

Anadromy versus non-anadromy in the Canadian Arctic: variation in the lake ecology and life history of two allopatric Arctic charr (*Salvelinus alpinus*) populations in Cumberland Sound on South Baffin Island, Nunavut

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ABSTRACT

The lake ecology of Arctic charr in the Canadian Arctic is poorly defined. This research examined and compared the lake ecology and biological parameters of two differing charr populations (anadromous and landlocked) in Cumberland Sound, Nunavut. Growth differed between the populations, with anadromous charr being larger and having higher overall growth rates. Stomach contents indicated that landlocked charr feed in both fall and winter while anadromous charr did not feed within freshwater. Two discrete size at age classes were detected within the anadromous population, suggesting that significant morphological changes occur following first migration. Three discrete size at age classes were detected within the landlocked population indicative of ontogenetic shifts in diet from invertebrate feeding to piscivory. Littoral habitat was found to be important to all sizes of landlocked charr in both seasons, whereas the littoral habitat was only important for small fish in the winter within the anadromous population.

For Autumn and Finlay – may you never lose your sense of wonder,

and

for Jer, whose love for the natural world is a constant inspiration.

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Chapter 1: Literature Review

How an animal uses its environment, specifically, the variety of habitats it occupies, the types of food it consumes and the driving mechanisms behind these choices and behaviors has long been central to the study of ecology (Johnson 1980a; Huey 1991). Organisms seek optimal habitats for critical life history stages, and how well a habitat meets the needs of the organism during each stage in the life cycle will affect its overall fitness and survival. Fish, like most animals, require suitable reproductive habitats and favorable ecological conditions for their offspring. In later life stages, fish require habitats that maximize growth and maturation (Miller and Brannon 1981; Stearns 1993). Lacustrine (“lake”) systems offer food and habitats suitable for meeting some or all of the life cycle needs of many fish species. However, freshwater fishes at high-latitudes face additional challenges regarding growth, fitness and survival in lacustrine systems given that Arctic lakes are low production and are ice covered for most of the year (Power *et al.* 2008). For many Arctic freshwater fish species, lacustrine environments play a critical role in the life cycle by providing the necessary reproductive, rearing and overwintering habitats (Power *et al.* 2008). As such, the lake ecology of freshwater Arctic fishes is uniquely dynamic but remains poorly defined in some species.

This review of the literature outlines the abiotic and biotic factors which are commonly used to define and describe fish habitats within high-latitude lacustrine systems; the factors related to the life histories of Arctic Salmonids; and an overview of the general lake ecology of Arctic charr throughout their range.

Arctic Lacustrine Environments

The Arctic is a geographical region located at the northernmost part of the earth wherein Canada, the United States, Greenland, Russia, Finland, Norway, Sweden and Iceland are either partially or wholly located (Vincent *et al.* 2008). This region can be defined by extreme variation in climate and weather, exhibiting extreme seasonality and exceptionally low temperatures; the persistence of seasonal ice and snow cover (Wrona *et al.* 2005); and decreased or complete absence of sunlight in winter and long days in the summer (McBean *et al.* 2005). Arctic lakes have been referred to as the “ecological theatre of the lacustrine north where evolutionary plays continuously take place” (Klemetsen 2013). Freshwater Arctic lakes are geologically young (<10,000 years) and have only been accessible to fishes since the end of the last glaciation (Kristjánsson *et al.* 2011). Most high-latitude lacustrine environments are oligotrophic; characterized by soft waters, few nutrients, low biomass, low species diversity (Vincent *et al.* 2008) and many experience water temperatures close to 0°C for much of the year, especially when under ice cover (Power *et al.* 2008). In these environments, the variation in biological communities is dictated by the variation in physical properties (lake area, depth, temperature, lake zones, wind exposure, ice cover) and chemical properties (nutrients, oxygen, pH) (Klemetsen 2013). These environments are also indicative of highly seasonal feeding opportunities and a high degree of environmental stochasticity.

