice concentration over the southern Beaufort Sea in June was negatively correlated with Dolly Varden growth. A decline in sea ice concentration may result in greater phytoplankton production through increased nutrient and light availability and decreased production of ice algae (Carmack and MacDonald 2002). Increases in primary productivity associated with decreased ice concentrations may facilitate greater Dolly Varden growth, and vice versa, if this production (or lack thereof) is transferred through adjacent trophic levels (Arrigo et al. 2008). Additionally, sea ice cover likely contributes to the thermal characteristics of the underlying water. Lower concentrations of ice in June may contribute to higher water temperatures that can facilitate increased growth through reductions in swimming costs and increases in the rate at which forage is captured, assimilated, and evacuated (Brett 1976; Beamish 1980; Jobling 1994).

While the results of this research are intriguing, several limitations imposed by the opportunistic nature by which samples were gathered limit our conclusions. First, the temporal and spatial continuity of growth data used in this research reflected the discreet nature by which most biological studies are designed and implemented. Limited sample sizes among locations and years necessitated pooling data among locations so that even the most basic statistical analyses could be implemented. By pooling data, we introduced the assumption that growing conditions, primarily forage abundance, temperature, and salinity experienced by Dolly Varden, were similar throughout nearshore areas during summer months. Evidence of high forage densities and dietary overlap among secondary consumers suggest that forage may not be limiting (Craig 1989). However, given our knowledge of the physical structure of nearshore systems, the homogeneity of other abiotic conditions is unlikely (Hale 1990; Gallaway et al. 1991).

The nearshore estuarine environment has been likened to a constantly changing mosaic of temperature and salinity patches (Maughan 1990). At large scales, the proximity to and quantity of freshwater inputs influences the size of the estuarine band while prevailing winds modify its location and composition by pushing or pulling it to and from shore (Gallaway et al. 1991; Carmack and MacDonald 2002). Broad-scale conditions are modified locally by lagoon bathymetry and barrier islands that trap or promote water exchange between the lagoon and the marine environment (Hale 1990; Gallaway et al. 1991). As a result of these modifying factors, nearshore habitats are diverse and highly dynamic in both spatial and temporal scales (Hale 1990). However, the dynamic and spatially heterogeneous nature of nearshore habitats may not translate directly to variability in the collective environmental conditions experienced by fish if individuals select for preferred subsets of available conditions. Assuming that individuals of the same age have similar habitat preferences, directed occupancy of a selected subset of preferred conditions may dampen differences in individual environmental histories (Neill 1979). However, it is not currently known if, or the degree to which, Dolly Varden behaviorally select habitats. While behavioral regulation may mediate some differences among individuals, it seems unlikely that this mechanism could completely homogenize environmental histories and validate our assumption that the biotic and abiotic environments experienced by fish are similar among locations.

Despite pooling samples across locations within years, sample sizes remained small. Overwintering aggregations of Dolly Varden from the Ivishak River have been estimated to be in excess of 20,000 individuals in some years (Viavant 2009). Sampling only 12 fish, on average, within each year most likely is not representative of North Slope Dolly Varden populations, especially considering that the Ivishak River aggregation is but one, albeit the largest, of many overwintering aggregations on the North Slope (Viavant 2009). Because of the reliance upon otoliths collected in previous research and surveys, little control could be exerted over the number of samples available for use.

Environmental data were also limiting, not in time, but in space. For example, air temperature and wind data were only available from the Deadhorse airport. By using these data we were forced to assume that air temperature and wind conditions in Deadhorse were representative of conditions throughout the roughly 300 km of Beaufort Sea coast where Dolly Varden were sampled. Such an assumption is unlikely to be valid given variability in topography and local weather conditions throughout such a vast area. New weather stations have recently come online within Arctic Alaska, and will aid in the description of environmental variability over space and time. However, it will be many years before such stations can accumulate a temporal record suited to more robust long-term analyses. Sea surface temperature and ice concentration data, while spatially adequate, were quite coarse. These data were collected on a 1 x 1 degree grid (Reynolds and Smith 1994), which translates to an average cell size of roughly 64 by 64 km. At this resolution, each cell is dominated by marine information as nearshore environments only comprise a small fraction of the area of such a large cell. In using these data, we must assume that marine SST is representative of nearshore SST which may be unlikely given the influence of freshwater input within nearshore habitats (Hale 1990). Finer resolution images, such as those collected by the Landsat satellites or the Advanced Very High Resolution Radiometer (AVHRR), may be more capable of measuring nearshore SST. However, persistent cloud cover over coastal areas of the Alaskan Arctic inhibits the collection of a spatially or temporally continuous SST record (Prakash et al. 2008). Analysis of partial records will be further inhibited by thermal stratification and our incomplete understanding of Dolly Varden behavioral thermoregulation and movement patterns.

The application of growth chronology techniques to such an ecologically complex and short-lived species is not ideal. In general, growth-chronology techniques are reserved for long-lived sedentary species (Strom et al. 2004; Black et al. 2005). The otoliths of long-lived fishes contain greater numbers of increments which permit the application of flexible functions to these data resulting in a more comprehensive analysis and removal of age and growth effects (Black et al. 2005). Furthermore, correlating these detrended data to environmental conditions may be more straightforward within sedentary fishes as growth will most likely be responsive to environmental variability at local scales. For Dolly Varden, first seaward migration represents a significant habitat shift that, due to productivity differences between freshwater and marine habitats, magnifies growth (Craig 1977). Relative to juvenile growth in freshwater, marine growth at the age at first migration, and in subsequent years, represents a substantial shift in the lifetime growth trajectories of individual fish that is recorded in the increment widths of otoliths (Bain 1974). However, variability in the age at first migration and the onset of the marine growth shift can result in very different ontogenetic growth patterns among individuals. Rigid negative exponential functions typically applied to increment chronologies of short-lived fish may not be suitable to account for the presence of this marine growth shift or variability in its location within each chronology. As a result, a different method to isolate and remove ontogenetic signals was needed. Assuming ontogenetic growth effects are similar among individuals of the same age, a single year of growth data from each individual was isolated for analyses. These growth data were standardized to the size of the otolith at the beginning of that year to account for potential differences in growth resulting from size differences among individuals. While this approach may be supported in theory, its application is largely unprecedented in the literature (Boehlert et al. 1989).

In conclusion, Dolly Varden growth data inferred from otoliths were tabulated for two general periods: 1980 to 1989 and 2003 to 2009, with the exception of 2005. Increases in Dolly Varden growth observed during the 1980s were mirrored in age-0 Arctic cisco and Dolly Varden smolts captured from the Alaskan Arctic over similar time intervals (Fechhelm et al. 2004; Von Biela et al. 2011). Significant correlations were observed between growth and air and sea surface temperature, discharge, and ice concentration. However, due to limitations in sample size and methodology, these results should be considered tenuous, but may be useful to guide future research investigating Dolly Varden-habitat interactions. Future efforts should focus on investigating if, or the degree to which, Dolly Varden behaviorally regulate their exposure to the abiotic environment. This information may provide insight into the ability of Dolly Varden to avoid deleterious thermal environments, a behavior that may become increasingly important if projected temperature increases within Arctic environments are realized (Solomon et al. 2007).

## Acknowledgements

We thank the USFWS Fairbanks Fisheries Resource Office for access to otolith collections, and the use of laboratory facilities. Otolith sectioning expertise was provided by Randy Brown, Dave Daum, and Bill Carter. Funding for this study was provided by the USFWS, Arctic National Wildlife Refuge and the Fairbanks Fisheries Resource Office. The use of trade names of commercial products in this report does not constitute endorsement or recommendation for use.

## References

Arrigo, K. R., G. van Dijken, and S. Pabi. 2008. Impact of a shrinking Arctic ice cover on marine primary production. Geophysical Research Letters 35:L19603.

Bain, L. H. 1974. Life histories and systematics of Arctic char (*Salvelinus alpinus*, L.) in the Babbage River system, Yukon Territory. Pages 1 - 156 *in* P. J. McCart, editor. Life Histories of Three Species of Freshwater Fishes in Beaufort Sea Drainages, Yukon Teritory, Aquatic Environments Limited, Arctic Gas Biological Report Series, Volume 18. Calgary, Alberta.

Beamish, F. W. H. 1980. Swimming performance and oxygen consumption of the charrs. Pages 739-748 *in* E. K. Balon, editor. Charrs. Salmonid fishes of the genus *Salvelinus*. Dr W. Junk, The Hague, The Netherlands.

Bevelhimer, M. S., and S. Adams. 1993. A bioenergetics analysis of diel vertical migration by kokanee salmon, *Oncorhynchus nerka*. Canadian Journal of Fisheries and Aquatic Sciences 50:2336-2349.

Black, B. A., G. W. Boehlert, and M. M. Yoklavich. 2005. Using tree-ring crossdating techniques to validate annual growth increments in long-lived fishes. Canadian Journal of Fisheries and Aquatic Sciences 62:2277-2284.

Boehlert, G. W., M. M. Yoklavich, and D. B. Chelton. 1989. Time series of growth in the genus *Sebastes* from the Northeast Pacific Ocean. Fishery Bulletin 87:791-806.

Boivin, T. G., and G. Power. 1990. Winter condition and proximate composition of anadromous Arctic charr (*Salvelinus alpinus*) in eastern Ungava Bay, Quebec. Canadian Journal of Zoology 68:2284-2289.

Boudrias, M. A., and A. G. Carey. 1988. Life history patterns of *Pseudalibrotus litoralis* (Crustacea: Amphipoda) on the inner continental shelf SW Beaufort Sea. Marine Ecology - Progress Series 49:249-257.

Brett, J. R. 1976. Energetic responses to temperature: a study of some thermal relations in the physiology and freshwater ecology of sockeye salmon. American Zoologist 11:99-113.

Cabin, R. T., and R. J. Mitchell. 2000. To Bonferroni or not to Bonferroni: when and how are the questions? Bulletin of the Ecological Society of America 81:246–248.

Carmack, E. C., and R. W. Macdonald. 2002. Oceanography of the Canadian Shelf of the Beaufort Sea: a setting for marine life. Arctic 55:29-45.

Craig, P. C. 1977. Ecological studies of anadromous and resident populations of Arctic char in the Canning river drainage and adjacent coastal waters of the Beaufort Sea, Alaska. Pages 1-116 *in* P. McCart editor. Fisheries Investigations along the North Slope and Beaufort Sea coast in Alaska with emphasis on Arctic char, Aquatic Environments Limited, Arctic Gas Biological Report Series, Volume 41. Calgary, Alberta.

Craig, P. C. 1989. An introduction to anadromous fishes in the Alaskan Arctic. Biological Papers of the University of Alaska 24:27-54.

Craig, P. C., W. B. Griffiths, L. Haldorson, and H. McElderry. 1982. Ecological studies of Arctic cod (*Boreogadus saida*) in Beaufort Sea coastal waters, Alaska. Canadian Journal of Fisheries and Aquatic Sciences 39:395-406.

Devries, D. R., and R. V. Frie. 1996. Determination of age and growth. Pages 483 -508 *in* B. R. Murphy and D. W. Willis, editors. Fisheries techniques, second edition. American Fisheries Society, Bethesda, Maryland.

Dunton, K. H., S. V. Schonberg, and L. W. Cooper. 2012. Food web structure of the Alaskan nearshore shelf and estuarine lagoons of the Beaufort Sea. Estuaries and Coasts 35:416-435.

Dunton, K. H., T. Weingartner, and E. C. Carmack. 2006. The nearshore western Beaufort Sea ecosystem: circulation and importance of terrestrial carbon in Arctic coastal food webs. Progress in Oceanography 71:362-378.

Fechhelm, R. G., J. D. Bryan, W. B. Griffiths, and L. R. Martin. 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 54:1103-1110.

Fechhelm, R. G., W. B. Griffiths, B. E. Haley, and M. R. Link. 2004. Nearshore Beaufort Sea fish monitoring in the Prudhoe Bay region, 2003. Report for BP Exploration (Alaska) Inc. by LGL Alaska Research Associates, Inc., Anchorage.

Fechhelm, R. G., B. Streever, and B. J. Gallaway. 2007. The Arctic cisco (*Coregonus autumnalis*) subsistence and commercial fisheries, Colville River Alaska: a conceptual model. Arctic 60:421-429.

Gallaway, B. J., W. J. Gazey, J. M. Colonell, A. W. Niedoroda, and C. J. Herlugson. 1991. The Endicott Development Project - preliminary assessment of impacts from the first major offshore oil development in the Alaskan Arctic. American Fisheries Society Symposium 11:42-80.

Guyette, R. P., and C. F. Rabeni. 1995. Climate response among growth increments of fish and trees. Oecologia 104:272-279.

Hale, D. A. 1990. A description of the physical characteristics of nearshore and lagoonal waters in the eastern Beaufort Sea. National Oceanic and Atmospheric Administration, Office of Oceanography and Marine Assessment. Report to U.S. Fish and Wildlife Service, Anchorage, Alaska.

Hare, S. R., and N. J. Mantua. 2000. Empirical evidence for North Pacific regime shifts in 1977 and 1989. Progress in Oceanography 47:103-147.

Jarvela, L. E., and L. K. Thorsteinson. 1997. Movements and temperature occupancy of sonically tracked Dolly Varden and Arctic ciscoes in Camden Bay, Alaska. Pages 165-174 *in* J. Reynolds, editor. Fish ecology in Arctic North America. American Fisheries Society, Symposium 19, Bethesda, Maryland.

Jobling, M. J. 1994. Fish bioenergetics. Fish and Fisheries Series 13. Chapman & Hall, London, United Kingdom.

Krueger, C. C., R. L. Wilmot, and R. J. Everett. 1999. Stock origins of Dolly Varden collected from Beaufort Sea coastal sites of Arctic Alaska and Canada. Transactions of the American Fisheries Society 128:49-57.

Larsson, S. 2005. Thermal preference of Arcti charr, *Salvelinus alpinus*, and brown trout, *Salmo trutta*-implicatios for their niche segregation. Environmental Biology of Fishes 73:89-96.

Larsson, S., and I. Berglund. 1998. Growth and food consumption of 0+ Arctic charr fed pelleted or natural food at six different temperatures. Journal of Fish Biology 52: 230-242.

LeBreton, G. T. O., and F. W. H. Beamish. 2000. Interannual growth variation in fish and tree rings. Canadian Journal of Fisheries and Aquatic Sciences 57:2345-2356.

Lee, R. M. 1912. An investigation into the methods of growth determination in fishes. Conseil permanent international pour l'Explororation de la Mer Publication Circulaire 63:1-35.

Magnuson, J. J., D. M. Robertson, B. J. Benson, R. H. Wynne, D. M. Livingstone, T. Arai, R. A. Assel, R. G. Barry, V. Card, E. Kuusisto, N. G. Granin, T. D. Prowse, K. M. Stewart, and V. S. Vuglinski. 2000. Historical trends in lake and river ice cover in the northern hemisphere. Science 289:1743-1746.

Maughan, O. E. 1990. Habitat. Pages 85-96 *in* MBC Applied Environmental Sciences editors. A synthesis of environmental information on causeways in the nearshore Beaufort Sea. U.S. Department of the Interior, Minerals Management Service, OCS Study MMS 89-0038, Anchorage, Alaska.

Maxwell, J. B., and L. A. Barrie. 1989. Atmospheric and climatic change in the Arctic and Antarctic. Ambio 18:42-49.

McCart, P. J. 1980. A Review of the systematic and ecology of Arctic char, *Salvelinus alpinus*, in the western Arctic. Canadian Technical Report of Fisheries and Aquatic Sciences No. 935, Winnipeg, Manitoba.

Miller, J. R., and G. L. Russell. 1992. The impact of global warming on river runoff. Journal of Geophysical Research 97:2757-2764.

Minobe, S. 2002. Interannual to interdecadal changes in the Bering Sea and concurrent 1998/1999 changes over the North pacific. Progress in Oceanography 55:45-64.

Mittelbach, G. G., and L. Persson. 1998. The ontogeny of piscivory and its ecological consequences. Canadian Journal of Fisheries and Aquatic Sciences 55:1454:1465.

Mortensen, A., O. Ugedal, and F. Lund .2007. Seasonal variation in the temperature preference of Arctic charr (*Salvelinus alpines*). Journal of Thermal Biology 32:314-320.

Murphy, S. M., F. J. Mueter, S. R. Braund, L. Lampe, A. K. Prichard B. A. Anderson, and J. C. Seigle. 2007. Variation in the abundance of Arctic cisco in the Colville River:analysis of existing data and local knowledge. U.S. Department of the Interior, Minerals Management Service, Alaska OCS Region, Technical Report Number MMS 2007-042, Anchorage.

National Climate Data Center. 2012. www.ncdc.noaa.gov/oa/dataaccesstools.html (accessed 2, March 2012).

National Water Information System database. 2012. http://waterdata.usgs.gov/nwis (accessed 3 March 2012).

Neill, W. H. 1979. Mechanisms of fish distribution in heterothermal environments. American Zoologist 19:305-317.

Neill, W. H. and B. J. Gallaway. 1989. "Noise" in the distributional responses of fish to environment: an exercise in deterministic modeling motivated by the Beaufort Sea experience. Biological Papers of the University of Alaska 24:123-130.

Neverman, D., and W. A. Wurtsbaugh. 1994. The thermoregulatory function of diel vertical migration for a juvenile fish, *Cottus extensus*. Oecologia 98:247-256.

NOAA Earth Systems Research Laboratory. 2012. http://www.esrl.noaa.gov/psd/data/gridded/data.noaa.oisst.v2.html (accessed 5 March 2012).

NOAA National Weather Service Climate Prediction Center. 2012. http://www.cpc.ncep.noaa.gov/products/precip/CWlink/daily_ao_index/ao_index.html (accessed 3 March 2012).

Pabi, S., G. L. van Dijken, and K. R. Arrigo. 2008. Primary production in the Arctic Ocean, 1998-2006. Journal of Geophysical Research 113:C08005.

Prakash, A., K. Engle, S. Panda, J. Margraf, and T. Underwood. 2008. Nearshore thermal habitat and general circulation mapping in Arctic Alaskan coasts using archived AVHRR images. Annual meeting of the American Geophysical Union, San Francisco, California

Prowse, T. D., F. J. Wrona, J. D. Reist, J. J. Gibson, J. E. Hobbie, L. M. J. Lévesque, and W. F. Vincent. 2006. Climate change effects on hydroecology of Arctic freshwater ecosystems. Ambio 35:347-358.

R Development Core Team. 2012. R: a language and environment for statistical computing. R foundation for Statistical Computing, Vienna. Availaible: www.R-project.org.

Reist, J. D., J. D. Johnson, and T. J. Carmichael. 1997. Variation and specific identity of char from northwestern Arctic Canada and Alaska. American Fisheries Society Symposium 19:250-261.

Reist, J. D., F. J. Wrona, T. D. Prowse, M. Power, J. B. Dempson, R. J. Beamish, J. R. King, T. J. Carmichael, C. D. and Sawatzky. 2006. General effects of climate change on Arctic fishes and fish populations. Ambio 35:370-380.

Reynolds, R. W., and T. M. Smith. 1994. Improved global sea surface temperature analyses using optimum interpolation. Journal of Climate 7:929-948.

Rypel, A. L. 2009. Climate-growth relationships for largemouth bass (*Micropterus salmoides*) across three southeastern USA states. Ecology of Freshwater Fish 18:620-628.

Serreze, M. C., J. E. Walsh, F. S. Chapin III, T. Osterkamp, M. Dyurgerov, V. Romanovsky, W. C. Oechel, J. Morison, T. Zhang, and R. G. Barry. 2000. Observational evidence of recent change in the northern high-latitude environment. Climate Change 46:159-207.

Solomon, S., D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M.Tignor, and H.L. Miller, editors. 2007. Climate change 2007: the physical science basis. Contribution of working group I to the fourth assessment report of the intergovernmental panel on climate change. Cambridge University Press, Cambridge, United Kingdom and New York.

Strom, A., R. C. Francis, N. J. Mantua, E. L. Miles, and D. L. Peterson. 2004. North Pacific climate recorded in growth rings of geoduck clams: a new tool for paleoenvironmental reconstruction. Geophysical Research Letters 31:L06206.

Thompson, D. W. J., and J. M. Wallace. 1998. The Arctic oscillation signature in the wintertime geopotential height and temperature fields. Geophysical Research Letters 25:1297-1300.

Thorsteinson, L. K., L. E. Jarvela, and D. A. Hale. 1991. Arctic fish habitat use investigations: nearshore studies in the Alaskan Beaufort Sea, summer 1990. National Oceanic and Atmospheric Administration, National Ocean Service, Office of Ocean Resources Conservation and Assessment, Annual report, Anchorage, Alaska.

Underwood, T. J., J. A. Gordon, M. J. Millard, L. A. Thorpe, and B. M. Osborne. 1995. Characteristics of selected fish populations of Arctic Wildlife Refuge coastal waters, final report, 1988-1991. U.S. Fish and Wildlife Service, Alaska Fisheries Technical Report No. 28, Fairbanks, Alaska.

Viavant, T. 2009. Aerial monitoring of Dolly Varden overwintering abundance in the Anaktuvik, Ivishak, Canning, and Hulahula rivers, 2006-2008. Alaska Department of Fish and Game, Fishery Data Series No. 09-21, Anchorage.

Wagner, A., and J. Benndorf. 2007. Climate-driven warming during spring destabilizes a Daphnia population: a mechanistic food web approach. Ocecologia 151:351-364.

Water Survey of Canada. 2012. www.climate.weatheroffice.gc.ca. (accessed 3 March, 2012).

Weslawski, J. M. 1989. Occurrence and life cycle of *Mysis oculata* (Crustacea) from Spitsbergen. Polske Archiwum Hydrobiologii 36:207-215.

West, R. L. 1987. Baseline histopathological and contaminant studies of four Arctic fish species in Beaufort Lagoon, Arctic National Wildlife Refuge, Alaska. U. S. Fish and Wildlife Service, Fairbanks Fishery Resources Progress Report Number FY86-4, Fairbanks, Alaska.

Wiens, J. A., and J. T. Rotenberry. 1981. Habitat associations and community structure of birds in shrubsteppe environments. Ecological Monographs 51:21-42.

Wiswar, D. W., and D. Fruge. 2006. Fisheries investigations in Western Camden Bay, Arctic National Wildlife Refuge, Alaska, 1987. U.S. Fish and Wildlife Service, Alaska Fisheries Data Series Number 2006-10, Fairbanks, Alaska.

Woodbury, D. 1999. Reduction of growth in otoliths of widow and yellowtail rockfish (*Sebastes entomelas and S. flavidus*) during the 1983 El Nino. Fishery Bulletin 97:680-689.

Von Biela, V. R., C. E. Zimmerman, and L. L. Moulton. 2011. Long-term increases in young-of-the-year growth of Arctic cisco *Coregonus autumnalis* and environmental influences. Journal of Fish Biology 78:39-56.

Yoshihara, H. T. 1973. Monitoring and evaluation of Arctic waters with emphasis on the North Slope drainages. Alaska Department of Fish and Game, Division of Sport Fish, Federal Aid in Fish Restoration, Project F-9-5, Annual Progress Report 1972-1973, Juneau.

**Table 3.1**: Summary of environmental data incorporated into analysis including units, location collected, coordinates collected, and online source.

| Environmental data | Units | Location described | Coordinates | Data source |
|---|---|---|---|---|
| Wind speed and direction | km/hr | Deadhorse, AK | 70.1917N -148.4722W | www.ncdc.noaa.gov/oa/dataaccesstools.html |
| Discharge | | | | |
| Sagavanirktok River | $m^3$/sec | Alyeska pump station 3 | 69.839722N -148.806944W | http://waterdata.usgs.gov/nwis |
| Mackenzie River | $m^3$/sec | Fort Simpson, NWT | 61.86833N -121.358889W | www.climate.weatheroffice.gc.ca |
| Arctic oscilation | NA | Throughout the Arctic | NA | http://www.cpc.ncep.noaa.gov |
| Sea surface temperature | ºC | Barrow, AK to Makenzie River mouth, NWT | 69.5 to 71.5N by -134.5 to -152.5W | http://www.esrl.noaa.gov |
| Ice concentration | % area covered | Barrow, AK to Makenzie River mouth, NWT | 69.5 to 71.5N by -134.5 to -152.5W | http://www.esrl.noaa.gov |

**Table 3.2**: Sample sizes of Dolly Varden otoliths age 5 or older organized by location and year in which age 4 growth occurred. Calendar years with fewer than four samples have been omitted.

| Year | Beaufort Lagoon | Bullet Point | Camden Bay | Ivishak River | Jago and Kaktovik Lagoons | Total |
|---|---|---|---|---|---|---|
| 1980 | 7 | 0 | 0 | 0 | 0 | 7 |
| 1981 | 13 | 0 | 0 | 0 | 0 | 13 |
| 1982 | 7 | 0 | 0 | 0 | 0 | 7 |
| 1983 | 7 | 2 | 4 | 0 | 1 | 14 |
| 1984 | 2 | 0 | 4 | 0 | 1 | 7 |
| 1985 | 1 | 0 | 9 | 0 | 1 | 11 |
| 1986 | 1 | 0 | 8 | 0 | 2 | 11 |
| 1987 | 1 | 0 | 3 | 0 | 12 | 16 |
| 1988 | 4 | 0 | 2 | 0 | 3 | 9 |
| 1989 | 8 | 0 | 0 | 0 | 0 | 8 |
| 2003 | 0 | 0 | 0 | 0 | 3 | 5 |
| 2004 | 0 | 0 | 0 | 1 | 10 | 11 |
| 2006 | 0 | 0 | 0 | 4 | 0 | 4 |
| 2007 | 0 | 0 | 0 | 22 | 0 | 22 |

**Table 3.2 continued:**

| | | | | | | |
|---|---|---|---|---|---|---|
| 2008 | 0 | 0 | 0 | 32 | 0 | 32 |
| 2009 | 0 | 0 | 0 | 26 | 0 | 25 |
| Total | 51 | 2 | 30 | 87 | 33 | 202 |

**Table 3.3**: Pearson's correlation coefficients and p values of significant pairwise comparisons of environmental characteristics and standardized Dolly Varden growth.

| Environmental characteristic | Pearson's r | P-value |
|---|---|---|
| June SST | 0.576 | 0.031 |
| July SST | 0.607 | 0.021 |
| August SST | 0.649 | 0.012 |
| August air temperature | 0.714 | 0.004 |
| June ice concentration | -0.598 | 0.024 |
| August discharge Mackenzie River | 0.636 | 0.008 |
| Mean discharge Mackenzie River | 0.504 | 0.046 |
| September discharge Sagavanirktok River | 0.596 | 0.024 |

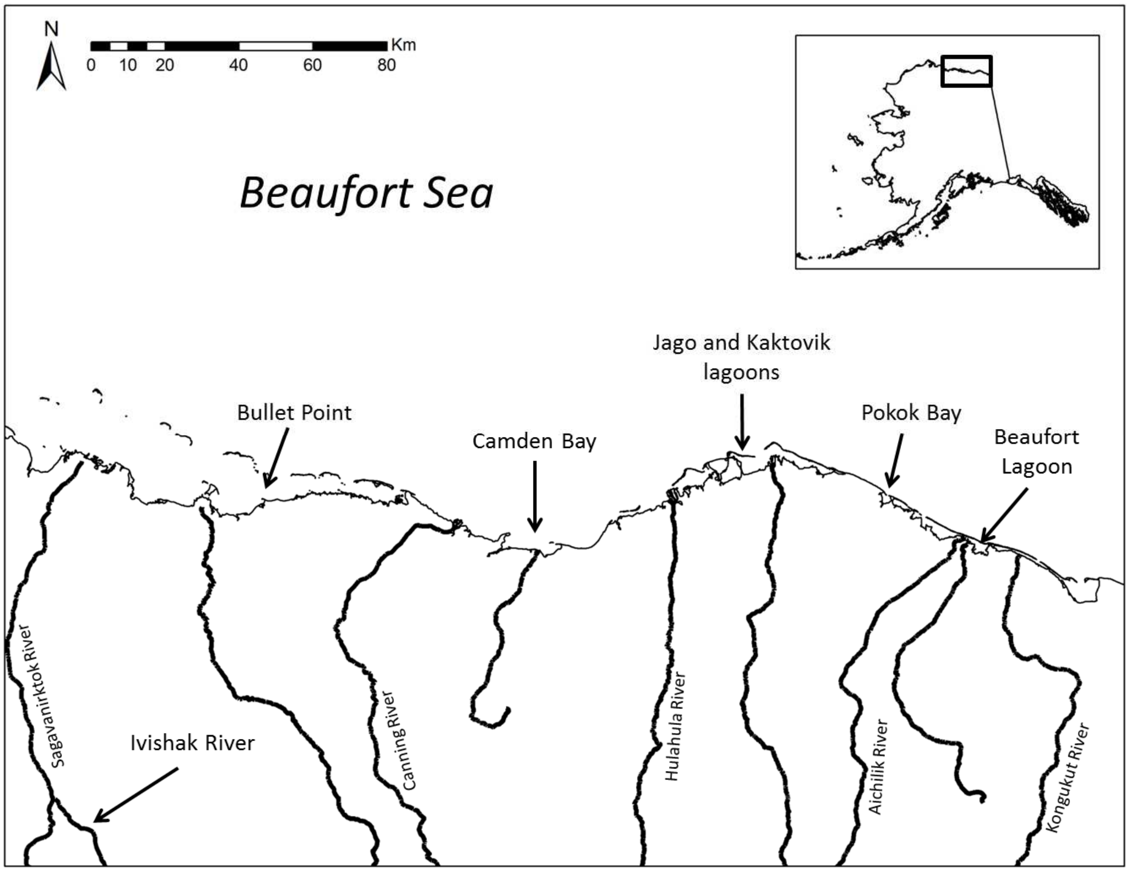

**Figure 3.1**: Map of nearshore and freshwater areas of the Alaskan Arctic with black arrows indicating the general locations where otoliths were collected in previous research and surveys.