Abiotic and Biotic Factors Influencing the Lake Ecology of Fishes

The lake ecology of fishes is influenced by abiotic and biotic factors. Lakes are divided in habitat zones within which abiotic and biotic factors fluctuate, with each zone

offering different food sources, water temperatures and dissolved oxygen concentrations (D.O.), and forms of cover (Jackson *et al.* 2001). Lake zones commonly used to describe fish habitat include littoral, pelagic, profundal, and benthic, as displayed in Figure 1.0. Generally speaking, the littoral zone is a shallow, warm water area associated with shoreline and is considered productive due to the large amount of light penetration it receives, and can offer various types of refugia (Karlsson and Byström 2005). Littoral zones tend to be inhabited by small, young fish (Scott and Crossman 1984; Byström *et al.* 2004). The pelagic zone (open water) is characterized by cold water, little cover and is typically occupied by large top predators (Girdler *et al.* 2010). The profundal zone is located below the thermocline and is characterized by colder water and decreased light penetration (Girdler *et al.* 2010). The benthic zone is the lake bottom characterized by small to large sized substrates, cold water, minimal light penetration and foraging opportunities in the form of benthos, which is ideal for bottom-feeders (Girdler *et al.* 2010).

Lake zones contain various abiotic factors which are comprised of both physical and chemical factors that can influence the distribution of fish species within the lake. Physical abiotic factors include bottom substrate and ice cover, with chemical abiotic factors including pH, salinity, water temperature and D.O.; all of which can influence the development and growth of fish (Jackson *et al.* 2001; Girdler *et al.* 2010). In regards to the abovementioned abiotic parameters, different species of fish have varying levels of tolerance to concentrations for each abiotic factor within their habitats. This research focused on water temperature and D.O. given the importance of these habitat variables within the Salmonidae.

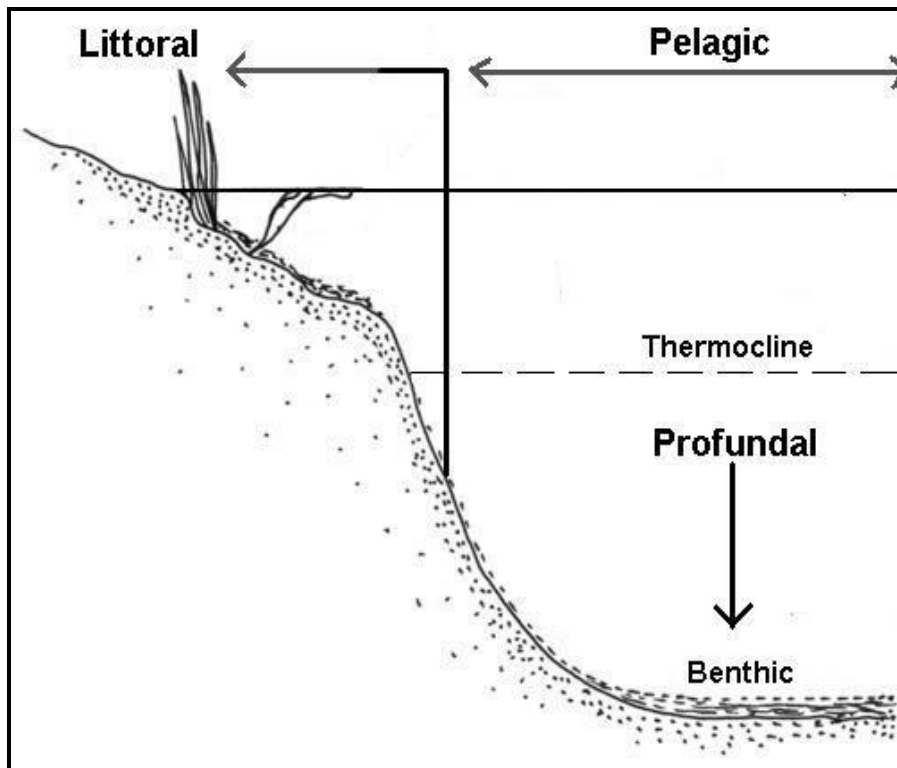


Figure 1.0 Diagram outlining lake zones commonly used to describe fish habitat: littoral, pelagic, profundal and benthic. Profundal zones depend on the presence of a thermocline.

Water temperature plays a critical role in defining fish habitat, as fish are ectothermic (depending on habitat temperatures to control body temperature), which in turn affects growth rate, food consumption and metabolic rate (Kausar and Salim 2006). Colder water is generally associated with lower metabolic rates, slower growth, and decreased food consumption rates, which is widely observed in Arctic lake freshwater fish (Power *et al.* 2008). Each fish species has a temperature range in which it achieves optimum growth rates (Kausar and Salim 2006), and to control body temperature fish utilize different areas of their habitat (Kausar and Salim 2006). Thus, temperature has been widely known to influence and often limit the distribution of species globally, including within lacustrine environments (Jackson *et al.* 2001).