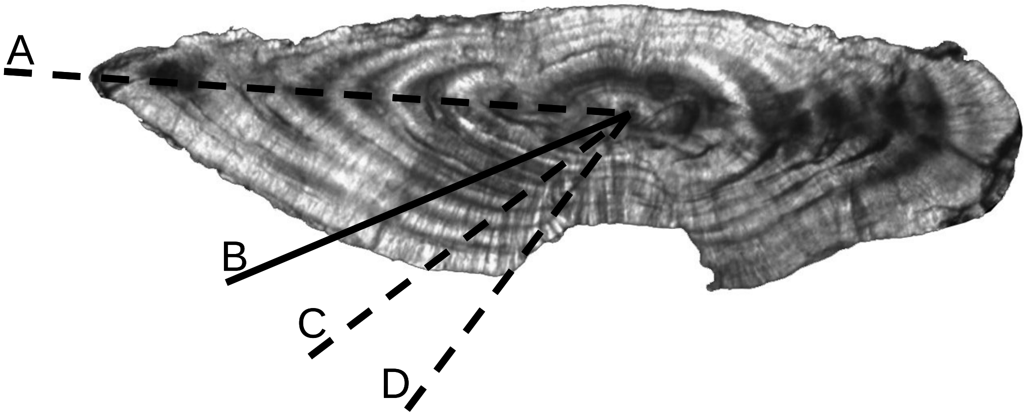

**Figure 3.2**: Transverse section of a Dolly Varden otolith depicting transects, each emanating from the focus, on which preliminary (dashed lines) and final (solid line) annuli measurements were taken. Transect B bisects the angle created by radii A and D joining at the focus and transect C bisects the angle created by radii B and D joining at the focus.

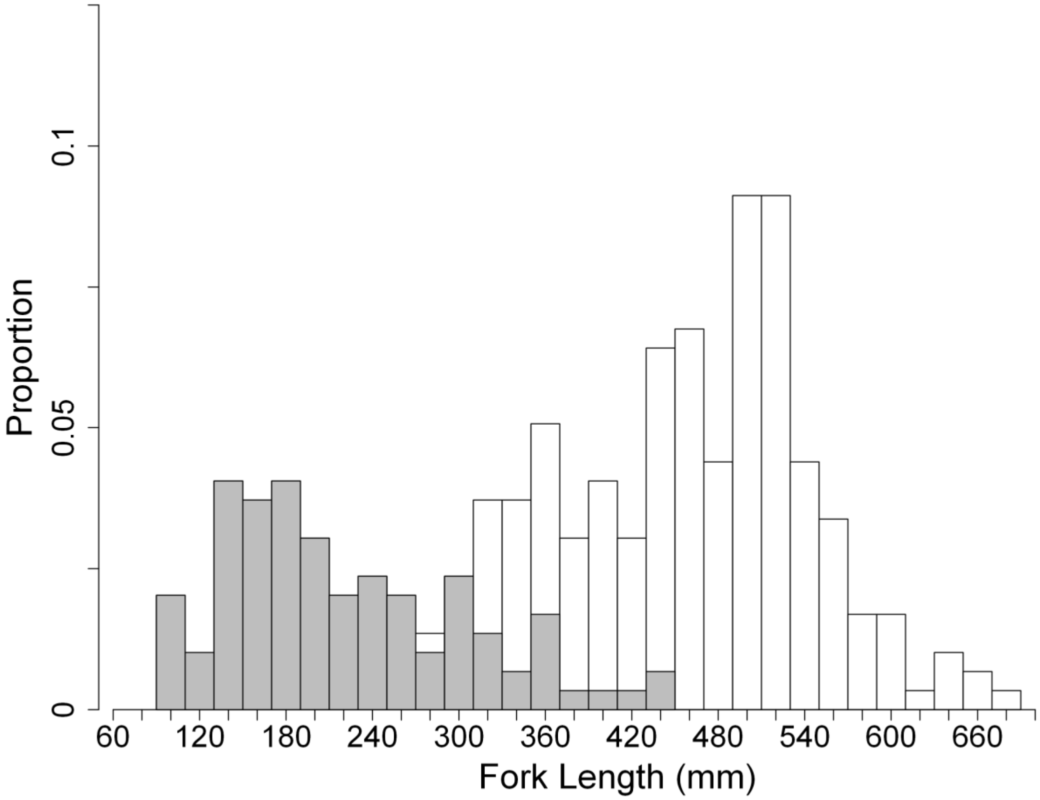

**Figure 3.3**: Stacked length-frequency histogram of Dolly Varden sampled from nearshore and freshwater habitats of the Alaskan Arctic conditioned by age. Open bars indicate fish older than age 4, while grey bars are fish age 4 and younger.

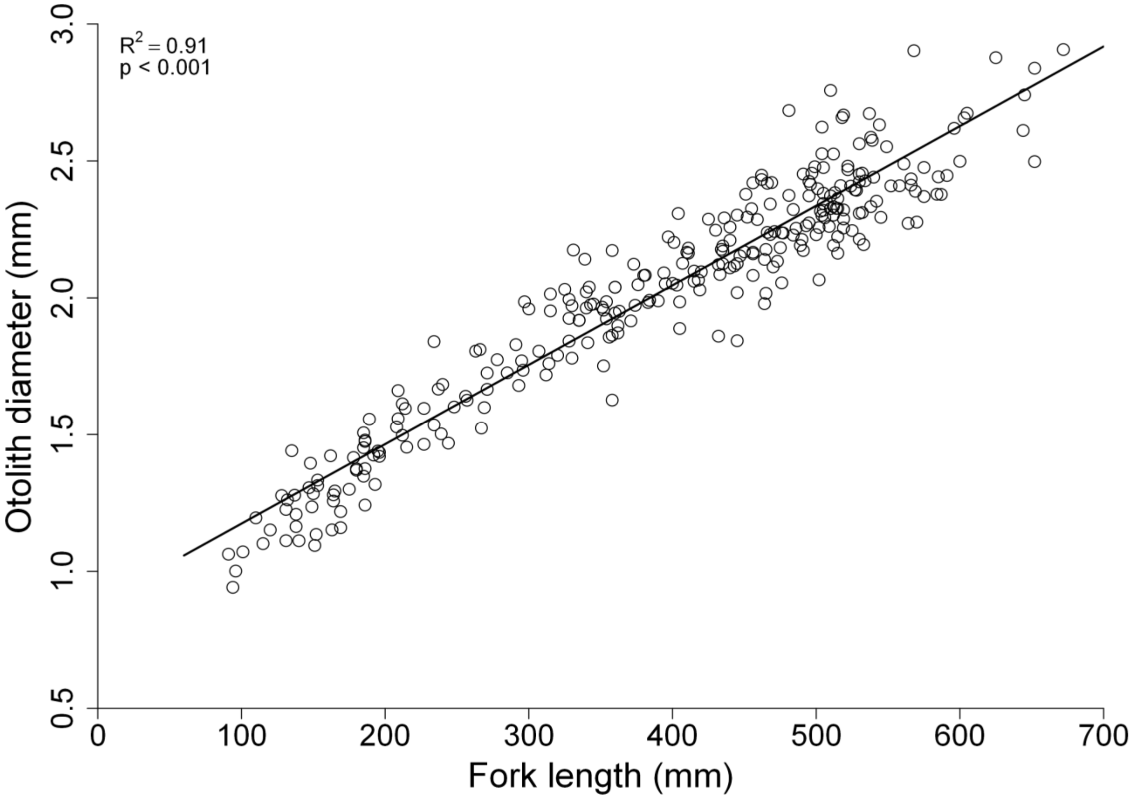

**Figure 3.4**: Otolith diameter as a function of fork length for all age-classes of Dolly Varden captured from freshwater and estuarine habitats of Arctic Alaska.

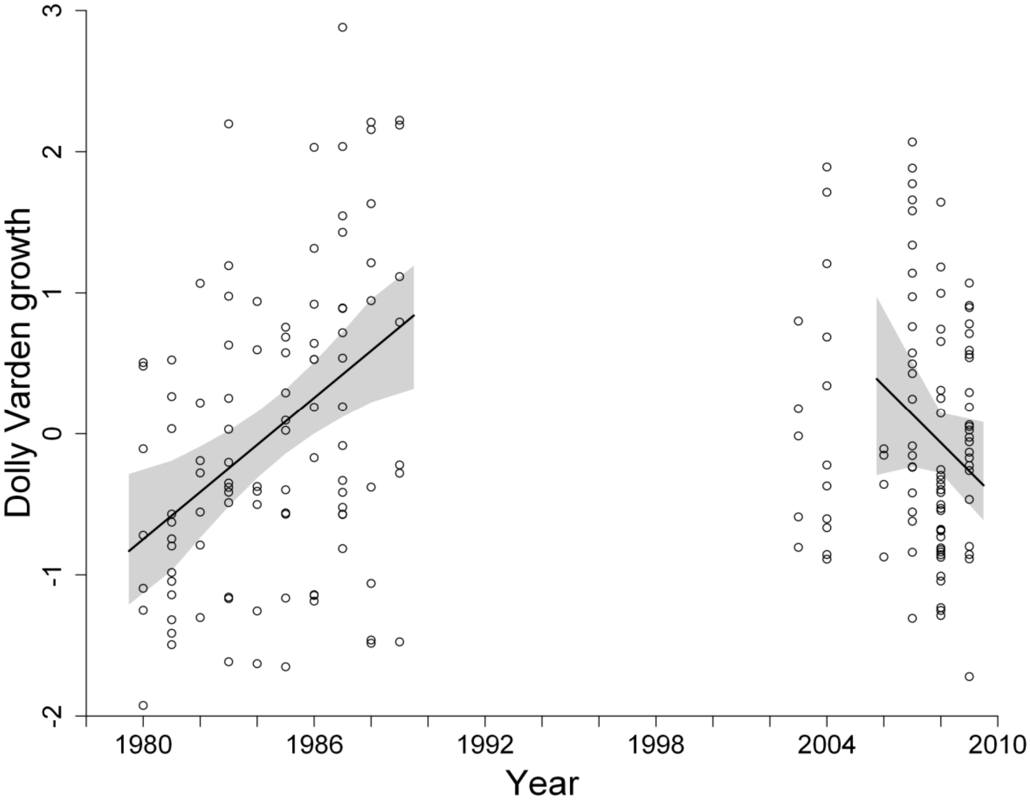

**Figure 3.5**: Weighted linear regressions with 95% confidence intervals (grey shading) of standardized, age-4 Dolly Varden growth and calendar year. Separate models were fit to data groupings spanning from 1980 to 1989 and from 2006 to 2009.

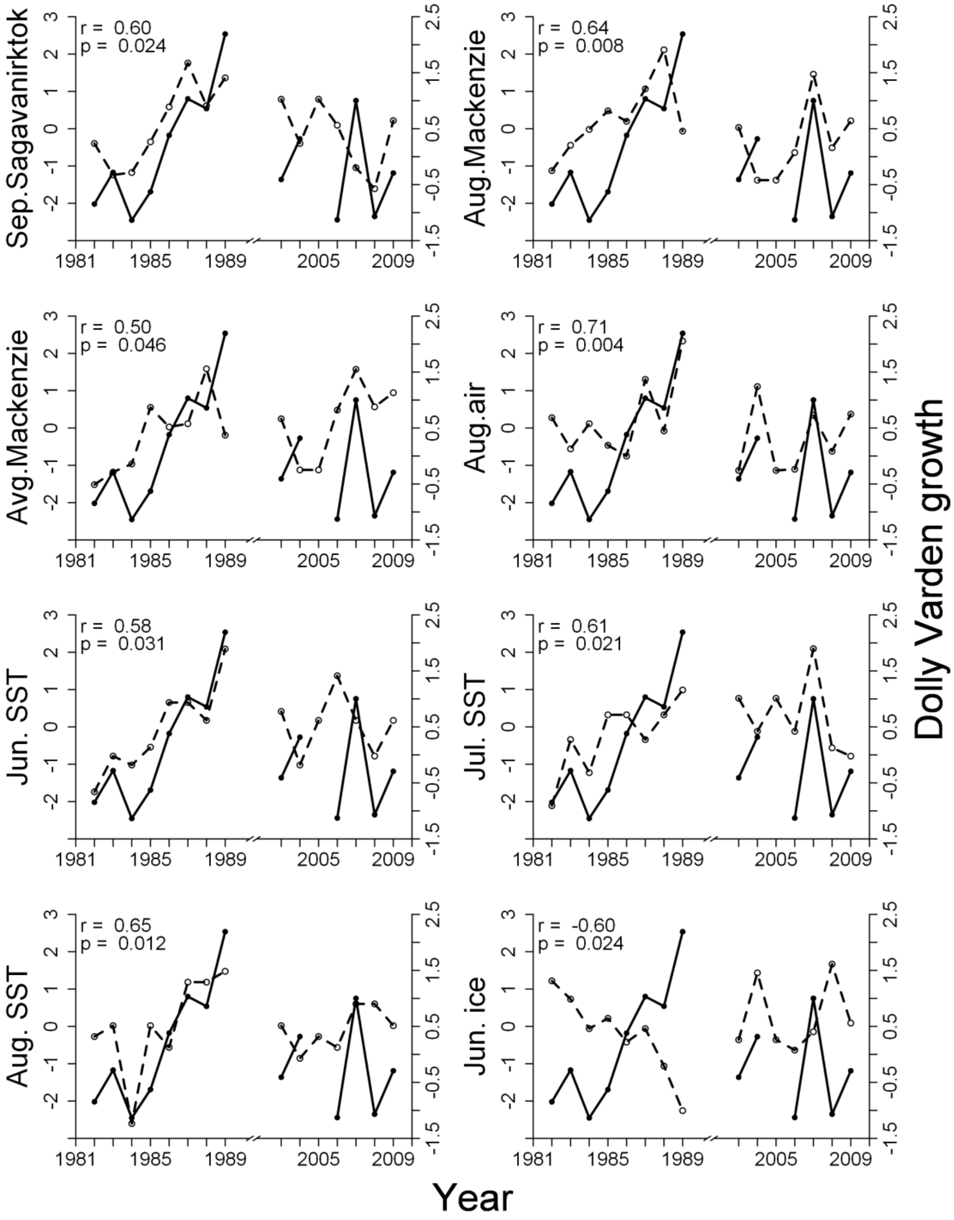

**Figure 3.6**: Standardized environmental characteristics (dashed line) and age-4 Dolly Varden growth (solid line) plotted by year with Pearson's correlation (r) and associated p values (p).