In addition to having a direct influence on fish habitat use, water temperature also influences the amount of D.O. a body of water can hold. Water in contact with the atmosphere has a partial pressure of D.O. equal to that of the air, reaching a saturation point at an approximate concentration of $10\text{mg O}_2\text{l}^{-1}$ at 15°C (Kramer 1987). The capacity of water to hold oxygen decreases as temperature increases; meaning colder water is more oxygenated (Jackson *et al.* 2001). Within aquatic habitats, the availability of oxygen (coupled with water temperature) has been identified as one of the most significant abiotic factors affecting the distribution of freshwater fish (Jones *et al.* 2008; Girdler *et al.* 2010). Oxygen has been shown to influence locomotion, growth and reproduction in fish; with low D.O. levels reducing these biological parameters (Kramer 1987). Given the abovementioned considerations, D.O. has been referred to as both a limiting factor (Fry 1971) and as a resource to fish (Tilman 1982; Andrewartha and Birch 1984).

The effects of water temperature and D.O. on habitat use of fish are taxa-specific with many cyprinids and percids shown to tolerate relatively low levels of D.O. and higher water temperatures. Salmonids on the other hand require higher D.O. (Jones *et al.* 2008) and generally prefer lower water temperatures (Reiser and Bjornn 1979). In the case of Lake Trout (*Salvelinus namaycush*), water temperature and D.O. are considered primary factors influencing habitat selection due to the narrow tolerance range of this species (Sellers *et al.* 1998; Plumb and Blanchfield 2009). Water depth has a direct influence on water temperature and D.O. concentration, where temperature generally decreases with depth and colder water holds more oxygen. Thus, in many temperate lakes, species requiring colder, oxygen-rich water (such as *S. namaycush*) are restricted to deep water habitats (Jackson *et al.* 2001). Temperature and D.O. requirements have been found to be so fundamental to fish habitat selection that governments use these parameters to describe habitat requirements of fish. For example, in Ontario temperature and D.O. are explicitly used to define *S. namaycush* habitat (Plumb and Blanchfield 2009).

Biotic factors play a significant role in the use of habitats by aquatic organisms in lacustrine environments during each life cycle stage. Predation and competition are common examples of biotic factors influencing the lake ecology of fish (Gillam and Fraser 1984; Jackson *et al.* 2001; Greig and Wissinger 2010). Habitat use of small fish is thought to be highly dependent on predation risk whereas habitat use by larger individuals is likely dependent on foraging gain (Skalski and Gilliam 2002; Byström *et al.* 2003; Byström *et al.* 2004; Keyse *et al.* 2007). This may be why young and small fish are often observed occupying low-risk habitats as compared to older and larger

conspecifics (Saksgård and Hesthagen 2004). For large fish which are not vulnerable to predation, habitat use is theorized to be determined by prey availability and associated energy exertion used searching for and capturing prey (Saksgård and Hesthagen 2004). Moreover, large piscivorous fish are thought to influence the habitat selection of their prey (Damsgård and Ugedal 1997).

Life History Variation

Many high-latitude fish species exhibit life history strategies reflective of the fluctuating environment they inhabit, such as: variable juvenile mortality; long life span, late maturity and reduced fecundity (Dutil 1986). Seasonality of food resources is a limitation within high-latitude environments that fish must adapt to (Gross 1987). To compensate, many fish have adapted alternative feeding strategies such as using multiple habitats, accessing seasonal habitats, or ontogenetic niche and/or prey shifts (Power *et al.* 2008). Shifts in diet at certain points in ontogeny can have significant bearing on the life history, as most of these strategies have a direct influence the age and size at maturity of the individual (Sánchez-Hernández *et al.* 2013). At high-latitudes, a common example of an ontogenetic shift in diet (and niche) for some coastal freshwater salmonids is the seasonal migration between freshwater and marine environments for the purpose of feeding (Chapman *et al.* 2012). Within lacustrine environments, a shift in prey at certain points in ontogeny such as the adoption of piscivory (Mittelbach and Persson 1998; Sánchez-Hernández *et al.* 2013) is a common observation within high-latitude freshwater Salmonids.