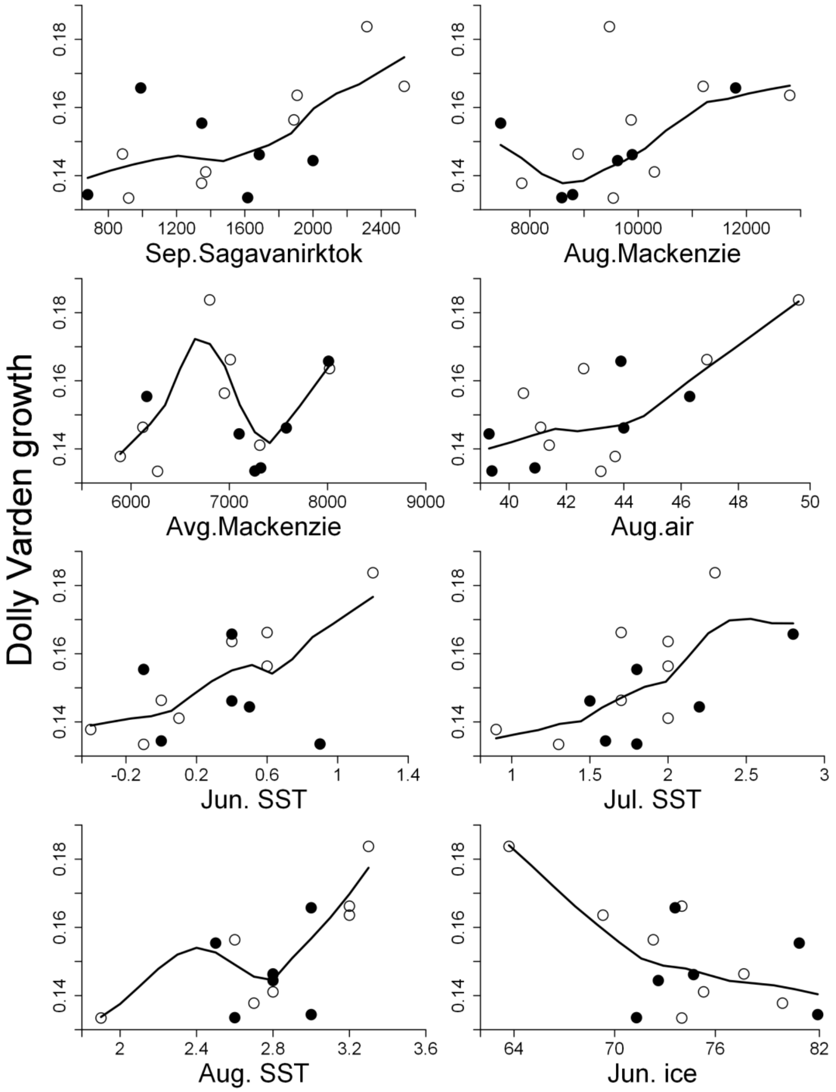

**Figure 3.7**: Standardized Dolly Varden growth plotted as a function of environmental characteristics, each fitted with a smoothed loess function. Solid points refer to data collected between 2003 and 2009, while empty points are data collected prior to 1990.

# Chapter 4: Dolly Varden whole body and tissue energy content: demographic effects and reproductive investment.

## Abstract

Seasonal and ontogenetic cycles of lipid storage and depletion likely influence Dolly Varden *Salvelinus malma* population structure and abundance through tradeoffs between reproductive output and post-spawning and overwintering mortality. To our knowledge, no data exists regarding variation in Dolly Varden whole body or tissue energy content among years or demographics (i.e. reproductive versus non-reproductive individuals). We quantified percent-based whole body proximate and tissue water content of reproductive and non-reproductive adult Dolly Varden (N = 90) collected in 2010 and 2011 from the Ivishak River, Alaska. The gonadal somatic index of reproductive and non-reproductive females increased significantly with fork length, but no significant trends were apparent for males of either reproductive status. Dolly Varden captured in 2010 were in overall poorer condition relative to 2011 and displayed significantly lower whole body estimates of lipid and greater estimates of carcass and viscera water content. In both years, non-reproductive fish contained greater proportions of lipid relative to reproductive fish, likely reflecting differences in freshwater residence times among the two groups. Furthermore, reproductive fish exhibited significantly greater percentages of carcass and viscera water content suggesting energy is mobilized from these tissues during reproduction and freshwater residence. Despite substantial

differences in whole body lipid content among years, reproductive fish invested similar amounts of energy (as a percentage of body weight) into gamete production. Tradeoffs between reproductive investment and post-reproductive and overwintering mortality are discussed.

## Introduction

Amphidromous northern-form Dolly Varden char *Salvelinus malma* (herein referred to as Dolly Varden) are a dominant member of the nearshore Arctic ichthyofauna and support one of the largest traditional subsistence fisheries in coastal Arctic communities (Craig et al. 1984; Pedersen and Linn 2005). During summer, adults undertake two to three month sojourns to sea where they forage heavily upon marine invertebrates and fish (Craig et al. 1984). The summer foraging season is a critical period for Dolly Varden as these fish must acquire close to 100% of their annual energy budgets while at sea (Craig 1989). The remaining portion of the year is spent subsisting upon endogenous energy reserves (primarily lipid) within deep pool habitats and spring areas of coastal rivers where little forage is consumed (Boivin and Power 1990). Seasonal patterns in lipid concentration, and to a lesser extent, morphological-based estimates of condition (Glass 1989; Brown 2008), often mirror these patterns in resource availability, with annual peaks and depressions occurring in late summer and early spring (Jobling et al. 1998).

Seasonal limitations in resource availability and energy costs associated with the lengthy overwintering period tax individual energy reserves within any given year (Glass 1989). Reproductive fish face a greater burden as they must allocate additional resources for gamete production and the formation of secondary sexual characteristics (Shul'man 1974; Dutil 1984). For example, Dutil (1986) noted that mature, non-reproductive Arctic char *Salvelinus alpinus* lost close to 30% of their energy reserves during winter compared to 52% for reproductive fish. High reproductive costs amid a temporally limited resource landscape likely inhibit Dolly Varden from accumulating energy reserves sufficient to reproduce in consecutive years (Furniss 1975; Dutil 1986). Thus, interwoven within the annual cycle of lipid accumulation and depletion is an ontogenetic lipid cycle operating at multi-year intervals and characterized by fish in two different states of energy accumulation, one en route to, and the other recovering from, reproduction.

To our knowledge, there are no data describing the size or magnitude of annual variability in Dolly Varden lipid content both within and among fish. Endogenous lipid dynamics reveal the relative importance and storage capacities of different tissues, including energy invested into gonads (Jørgensen et al. 1997; Jobling et al. 1998). At the organismal level, variability in lipid content among sexes and demographics (i.e. reproductive versus non-reproductive individuals) suggest possible mechanisms (post-reproductive and overwintering mortality) responsible for the regulation of population abundance or structure (Dutil 1984, 1986; Jonsson et al. 1997). Of particular importance may be the relationship between parental condition and reproductive investment as research suggests a linkage between parental condition, ova quality, and recruitment (as reviewed by Kamler 2005). To obtain a greater understanding of Dolly Varden energy dynamics and their potential effect on mortality and reproductive investment, we quantified whole body and tissue composition among demographics, sexes, and years for Dolly Varden collected from the Ivishak River in 2010 and 2011.

## Methods

### Fish sampling

Sampling occurred at overwintering habitats on the Ivishak River, Alaska. The Ivishak River originates in the Brooks Mountain range, and is a north-flowing tributary of the Sagavanirktok River, which empties into the Beaufort Sea at Prudhoe Bay (Figure 4.1). The Ivishak River is generally thought to contain the largest overwintering aggregation of Dolly Varden on the North Slope of Alaska (Viavant 2005).

Mature Dolly Varden (> 400-mm fork length) were captured by angling during multiple sampling events in late August and early September 2010 and 2011 (Underwood et al. 1996). The sample was to be partitioned equally among combinations of demographic and sex. Reproductive fish were defined as those that contained ripe gonads and would spawn that year, while non-reproductive fish were defined as fish that contained developing gonads and would not spawn in the given year. Sex and demographic were determined visually from external characteristics, such as coloration and presence or absence of secondary sexual characteristics. The first 12 to 15 individuals caught within each combination of demographic and sex were retained for this study. Upon capture, fish were sacrificed via cranial concussion, weighed to the nearest 1 g, and measured to the nearest 1 mm in fork length. Each fish was individually labeled, wrapped in plastic, and transported to the University of Alaska Fairbanks where they were frozen at -40°C prior to subsequent laboratory analyses.

## Laboratory methods

In the laboratory, fish were thawed and dissected, stomachs were excised, and forage items were removed to eliminate variability in energy content associated with the quantity or quality of forage. Viscera, including the stomach and swim bladder, gonads, and the remaining carcass, were weighed separately to the nearest 1g. Egg diameter was measured as the mean length in mm of 10 non-water swollen ova, and fecundity was assessed using the gonadal somatic index (GSI), calculated as the ratio of the wet weight of the gonads versus the wet weight of the fish. Sectioned carcasses, gonads, and viscera were desiccated in a freeze drier to a constant weight. Percent water content was calculated as the quotient of the difference between sample wet- and dry-weight and wet weight. The carcass, viscera, and gonads were then combined and homogenized using an industrial blender, and subsamples (0.5 to 1.5 g) were taken for analysis of proximate composition following standardized methods (AOAC 1990). Lipid was extracted using the soxhlet method, and protein content was estimated from nitrogen analysis following the application of a nitrogen:protein conversion factor of 6.25. Ash content was determined from weight differences following the combustion of a subsample in a muffle furnace operating at 550°C for 24 hours. All samples were run in triplicate, averaged, and expressed as a percentage of the dry weight of the subsample.

### Statistical analyses

Prior to analysis, all dependent variables were arcsine square root transformed to meet assumptions of normality. Differences in whole body proximate composition (i.e., percent lipid, protein, water and ash) and water content of anatomical subdivisions (i.e., carcass, gonad, and viscera) among sex, demographic, year, and their interactions were assessed separately using multivariate analysis of variance (MANOVA) at an alpha = 0.05. If interaction effects were significant, sequential tests of analysis of variance (ANOVA) were used to test each dependent variable separately (Jonson and Wichern 2007). Sequential tests were evaluated at a Bonferroni corrected alpha = 0.05/ t, where t = the number of sequential tests performed. Length-based trends in GSI were tested using ordinary least squares regression and evaluated at an alpha = 0.05. All statistical analyses were conducted using the statistical software package R (R development Core Team 2012).

### Results

A total of 90 Dolly Varden were collected in 2010 and 2011 and were apportioned somewhat unequally among different combinations of demographic and sex (Table 4.1). Reproductive males were particularly difficult to capture and thus were poorly represented in the sample. Furthermore, visual discrimination between reproductive and non-reproductive females was also difficult and contributed to sample inequality. Dolly Varden included into the study ranged in length between 400 mm (the lower size limit for inclusion) and 680 mm and in weight between 530 and 2,776 g (Figure 4.2, 4.3). Gonadal somatic index was significantly related to fork length within reproductive ($F = 7.55$; $p = 0.011$) and non-reproductive ($F = 11.79$; $p = 0.002$) females (Figure 4.4). No significant trends were observed in GSI data in reproductive ($F = 0.46$; $p = 0.519$) or non-reproductive ($F = 1.70$; $p = 0.204$) males (Figure 4.4).

Multivariate analysis of variance of whole body estimates of proximate constituents (i.e., lipid, protein, water, and ash) indicated significant interactions among the independent variables sex, demographic, and year. As a result, each dependent variable was tested separately using ANOVA. Analysis of variance indicated that whole body estimates of lipid, protein, and water differed significantly ($P < 0.013$) among years and demographics while ash content differed significantly only among demographics (Table 4.2). More specifically, lipid content was significantly lower in 2010 relative to 2011($F = 98.63$; $p < 0.001$) and among both years, non-reproductive fish exhibited significantly greater percentages of lipid ($F = 36.90$; $p < 0.001$) relative to reproductive fish (Figure 4.5). Whole body estimates of protein and water content were significantly greater in 2010 relative to 2011 ($F = 74.20$; $p < 0.001$; $F = 108.03$; $p < 0.001$), while among both years, non-reproductive fish exhibited significantly lower percentages of protein ($F = 36.45$; $p < 0.001$) and water ($F = 7.39$; $p = 0.007$). Reproductive fish exhibited significantly greater percentages of ash ($F = 14.81$; $p < 0.001$) relative to non-reproductive fish among both years (Figure 4.5).

Multivariate analysis of variance of tissue subdivision (i.e., carcass, viscera, and gonad) water content also indicated significant interactions among the independent variables sex, demographic, and year. Analysis of variance results of carcass and viscera water content suggests these metrics were significantly ($p < 0.017$) greater in 2010 relative to 2011 ($F = 84.78$; $p < 0.001$; $F = 117.36$; $p < 0.001$; Figure 4.6). Among both years, reproductive fish exhibited significantly greater percentages of water within carcass ($F = 15.12$; $p < 0.001$) and viscera ($F = 117.36$; $p < 0.001$) tissues (Figure 4.6). Significant interactions between sex and demographic prompted analysis of gonad water content to be conducted separately among demographics. No differences in gonad water content within non-reproductive fish were detected among sex, year, or their interaction. Gonad water content of reproductive females was significantly ($P < 0.01$) lower than that of reproductive males ($F = 549.20$; $p < 0.001$) and did not differ among years ($F = 0.03$; $p = 0.858$; Figure 4.7).

## Discussion

During periods when metabolic costs exceed rates of energy consumption, stored energy (primarily lipid) is allocated to cover deficits resulting in a decline in proportion of body lipid (Shul’Man 1974). Research suggests that many salmonids may reduce or completely curtail foraging activities for some time prior to reproduction (Brett 1995; Kadri et al. 1996; Tveiten et al. 1996). Within North Slope Dolly Varden populations, reproductive fish generally precede non-reproductive fish at spawning and overwintering grounds by up to a month (Glova and McCart 1974; McCart 1980). Certain segments of Dolly Varden populations in northwestern Alaska are known to forgo seaward entry entirely during the summer in which they are to reproduce (DeCicco 1997). Upon or possibly prior to freshwater entry, Dolly Varden cease to consume forage (Boivin and Power 1990; J. Stolarski, University of Alaska Fairbanks [UAF], unpublished data). Thus, the lower lipid content observed within reproductive relative to non-reproductive Dolly Varden may be a result of longer freshwater residence periods. However, differences may also, in part, reflect energy deficits incurred during vitellogenesis and the endogenous processing and transport of lipid in support of morphological alterations and the development of ova (Jonsson et al. 1991; Jobling 1994; Tocher 2003). Regardless of their origin, energetic deficits within reproductive fish likely contribute to greater rates of post-reproductive and overwintering mortality within this demographic (Furniss 1975; McCart 1980). Boivin and Power (1990) noted that in late winter, reproductive Arctic char exhibited lower body condition relative to non-reproductive char. Given that these fish had already spawned, reduced condition might be expected due to the energetic costs of agonistic behaviors, ova release, and the development of secondary sexual characteristics (Jonsson et al. 1991). However, our research suggests that energetic deficits within reproductive fish may already exist in early fall, prior to the release of gametes. These results suggest that the cessation of foraging and freshwater residency may play a larger role in energy depletion of reproductive fish than previously thought (Dutil 1984).

Trends in other whole body proximate constituents among years and demographics are more difficult to interpret due to their inherent interrelationships. Lipid, protein, and ash content were expressed as a percentage of dry weight, thus changes to one component will invariably alter the relative values of others (Shearer 1994). During fall, lipid undergoes the greatest percent change as it is selectively consumed in the early stages of starvation and during the production of gametes (Shul'Man 1974; Navarro and Gutierrez 1995). Alternatively, ash content may change relatively little among fish of similar sizes (Shearer 1994). Trends in protein content among years and demographics are opposite that of lipid, which suggests these trends are more reflective of lipid dynamics rather than true energetic phenomenon (Shearer 1994). Previous research suggests that protein metabolism increases during the latter stages of starvation after lipid stores have been largely depleted (Shul'man 1974; Castellini and Rea 1992; Navarro and Gutierrez 1995; Hendry et al. 2000).

Estimates of water content among tissues indicate the proportion of energy (primarily lipid) contained therein due to the inverse relationship between whole body and tissue energy and water content (Medford and Mackay 1978; Jonsson et al. 1997; Hartman and Margraf 2008). Greater proportions of water within the carcasses of reproductive Dolly Varden suggest that the carcass is an important store from which energy is mobilized within reproductive fish (Jørgensen et al. 1997; Jobling et al. 1998; Hendry et al. 2000). The majority of this energy is most likely used to fuel gamete production in the case of females and to cover the metabolic costs of agonistic behavior and the development of secondary sexual characteristics in males (Shul'man 1974;

Jonsson et al. 1991). Viscera water content exhibited similar trends among years and demographics as carcass water content, suggesting that lipid is mobilized from this depot as well (Shul'man 1974; Boivin and Power 1990). However, relative to contributions from muscle or skeletal tissues, visceral lipid may comprise only a small fraction of mobilized energy (Jørgensen et al. 1997; Jobling et al. 1998).

Given the energetic differences between ova and milt, it is not surprising that reproductive males exhibited greater gonad water content relative to reproductive females (Wootton 1998). However, no relationship existed between whole body lipid and reproductive investment (gonad water content) within spawning fish. For example, Dolly Varden collected in 2010 exhibited significantly lower whole body and tissue energy content relative to 2011, yet reproductive investment presumably remained similar among years. The parental effects hypothesis proposes that parental condition is conveyed to offspring through alterations in the amount of energy allocated to reproduction and predicts that reproductive fish in greater condition should invest more energy into gamete production, resulting in higher quality products (as reviewed by Kamler 2005). While seemingly intuitive, support for this hypothesis has not been universal, and may not apply to Dolly Varden (Keckeis et al. 2000; Ouellet et al. 2001; Bunnel et al. 2005; Moles et al. 2007; Wiegand et al. 2007; Muir et al. 2010). However, such a relationship might be masked if reproductive investment, or the decision to reproduce at all, was dependent upon lipid status at some point earlier in the seasonal cycle (Moles et al. 2007).

Dutil (1986) and others have hypothesized that there exists a threshold body condition below which gamete production is not initiated (Kadri et al. 1995; Tveiten et al. 1996). Temporal patterns in egg diameter among reproductive and non-reproductive Dolly Varden captured in nearshore habitats indicate that ova begin to ripen in early summer (Craig and Haldorson 1981). This suggests that reproductive decisions (i.e., the assessment of endogenous energy stores) are made during spring, prior to marine residence. These periods correspond to seasonal nadirs in Dolly Varden condition resulting from the exclusive reliance upon endogenous resources during the previous winter (Dutil 1986; Boivin and Power 1990). Thus, the decision to mature will largely depend upon energy reserves acquired in past years (Dutil 1986). Individuals not meeting energetic thresholds will defer maturation, while maturing fish will begin to allocate resources according to the abundance of their individual internal stores. Sampling data suggests that reproductive fish may only spend brief amounts of time within marine environments the year they are to spawn, if they migrate to sea at all (Glova and McCart 1974; DeCicco 1997). Dolly Varden acquire close to 100% of their energy from the marine environment, thus, the failure to fully exploit this resource may suggest that, in spring, reproductive fish already possess the majority of energy required for spawning later that fall. Individuals with energy levels close to but not exceeding critical thresholds may then undertake protracted seaward migrations to supplement energy stores with failure to acquire sufficient energy resulting in gonad reabsorption. By scaling reproductive effort according to body reserves, this strategy would maximize individual reproductive effort. However, if during this process somatic growth is not realized or overwintering energy stores are compromised, future reproductive effort may be affected through reductions in fecundity and increased post-spawning and overwintering mortality (Dutil 1986; Wootton 1998). Because reproductive decisions may be made at a time when Dolly Varden are at seasonal nadirs in condition, the amount of energy invested into reproduction may always be relatively small, especially if maturing fish undertake only limited seaward excursions the year they are to reproduce (Johnson 1980).

The lack of a clear relationship between body lipid and gonad energy content and similarities in reproductive investment among years could also indicate an upper limit to gonad energy density. Energy accumulated in excess of reproductive requirements might then be allocated to somatic growth or used to bolster overwintering reserves. Because gonad size increases with fish size, absolute energy investment will increase with fish size and possibly lead to reductions in somatic growth, condition, and senescence within older fish (Dutil 1986). Given temporal limitations to forage and the energetic costs of the lengthy overwintering period, a conservative and cautious approach to the maintenance of sufficient energy stores is certainly warranted. Future research should attempt to collect Dolly Varden during spring while in freshwater. The tissue and whole body energy content of these fish may reveal, in greater detail, reproductive investment strategies and the critical energy level that must be attained before reproduction is initiated.

## Acknowledgements

We thank Dave Sowards for assistance in capturing fish in the field, and Peter Bechtel, Lara Hortsmann-Dehn, and Matthew Wooler for the use of their laboratory facilities. Scientific sampling was conducted under the authority of Alaska Department of Fish and Game Fishery Resource Permit SF2010-088 and SF2011-046. Funding for this study was provided by the U.S. Fish and Wildlife Service, Arctic National Wildlife Refuge and the Fairbanks Fisheries Resource office. Care and handling of all fish included in this study was in accordance with approved protocols of the University of Alaska Fairbanks Institutional Animal Care and Use Committee assurance 175440-3.

**References**

Association of Official Analytical Chemists (AOAC). 1990. Official methods of analysis. Association of Official Analytical Chemists, Washington, D.C.

Boivin, T. G., and G. Power. 1990. Winter condition and proximate composition of anadromous Arctic char (*Salvelinus alpinus*) in eastern Ungava Bay, Quebec. Canadian Journal of Zoology 68:2284-2289.

Brett, J. R. 1995. Energetics. Pages 1-66 *in* C. Groot, L. Margolis, and W. C. Clarke, editors. Physiological ecology of Pacific salmon. University of British Columbia Press, Vancouver.

Brown, R. J. 2008. Life history and demographic characteristics of Arctic cisco, Dolly Varden, and other fish species in the Barter Island region of northern Alaska. U.S. Fish and Wildlife Service, Alaska Fisheries Technical Report No. 101, Fairbanks, Alaska.

Bunnell, D. B., M. A. Scantland, and R. A. Stein. 2005. Testing for evidence of maternal effects among individuals and populations of white crappie. Transactions of the American Fisheries Society 134:607-619.

Castellini, M. A., and L. D. Rea. 1992. The biochemistry of natural fasting and its limits. Experientia 48:575-581.

Craig, P.C. 1989. An introduction to anadromous fishes in the Alaskan Arctic.  Biological Papers of the University of Alaska 24:27-54.

Craig, P. C, W. B. Griffiths, S. R. Johnson, and D. M. Schell. 1984. Trophic dynamics in an Arctic lagoon. Pages 347-380 *in* P. W. Barnes, D. M. Schell, and E. Reimnitz, editors. The Alaskan Beaufort Sea: ecosystems and environments. Academic Press, New York.

Craig, P. C., and L. Haldorson. 1981. Fish. Pages 384-678 *in* S. R. Johnson and W. J. Richardson, editors. Beaufort Sea barrier island-lagoon ecological process studies: final report, Simpson Lagoon, part 4. Environmental assessment of the Alaskan continental shelf, final report of principal investigators vol. 8: Biological Studies. National Oceanic and Atmospheric Administration, Outer Continental Shelf Environment Assessment Program, and Bureau of Land Management, Boulder, Colorado.

DeCicco, A. L. 1997. Movements of postsmolt anadromous Dolly Varden in Northwest Alaska. American Fisheries Society Symposium 19:175-183.

Dutil, J. D. 1984. Energetic costs associated with the production of gonads in the anadromous Arctic charr (*Salvelinus alpinus*) of the Nauyuk Lake basin, Canada. Pages 263-276 *in* L. Johnson and B. L. Burns, editors. Biology of the Arctic Charr. University of Manitoba Press, Winnipeg.

Dutil, J. D. 1986. Energetic constraints and spawning interval in the anadromous Arctic charr (*Salvelinus alpinus*). Copeia 4:945-955.

Furniss, R. A. 1975. Inventory and cataloging of Arctic area waters. Alaska Department of Fish and Game, Federal Aid in Fish Restoration, Project F-9-7, Annual Report of Progress, Anchorage.

Glass, D. R. 1989. Changes in the condition and physiological parameters of anadromous fish species in the central Beaufort Sea during the overwintering period. Part I, Chapter II *in* Endicott Environmental Monitoring Program - 1987. Report by Envirosphere Company for the U.S. Army Corps of Engineers, Anchorage, Alaska.

Glova, G., and P. McCart. 1974. Life history of Arctic char (*Salvelinus alpines*) in the Firth River, Yukon Territory. Pages 1-51 (Chapter 3) *in* P. J. McCart, editor. Life histories of anadromous and freshwater fish in the Western Arctic. Biological Report Series, Volume 20. Canadian Arctic Gas Study Limited/Alaskan Arctic Gas Study Company, Calgary, Alberta.

Hartman, K. J., and F. J. Margraf. 2008. Common relationships among proximate composition components in fishes. Journal of Fish Biology 73:2352-2360.

Hendry, A. P., A. H., Dittman, and R. W. Hardy. 2000. Proximate composition, reproductive development, and a test for trade-offs in captive sockeye salmon. Transactions of the American Fisheries Society 129:1082-1095.

Jørgensen, E. H., S. J. S. Johansen, and M. Jobling. 1997. Seasonal patterns of growth, lipid deposition and lipid depletion in anadromous Arctic charr. Journal of Fish Biology 51:312-326.

Jobling, M. J. 1994. Fish bioenergetics. Chapman and Hall, London, United Kingdom.

Jobling, M., S. J. S. Johansen, H. Foshaug, I. C. Burkow, and E. H. Jørgensen. 1998. Lipid dynamics in anadromous Arctic Char, *Salvelinus alpinus* (L.): seasonal variations in lipid storage depots and lipid class composition. Fish physiology and biochemistry 18:225-240.

Johnson, L. 1980. The Arctic char, *Salvelinus alpinus*. Pages 15-98 *in* U. K. Balon editor. Charrs: Salmonid Fishes of the Genus *Salvelinus*. Dr. W. Junk bv Publishers, The Hague, The Netherlands.

Jonson, R. A., and D. W. Wichern 2007. Applied multivariate statistical analysis. Prentice-Hall, London.

Jonsson, N., B. Jonsson, and L. P. Hansen. 1991. Energetic cost of spawning in male and female Atlantic salmon (*Salmo salar* L.). Journal of Fish Biology 39:739-744.

Jonsson, N., B. Jonsson, and L. P. Hansen. 1997. Changes in proximate composition and estimates of energetic costs during upstream migration and spawning in Atlantic salmon *Salmo salar*. Journal of Animal Ecology 66:425-436.

Kadri, S., N. B. Metcalfe, F. A. Huntingford, and J. E. Thorpe. 1995. What controls the onset of anorexia in maturing adult female Atlantic salmon? Functional Ecology 9:790-797.

Kadri, S., D. F. Mitchell, N. B. Metcalfe, F. A. Huntingford, and J. E. Thorpe. Differential patterns of feeding and resource accumulation in maturing and immature Atlantic salmon, *Salmo salar*. Aquaculture 142:245-257.

Kamler, E. 2005. Parent-egg-progeny relationships in telost fishes: an energetics perspective. 2005. Reviews in Fish Biology 15:399-421.

Keckeis, H., E. Bauer-Nemeschkal, V. V. Menshutkin, H. L. Nemeschkal, and E. Kamler. 2000. Effects of female attributes and egg properties on offspring viability in a rheophilic cyprinid, *Chondrostoma nasus*. Canadian Journal of Fisheries and Aquatic Sciences 57:789-796.

McCart, P. J. 1980. A Review of the systematic and ecology of Arctic char, *Salvelinus alpinus*, in the western Arctic. Canadian Technical Report of Fisheries and Aquatic Sciences No. 935, Winnipeg, Manitoba.

Medford, B. A., and W. C. Mackay. 1978. Protein and lipid content of gonads, liver, and muscle of northern pike (*Esox lucius*) in relation to gonad growth. Journal of the Fisheries Research Board of Canada 35:213-219.

Muir A. M., T. M., Sutton, M. T. Arts, R. M. Claramunt, M. P. Ebener, J. D. Fitzsimons, T. B. Johnson, R. E. Kinnunen, M. A. Koops, and M. M. Sepulveda. 2010. Does condition of Lake Whitefish spawners affect physiological condition of juveniles? Journal of Great Lakes Research 36:92-99.

Navarro, I., and J. Gutierrez. 1995. Fasting and starvation. Pages 393-434 *in* P. W. Hochachika and T. P. Mommsen, editors. Biochemistry and molecular biology of fishes, volume 4, metabolic biochemistry. Elsevier, Amsterdam.

Ouellet, P., Y. Lambert, and I. Be´rube´. 2001. Cod egg characteristics and viability in relation to low temperature and maternal nutritional condition.  ICES Journal of Marine Science 58:672-686.

Pedersen, S., and A. Linn, Jr. 2005. Kaktovik 2000-2001 Subsistence Fishery Harvest Assessment. U.S. Fish and Wildlife Service, Office of Subsistence Management, Fishery Information Services Division, Federal Subsistence Fishery Monitoring Program, Final Project Report No. FIS 01-101, Anchorage, Alaska.

R Development Core Team. 2012. R: a language and environment for statistical computing. R foundation for Statistical Computing, Vienna. Availaible: www.R-project.org.

Shearer, K. D. 1994. Factors affecting the proximate composition of cultured fishes with emphasis on salmonids. Aquaculture 119:63-88.

Shul'man, G. E. 1974. Life cycles of fish, physiology and biochemistry. Wiley, New York.

Tocher, D. R. 2003. Metabolism and functions of lipids and fatty acids in telost fish. Reviews in Fisheries Science 11:107-184.

Tveiten, H., H. K. Johnsen, and M. Jobling. 1996. Influence of maturity status on the annual cycles of feeding and growth in Arctic char reared at constant temperature. Journal of Fish Biology 48:910-924.

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

Viavant, T. 2005. Eastern North Slope Dolly Varden stock assessment. Alaska Department of Fish and Game, Fishery Data Series Number 05-07, Anchorage.

Wiegand, M. D., T. A., Johnston, W. C. Leggett, K. E. Watchorn, A. J. Ballevona, L. R. Porteous, and J. M. Casselman. 2007. Contrasting strategies of ova lipid provisioning in relation to maternal characteristics in three walleye (*Sander vitreus*) populations. Canadian Journal of Fisheries and Aquatic Sciences 64:700-712.

Wootton, R. J. 1998. The ecology of teleost fishes. Kluwer Academic Publishers, Dordrecht, The Netherlands.

**Table 4.1**: Sample size of Dolly Varden collected from the Ivishak River in 2010 and 2011 for each demographic and sex combination.

|  | 2010 |  | 2011 |  |
|---|---|---|---|---|
| Sex | Spawner | Non-spawner | Spawner | Non-spawner |
| Male | 5 | 14 | 5 | 11 |
| Female | 13 | 9 | 15 | 18 |

**Table 4.2**: F values and associated p values for significant ($p < 0.013$) coefficients of ANOVA models investigating differences in whole body proximate constituents as a function of sex, year, demographic and their interactions.

| | Year | | Demographic | |
|---|---|---|---|---|
| Constituent | F | p value | F | p value |
| Whole body lipid | 98.63 | < 0.001 | 36.9 | < 0.001 |
| Whole body protein | 74.2 | < 0.001 | 36.45 | < 0.001 |
| Whole body water | 108.03 | < 0.001 | 7.38 | 0.007 |
| Whole body ash | …. | …. | 14.82 | < 0.001 |

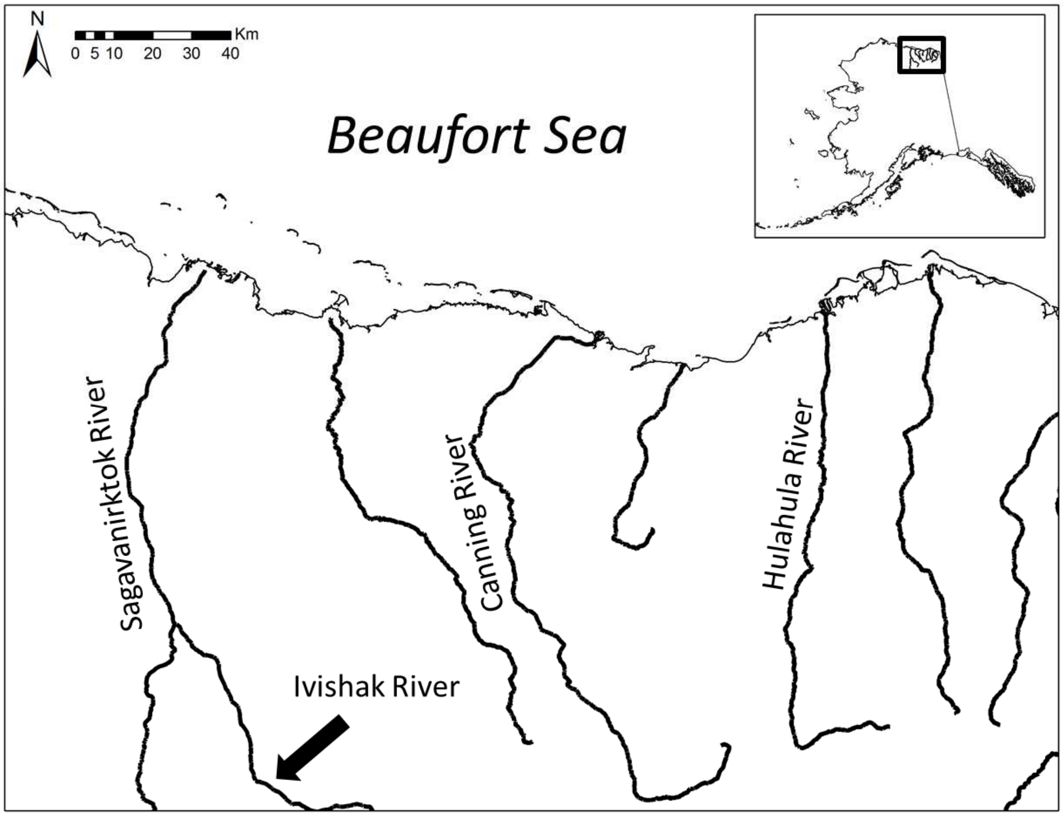

**Figure 4.1**: Map of major rivers on the Eastern North Slope of Alaska, with a black arrow indicating the general location on the Ivishak River where adult Dolly Varden were captured in 2010 and 2011.

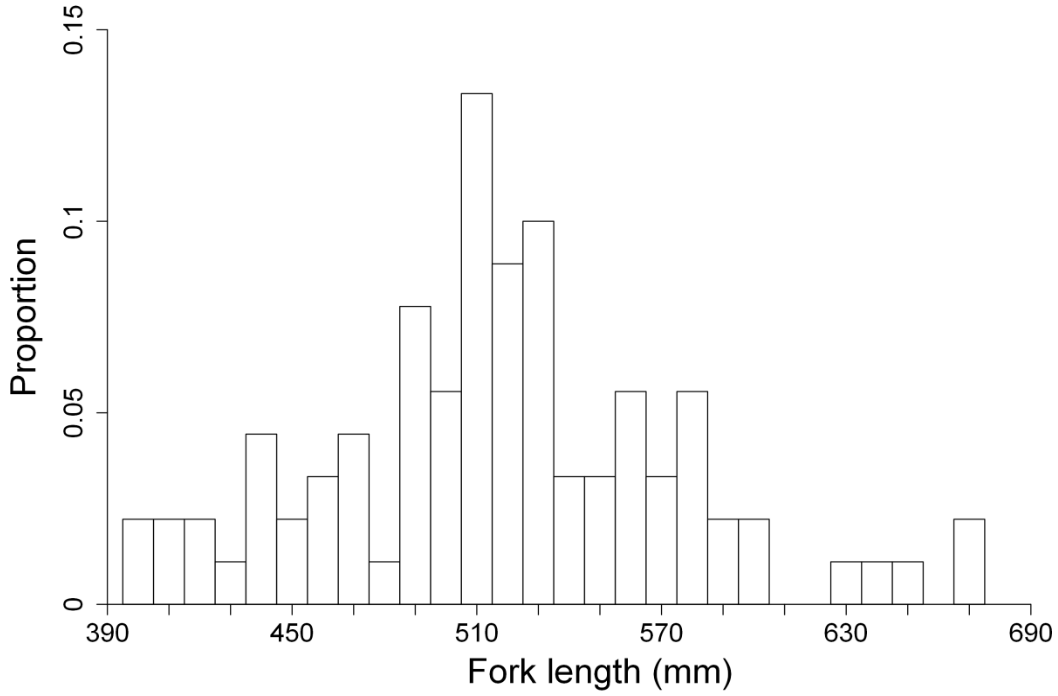

**Figure 4.2**: Composite length data plotted against sample proportion for Dolly Varden collected from the Ivishak River in fall of 2010 and 2011.

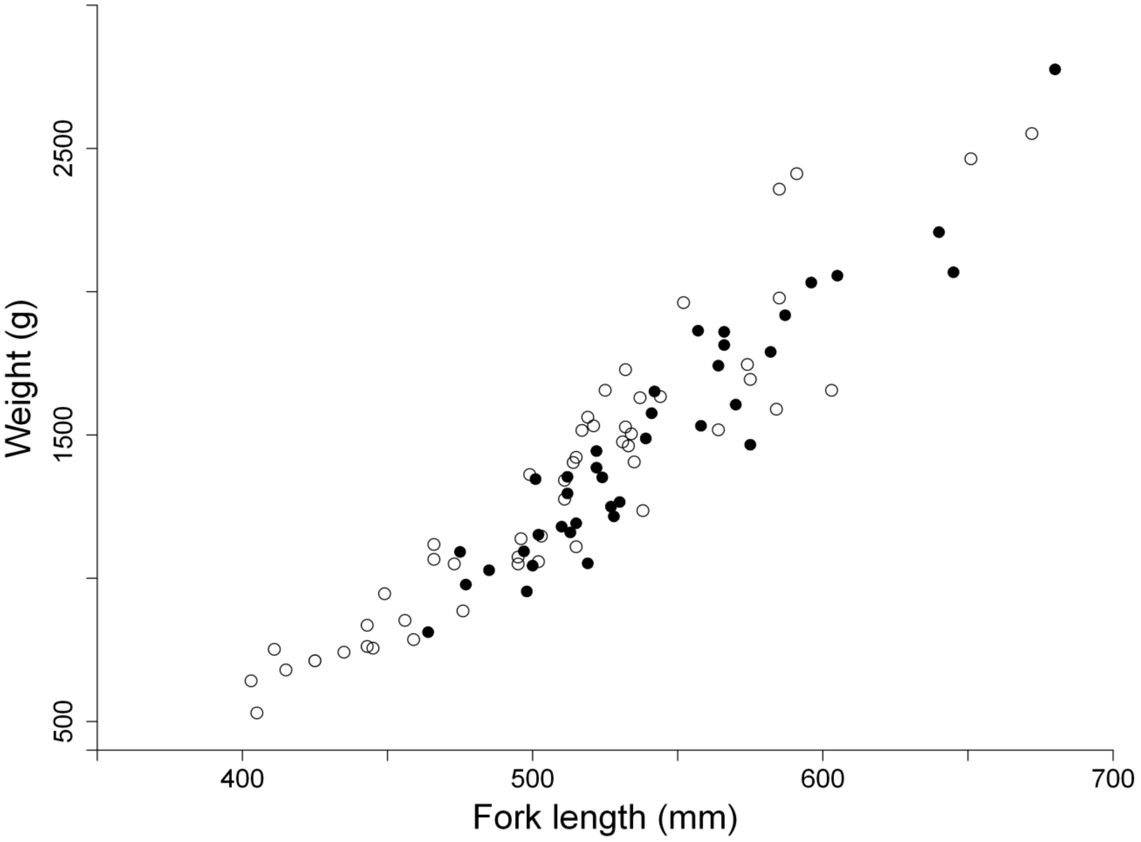

**Figure 4.3**: Weight-length relationship for reproductive (solid points) and non-reproductive (open points) Dolly Varden collected from the Ivishak River in fall of 2010 and 2011.

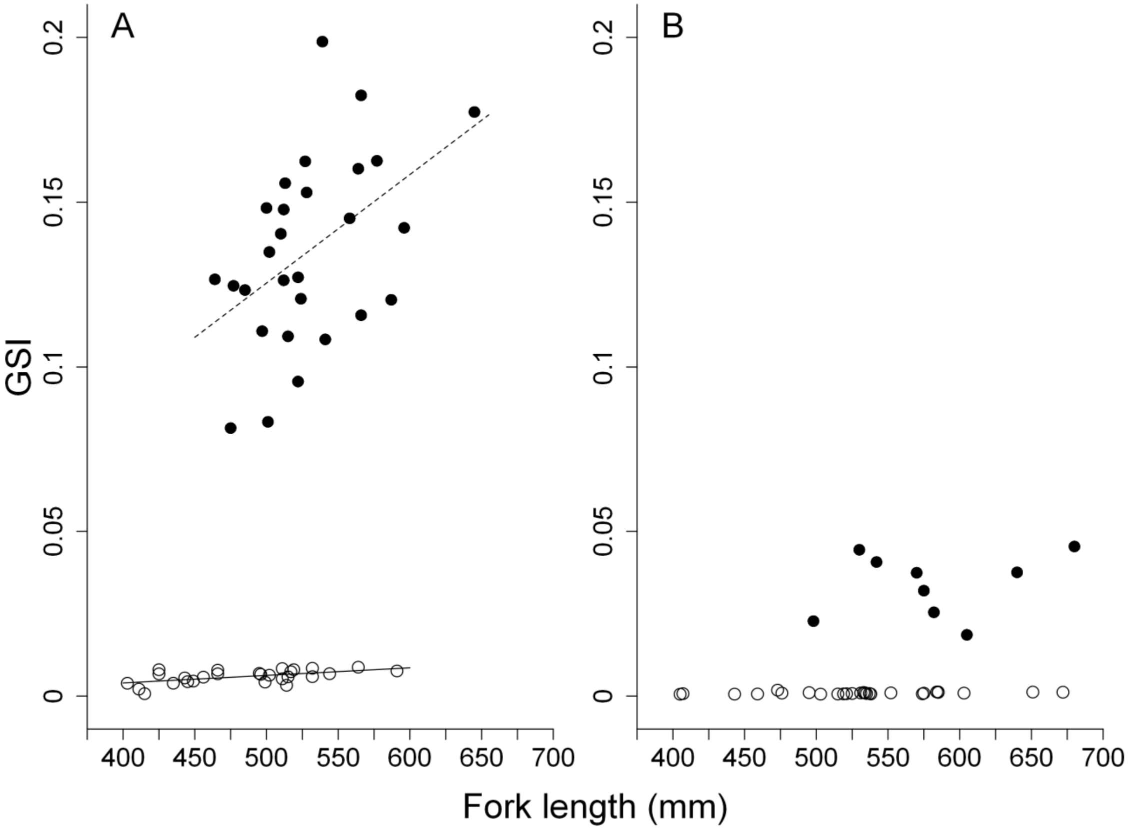

**Figure 4.4**: Gonadal somatic index of reproductive (solid points) and non-reproductive (open points) individuals plotted as a function of fork length for female (A) and male (B) Dolly Varden collected from the Ivishak River in 2010 and 2011. Trend lines are presented for significant ($P < 0.05$) correlations of length and GSI for reproductive (broken line) and non- reproductive (solid line) fish.

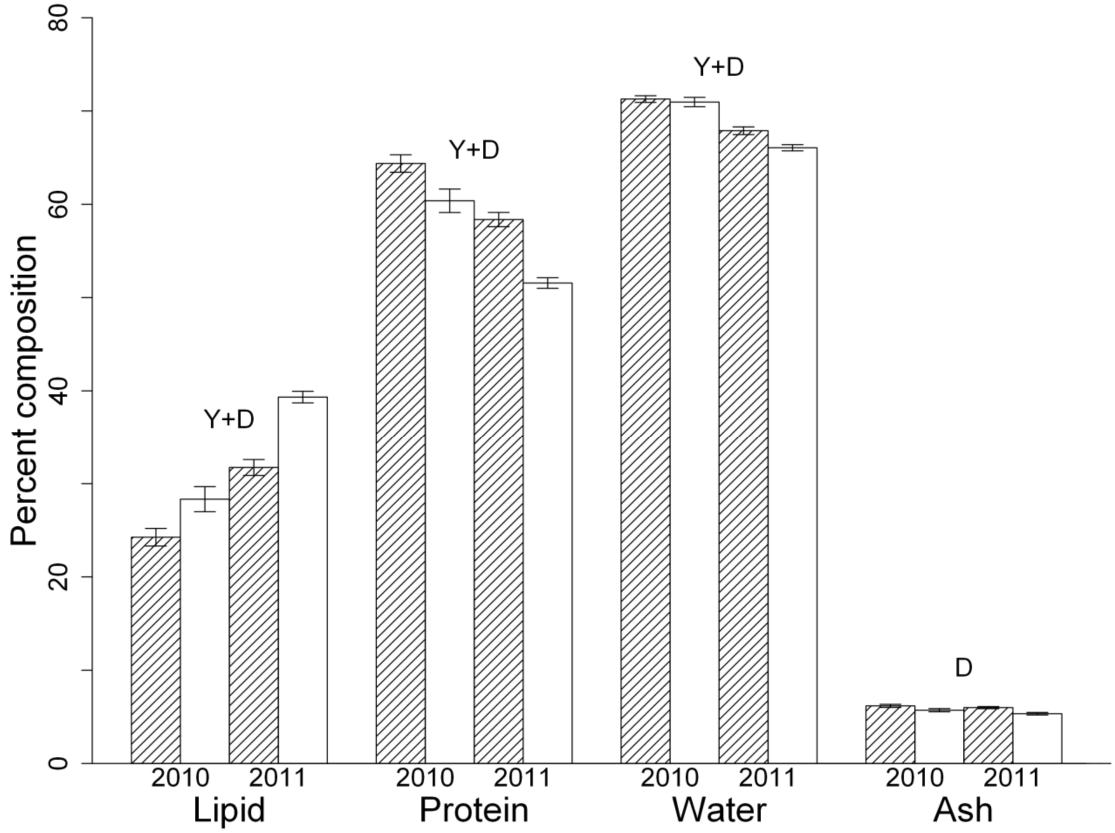

**Figure 4.5**:Percent composition (with standard error bars) of whole body estimates of proximate constituents from reproductive (striped bars) and non-reproductive (empty bars) Dolly Varden collected in 2010 and 2011 from the Ivishak River. Letters signify significant ($p < 0.013$) differences in a particular percent constituent among years (Y) and/or demographics (D).

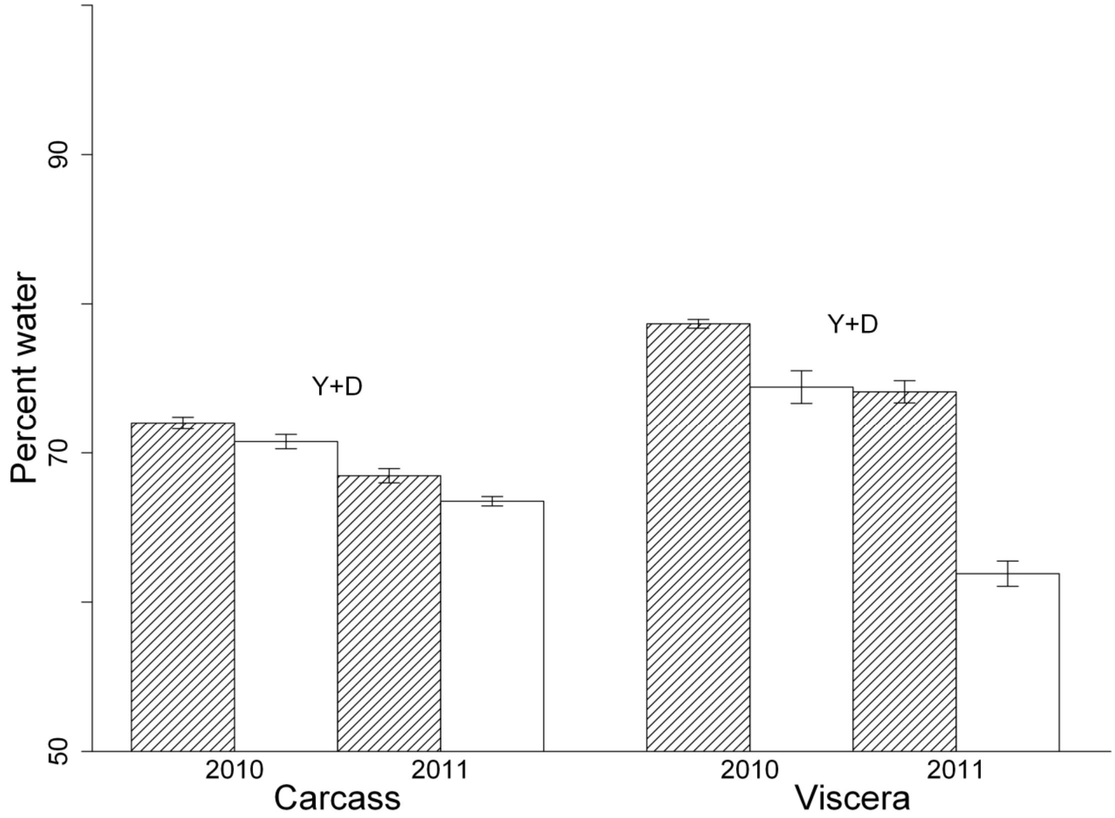

**Figure 4.6**: Carcass and viscera water content of reproductive (striped bars) and non-reproductive (empty bars) Dolly Varden expressed as a percentage of tissue wet weight with standard error bars. Letters signify significant ($p < 0.017$) differences in percent water content of a particular tissue among years (Y) and/or demographics (D).

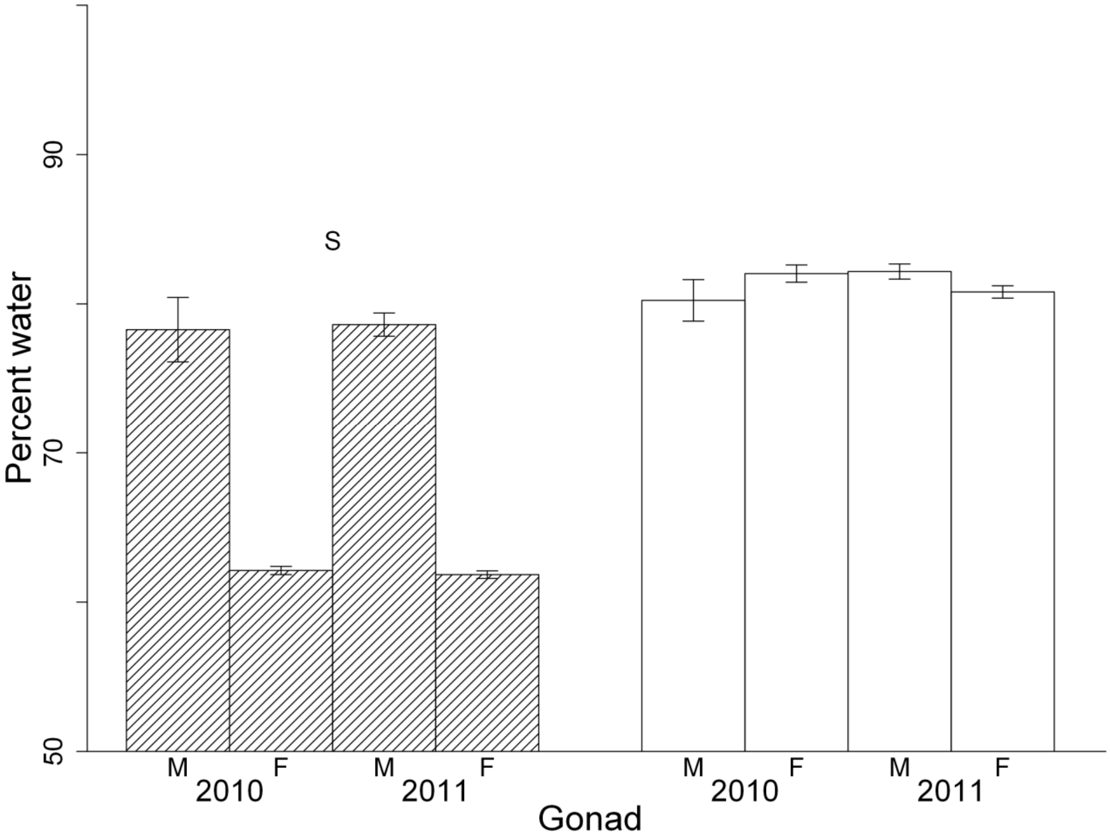

**Figure 4.7**: Gonad water content of reproductive (striped bars) and non-reproductive (empty bars) Dolly Varden expressed as a percentage of tissue wet weight, with standard error bars. Letters signify significant ($p < 0.01$) differences in percent water content among sexes (S).

## Conclusion

With this research, I have developed and applied new tools and techniques with which to measure and partition variability in Dolly Varden biological statistics among ecologically relevant sub-groupings. Scale-based aging techniques will permit the collection of age information from a greater proportion of individuals within population, which will contribute to more precise age-based biological statistics such as growth and condition. Furthermore, the successful identification of trends in Dolly Varden energy content among years and demographics (i.e. reproductive versus non-reproductive individuals) highlight the utility of proximate analysis. Future efforts examining this metric will be greatly simplified by the use of bioelectrical impedance analysis (BIA) models developed here to predict estimates of energy content from easily collected field data (Cox and Hartman 2005). Finally, retrospective growth analysis identified environmental variables correlated to Dolly Varden growth which may serve as the impetus for more in-depth studies of growth dynamics in the future.

Despite this work, however, substantial gaps remain in our current understanding of Dolly Varden ecology and life history that will hamper future research and monitoring programs (Holland-Bartels and Pierce 2011). Foremost among these is a lack of information regarding migration timing and patterns and movement rates within North Slope Dolly Varden populations, particularly that of reproductive fish. Egg size and testes weight data indicate that at least some reproductive fish enter nearshore habitats during the summer they are to spawn (Griffiths et al. 1977; Craig and Haldorson 1981). Catch per unit effort of these fish is generally small relative to non-reproductive individuals, which may in part reflect sampling bias, but could also indicate that relatively fewer reproductive fish frequent marine environments the year they are to spawn (Craig 1977; Craig and Haldorson 1981). During fall, reproductive Dolly Varden precede non-reproductive fish by up to a month at freshwater spawning and overwintering grounds, suggesting that if these fish do migrate all the way to sea, residency within the marine environment must be short lived (Glova and McCart 1974; Griffiths 1975). Particular segments of Dolly Varden populations within Northwestern Alaska may defer seaward migration entirely the year in which they are to spawn (DeCicco 1997). Following break-up, these fish ascend from overwintering habitats in lower river reaches to spawning grounds where reproduction occurs during July and August (DeCicco 1997). The presence of mature Dolly Varden within North Slope rivers during summer is largely supported by anecdotal evidence and observations (McCart 1980), and has been recently confirmed scientifically for a single fish in the Hulahula River (R. J. Brown, U. S. Fish and Wildlife Service, unpublished data). However, the significance of this life-history variant within North Slope populations is unknown, as large numbers of mature summer freshwater residents or summer spawning populations have not been confirmed scientifically. Efforts to identify such aggregations during summer are hampered by high water, turbidity, poor weather, and the logistical challenges and costs associated with sampling in remote locations (West and Wiswar 1985; Wiswar 1994). These investigations will further our understanding of life-history variation within North Slope populations and provide important information to managers charged with the protection and sustainability of all Dolly Varden populations.

Once at sea, Dolly Varden roam nearshore habitats foraging upon epibenthic prey during which time relatively little is known regarding their specific movements, habitat preferences, or foraging ecology (Craig 1984). Dolly Varden temperature preference may be of particular interest as external temperature plays a dominant role in regulating key physiological rates, including growth, within ectothermic organisms (Brett 1976; Elliot 1976; Jobling 1994). Nearshore environments may be warming as a result of global climate change which, all things being equal, has the potential to dramatically alter the growth rates of a stenothermic species such as Dolly Varden (Zhang et al. 1998; Reist et al. 2006). Assessment or prediction of the potential effects of this warming is made difficult by the general lack of data regarding the thermal spectrum of Dolly Varden. Reist et al. (2006) hypothesized that greater temperatures would initially result in higher growth rates, but if temperatures began to exceed optima, growth would decline. Potential growth effects may be mediated, however, if Dolly Varden are capable of behaviorally regulating their thermal environments (Neill 1979). During summer, nearshore habitats offer a diverse array of thermal environments to occupy (Hale 1990; Maughn 1990). Thus, by restricting habitat occupation to only those thermal environments optimal to the joint conduct of physiological processes such as growth, Dolly Varden may be capable of avoiding any deleterious growth effects (Neill 1979; Bevelhimer and Adams 1993; Neverman and Wurtsbaugh 1994).

Recent investigations using acoustic and satellite tags to collect temperature and depth data remotely may provide more accurate thermal preference and tolerance data than previous research using passive capture gears (Houghton et al. 1990; Underwood et al. 1995; Spares et al. 2012; A. Seitz, University of Alaska Fairbanks, unpublished data). However, satellite and acoustic tags are relatively large, which restricts investigations to all but the largest and oldest members of a population. Archival tags, on the other hand, are smaller and can be surgically implanted within a wider range of fish sizes. Capturing information over a range of fish sizes is warranted as temperature preference likely varies as a function of ontogeny (Jobling 1994). However, for information to be retrieved from archival tags, individuals must be recaptured and the tags removed. This will likely restrict such analyses to relatively small rivers and is complicated by the tendency of some Dolly Varden not to return to the same drainage annually (Crane et al. 2005). While difficult to collect, thermal occupancy data is essential to understanding how a warming environment will affect the growth Dolly Varden on the North Slope of Alaska.

Temperature and depth occupancy data may also offer insight into aspects of Dolly Varden foraging ecology within nearshore environments (Spares et al. 2012). During summer, Dolly Varden aggregates roam nearshore areas feeding heavily upon epibenthic prey such as mysid shrimp and amphipods (Furniss 1975; Craig and Haldorson 1981). However, it is unknown if these summer movements exhibit any directional patterns. One hypothesis suggests that individuals simply travel within prevailing water currents (Hachmeister et al. 1991). Such a strategy would minimize energy expenditure while maintaining proximity to forage as the same water currents are thought to transport the majority of prey items into and out of nearshore areas (Craig et al. 1984). This hypothesis conforms to sampling data which suggests Dolly Varden show affinity to habitats immediately adjacent (< 40 m) to shore (Craig and Haldorson 1981;

Craig 1984). However, more distant and deeper habitats, particularly those outside barrier islands, are rarely sampled (Craig 1984; Jarvela and Thorsteinson 1999). Satellite, acoustic, and archival tags offer a novel means by which to collect habitat occupancy data which may shed new light onto movement patterns, their motivations, and the ecology of Dolly Varden within nearshore areas (Spares et al. 2012).

Obtaining a more detailed understanding of Dolly Varden ecology within nearshore areas is important given the rate at which Arctic habitats are changing. (Solomon et al. 2007). Recent research suggests that the structure and productivity of nearshore food webs in the Beaufort Sea is tightly coupled to terrestrial processes through freshwater input provided by coastal rivers (Dunton et al. 2006, 2012). Terrestrial organic matter fuels heterotrophic production and while suspended in the water column, limits autotrophic production by increasing turbidity (Dunton et al. 2012). Accelerated permafrost melt resulting from warmer temperatures may increase organic matter contributions to nearshore areas (Reist et al. 2006; Solomon et al 2007). However, changes in discharge resulting from glacier loss and patterns of precipitation may partially offset these increases (Peterson et al. 2002; Symon et al. 2005). Climate warming has also been implicated as the cause of reductions in sea ice which may also limit autotrophic production by decreasing ice algae abundance and increasing turbidity through increased storm frequency and the resuspension of benthic sediments (Solomon et al. 2007; Gradinger 2009; Dunton et al. 2012). Once again, however, this decrease may be offset by longer ice-free periods which will allow more light to penetrate into the water column, possibly spurring greater production. While the net response of these alterations remains unclear, predicting the potential consequences of such change within a mobile predator such as Dolly Varden will require a deeper understanding of their ecology within nearshore habitats.

Gaps in our knowledge of Dolly Varden ecology and life history make it difficult to assess the potential consequences of anthropogenic disturbances such as climate change and hydrocarbon extraction activities (Reist et al. 2006; Holland-Bartels and Pierce 2011). In the latter instance, these gaps prevent a thorough assessment of the risks involved in the extraction of oil and gas from nearshore areas (Holland-Bartels and Pierce 2011). Nearshore studies attempting to examine non-lethal effects of habitat alterations will always be complicated by the multi-stock nature of nearshore Dolly Varden aggregates during summer (Krueger et al. 1999). Without genetic analysis, isolating a single population within the marine environment may only be possible when targeting smolts within or adjacent to river mouths (Everett et al. 1997; Fechhelm et al. 1997). While minimizing inter-population variability in biological statistics, such protocols may do little to assess the effects of oil and gas extraction as structures associated with these activities may not always coincide with smolt habitat. Furthermore, non-lethal effects of habitat manipulations will likely differ within older and larger fish as these individuals may be more tolerant of, or capable of avoiding environmental extremes (Gallaway et al. 1991; DeCicco 1992). Scale-based aging and bioelectrical impedance techniques developed in our research may permit the collection and calculation of more accurate biological statistics (Cox and Hartman 2005). However, if inter-population variability exceeds variability associated with a particular phenomenon of interest, such as alterations in temperature, the effects of this phenomenon will likely be obscured.

Future research should continue to attempt to isolate populations whenever possible. Because some non-spawning and juvenile Dolly Varden may not overwinter in natal drainages, sampling reproductive or pre-smolt fish may be the only means by which to completely isolate a population in freshwater (Everett et al. 1997; Crane et al. 2005). As previously mentioned, nearshore sampling within or adjacent to river mouths targeting out-migrating smolts may also successfully isolate a single population (Fechhelm et al. 1997). These protocols, in conjunction with aging and condition techniques developed here and the continued application of remote data collection using data-logging tags, may permit the collection and calculation of more precise biological statistics. Applied over greater temporal scales within the context of a long-term research and monitoring program, these efforts may aid in the detection of spatial or temporal change in Dolly Varden populations (Fechhelm et al. 2006; Reist et al. 2006). Such an effort would be a large undertaking considering the costs and logistics associated with operating out of remote Arctic habitats. However, these investigations are warranted given the threats imposed by climate change and hydrocarbon extraction, and our current inability to properly assess the risks and effects of such disturbances (Prowse et al. 2006; Reist et al. 2006; Holland-Bartels and Pierce 2011).

## References

Bevelhimer, M. S., and S. Adams. 1993. A bioenergetics analysis of diel vertical migration by kokanee salmon, *Oncorhynchus nerka*. Canadian Journal of Fisheries and Aquatic Sciences 50:2336-2349.

Brett, J. R. 1976. Energetic responses to temperature: a study of some thermal relations in the physiology and freshwater ecology of sockeye salmon. American Zoologist 11:99-113.

Cox, K. M., and K. J. Hartman. 2005. Nonlethal estimation of proximate composition in fish. Canadian Journal of Fisheries and Aquatic Sciences 62:269-275.

Craig, P. C. 1977. Ecological studies of anadromous and resident populations of Arctic char in the Canning river drainage and adjacent coastal waters of the Beaufort Sea, Alaska. Pages 1-116 (Chapter 1) *in* P. McCart, editor. Fisheries investigations along the North Slope and Beaufort Sea coast in Alaska with emphasis on Arctic char, Aquatic Environments Limited, Arctic Gas Biological Report Series, Volume 41, Calgary, Alberta.

Craig, P. C. 1984. Fish use of the coastal waters of the Alaskan Beaufort Sea: a review. Transactions of the American Fisheries Society 113:265-282.

Craig, P. C, W. B. Griffiths, S. R. Johnson, and D. M. Schell. 1984. Trophic dynamics in an Arctic lagoon. Pages 347- 380 *in* P. W. Barnes, D. M. Schell, and E. Reimnitz, editors. The Alaskan Beaufort Sea: ecosystems and environments. Academic Press, New York.

Craig, P. C., and L. Haldorson. 1981. Fish. Pages 384-678 *in* Beaufort Sea barrier island-lagoon ecological process studies: final report, Simpson Lagoon, part 4. Environmental assessment of the Alaskan continental shelf, final report of principal investigators vol. 8: Biological Studies. National Oceanic and Atmospheric Administration, Outer Continental Shelf Environment Assessment Program, and Bureau of Land Management, Boulder, Colorado.

Crane, P., T. Viavant, and J. Wenburg. 2005. Overwintering patterns of Dolly Varden *Salvelinus malma* in the Sagavanirktok River in the Alaskan North Slop inferred using mixed-stock analysis. U.S. Fish and Wildlife Service, Alaska Fisheries Technical Report No. 84, Anchorage, Alaska.

DeCicco, A. L. 1992. Long-distance movements of anadromous Dolly Varden between Alaska and the U.S.S.R. Arctic 45:120-123.

DeCicco, A. L. 1997. Movements of postsmolt anadromous Dolly Varden in Northwest Alaska. American Fisheries Society Symposium 19:175-183.

Dunton, K. H., S. V. Schonberg, and L. W. Cooper. 2012. Food web structure of the Alaskan nearshore shelf and estuarine lagoons of the Beaufort Sea. Estuaries and Coasts 35:416-435.

Dunton, K. H., T. Weingartner, and E. C. Carmack. 2006. The nearshore western Beaufort Sea ecosystem: circulation and importance of terrestrial carbon in arctic coastal food webs. Progress in Oceanography 71:362-378.

Elliot, J. M. 1976. The energetics of feeding, metabolism and growth of brown trout (*Salmo trutta L.*) in relation to body weight, water temperature and ration size. Journal of Animal Ecology 45:923-948.

Everett, R. J., R. L. Wilmot, and C. C. Krueger. 1997. Population genetic structure of Dolly Varden from Beaufort Sea drainages of Northern Alaska and Canada. American Fisheries Society Symposium 19:240-249.

Fechhelm, R. G., J. D. Bryan, W. B. Griffiths, and L. R. Martin. 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 54:1103-1110.

Fechhelm, R. G., G. B. Buck, and M. R. Link. 2006. Year 24 of the long-term monitoring of nearshore Beaufort Sea fishes in the Prudhoe Bay region, 2006. Report for BP Exploration (Alaska) Inc. by LGL Alaska Research Associates, Inc., Anchorage.

Furniss, R. A. 1975. Inventory and cataloging of Arctic area waters. Alaska Department of Fish and Game, Federal Aid in Fish Restoration, Project F-9-7, Annual Report of Progress, Anchorage.

Gallaway, B. J., W. J. Gazey, J. M. Colonell, A. W. Niedoroda, and C. J. Herlugson. 1991. The Endicott Development Project - preliminary assessment of impacts from the first major offshore oil development in the Alaskan Arctic. American Fisheries Society Symposium 11:42-80.

Glova, G., and P. McCart. 1974. Life history of Arctic char (*Salvelinus alpines*) in the Firth River, Yukon Territory. Pages 1-51 (Chapter 3) *in* P. J. McCart, editor. Life histories of anadromous and freshwater fish in the Western Arctic. Biological Report Series, Volume 20. Canadian Arctic Gas Study Limited/Alaskan Arctic Gas Study Company, Calgary, Alberta.

Gradinger, R. 2009. Sea-ice algae: major contributors to primary production and algal biomass in the Chukchi and Beaufort Seas during May/June 2002. Deep Sea Research II 56:1201-1212.

Griffiths, W. B., J. K. DenBeste, and P. C. Craig. 1977. Fisheries investigations in a coastal region of the Beaufort Sea (Kaktovik Lagoon, Alaska). Pages 1-205 (Chapter II) *in* P. McCart, editor. Fisheries investigations along the north slope from Prudhoe Bay, Alaska to the Mackenzie Delta, N.W.T. Biological Report Series, Volume 40. Canadian Arctic Gas Study Limited/Alaskan Arctic Gas Study Company, Calgary.

Hachmeister, L. E., D. R. Glass, and T. C. Cannon. 1991. Effects of solid-gravel causeways on the coastal central Beaufort Sea environment. American Fisheries Society Symposium 11:81-96.

Hale, D. A. 1990. A description of the physical characteristics of nearshore and lagoonal waters in the eastern Beaufort Sea. National Oceanic and Atmospheric Administration, Office of Oceanography and Marine Assessment. Report to U.S. Fish and Wildlife Service, Anchorage, Alaska.

Holland-Bartels, L., and B. Pierce, editors. 2011. An evaluation of the science needs to inform decisions on Outer Continental Shelf energy development in the Chukchi and Beaufort Seas, Alaska. U. S. Department of the Interior, U.S. Geological Survey Circular 1370, Reston, Virginia.

Houghton, J. P., C. J. Whitmus, and A. W. Maki. 1990. Habitat relationships of Beaufort Sea anadromous fish: integration of oceanographic information and fish-catch data. Pages 73-88 *in* R. M. Meyer and T. M. Johnson, editors. Fisheries oceanography-a comprehensive formulation of technical objectives for offshore application in the Arctic. United States Department of the Interior, Minerals Management Service, OCS Study MMS 88-0042, Anchorage, Alaska.

Jarvela, L. E., and L. K. Thorsteinson. 1999. The epipelagic fish community of Beaufort Sea coastal waters, Alaska. Arctic 52:80-94.

Jobling, M. J. 1994. Fish bioenergetics. Chapman and Hall, London, United Kingdom.

Krueger, C. C., R. L. Wilmot, and R. J. Everett. 1999. Stock origins of Dolly Varden collected from Beaufort Sea coastal sites of Arctic Alaska and Canada. Transactions of the American Fisheries Society 128:49-57.

Maughan, O. E. 1990. Habitat. Pages 85-96 *in* MBC Applied Environmental Sciences, editors. A synthesis of environmental information on causeways in the nearshore Beaufort Sea. United States Department of the Interior, Minerals Management Service, OCS Study MMS 89-0038, Anchorage, Alaska.

McCart, P. J. 1980. A review of the systematic and ecology of Arctic char, *Salvelinus alpinus*, in the western Arctic. Canadian Technical Report of Fisheries and Aquatic Sciences No. 935, Winnipeg, Manitoba.

Neill, W. H. 1979. Mechanisms of fish distribution in heterothermal environments. American Zoologist 19:305-315.

Neverman, D., and W. A. Wurtsbaugh. 1994. The thermoregulatory function of diel vertical migration for a juvenile fish, *Cottus extensus*. Oecologia 98:247-256.

Peterson, B. J., R. M. Holmes, J. W. McClelland, C. J. Vörösmarty, R. B. Lammers, A. I. 451 Shiklomanov, I. A. Shiklomanov, and S. Rahmstorf. 2002. Increasing river discharge to theArctic Ocean. Science 298:2171-2173.

Prowse, T. D., F. J. Wrona, J. D. Reist, J. J. Gibson, J. E. Hobbie, L. M. J. Lévesque, and W. F. Vincent. 2006. Climate change effects on hydroecology of Arctic freshwater ecosystems. Ambio 35:347-358.

Reist, J. D., F. J. Wrona, T. D. Prowse, M. Power, J. B. Dempson, R. J. Beamish, J. R. King, T. J. Carmichael, C. D. and Sawatzky. 2006. General effects of climate change on Arctic fishes and fish populations. Ambio 35:370-380.

Solomon, S., D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M.Tignor, and H.L. Miller, editors. 2007. Climate change 2007: the physical science basis. Contribution of working group I to the fourth assessment report of the intergovernmental panel on climate change. Cambridge University Press, Cambridge, United Kingdom and New York.

Spares, A. D., M. J. W. Stokesbury, R. K. O'Dor, and T. A. Dick. 2012. Temperature, salinity, and prey availability shape the marine migration of Arctic char, Salvelinus alpinus, in a macrotidal estuary. Marine Biology 159:1633-1646.

Symon, C., L. Arris, and B. Heal, editors. 2005. Arctic climate impact assessment (ACIC). Cambridge University Press, 1042p. http://www.acia.uaf.edu.

Underwood, T. J., J. A. Gordon, M. J. Millard, L. A. Thorpe, and B. M. Osborne. 1995. Characteristics of selected fish populations of Arctic Wildlife Refuge coastal waters, final report, 1988-1991. U.S. Fish and Wildlife Service, Alaska Fisheries Technical Report No. 28, Fairbanks, Alaska.

West, R. L., and D. W. Wiswar. 1985. Fisheries investigations on the Arctic National Wildlife Refuge, Alaska, 1984. Pages 729-777 *in* G. W. Garner and P. E. Reynolds, editors. Arctic National Wildlife Refuge coastal plain resource assessment, 1984 update report, baseline study of the fish, wildlife, and their habitats. U.S. Fish and Wildlife Service, Anchorage, Alaska.

Wiswar, D. W. 1994. Summer distribution of Arctic fishes in the 1002 Area of the Arctic National Wildlife Refuge, Alaska, 1991 with emphasis on selected lakes, tundra streams, and the Sadlerochit River drainage. U.S. Fish and Wildlife Service. Alaska Fisheries Technical Report No. 27, Fairbanks, Alaska.

Zhang, J. D., D. A. Rothrock, and M. Steele. 1998. Warming of the Arctic Ocean by a strengthened Atlantic inflow: model results. Geophysical Research Letters 25 1745-1748.