The adoption of multiple life histories within a population is commonly observed in high-latitude populations of Salmonidae. Anadromy is a life history where fish hatch in freshwater, migrate to the sea to feed for short periods in the summer where they incur the majority of their growth; then return to freshwater to spawn and overwinter (McDowell 2009). Anadromy is commonly observed in many high latitude fish species (McDowell 2009; Rikardsen *et al.* 2000). This strategy is particularly useful for Arctic fishes as the marine environment offers increased foraging opportunities which directly influences growth and fitness (Power *et al.* 2008). Some Arctic freshwater systems will exhibit partially anadromous populations of Salmonid species, where some individuals will adopt an anadromous life history while others will choose to remain in fresh water for their entire life cycle as lake residents (Chapman *et al.* 2012). Many fish of high-latitude lakes do not have access to the marine environment and its advantageous feeding opportunities making them landlocked. Fish populations in landlocked lakes remain in fresh water for their entire life cycle and exhibit landlocked life histories; such as younger age at maturity, smaller size at maturity, and lower fecundity (Johnson 1980*b*). Given the marked difference in resources between high-latitude freshwater and marine environments, noticeable difference in growth and other life history characteristics are commonly observed between fishes with anadromous and lake-resident life histories (Tallman and Surette 1996).

Morphological Variation

An organism's environment will ultimately shape its life history, with biotic and abiotic factors shaping lacustrine species biodiversity (Jackson *et al.* 2001). In order to

persist in unpredictable and highly variable lacustrine systems, species must be highly adaptable. Adaptations to effectively utilize available niches will influence an organism's life history during its life cycle (Miller and Brannon 1981). Dietary-morphological relationships are an adaptation which have been widely studied in the field of animal biology with the divergence of beak morphology in Darwin's ground finches (*Geospiza* spp.) as one of the most infamous examples, where beak morphology and feeding behavior was related to feeding on specific seeds by ground finches in the Galapagos Islands (Grant 1999). These findings subsequently led to the theory of natural selection (Darwin 1859) and similar dietary-morphological relationships have since been observed in other vertebrates (Skulason and Smith 1995) including mammals (Andrews *et al.* 1979; Reed 1998; Mendoza *et al.* 2005) and fish (Snorasson *et al.* 1994; Reichman and Nosil 2003; Karachle and Stergiou 2012). Phenotypic plasticity, defined as the phenotype expressed by a given genotype in concert with variation in environmental conditions (Nussey *et al.* 2007), will influence dietary-morphological relationships within a species with plastic species often displaying characteristics indicative of their environment and prey choice. Fish are known to demonstrate a high degree of phenotypic plasticity in many life history traits relating to environmental variability (Karjalainen *et al.* 2016), with members of the family Salmonidae in the Northern Hemisphere as common examples of taxa which demonstrate a high degree of within-species dietary-morphological variability (Skulason and Smith 1995).

Within-species biodiversity is influenced by adaptation and acclimatization for the exploitation of a range of environments (Kissinger 2107). Life history variation is highly

influenced by an animal's environment (Stearns 1993), and given the vast differences in diet exhibited between fish with migratory and non-migratory life histories, it is no surprise that morphological variation within and between these populations has been observed (Reist *et al.* 1995; Loewen *et al.* 2009). Most morphological adaptations in fishes tend to occur concurrently with a change in diet at some point in ontogeny for the purpose of allowing the individual to adequately catch prey, optimize energetic return and improve growth (Werner and Gillam 1984; Kimirei *et al.* 2013). Morphological characters associated directly with feeding and prey capture are deemed the most important to the feeding ecology of fishes (Ward-Campbell and Beamish 2004). These include features commonly associated with maneuverability and facilitation of the capture of prey such as those related to body dimensions (body depth, caudal peduncle width, fin size, etc.) (Ward-Campbell and Beamish 2004; Kimirei *et al.* 2013) and mouth dimensions (Keeley and Grant 2001). Mouth dimension, in particular gape size, is the main feature associated with prey size (Keeley and Grant 2001; Ward-Campbell and Beamish 2004), larger gape allows fish to eat larger prey. Fish that are able to adapt body morphology to best exploit their environment attain higher fitness resulting in better survival.

Biology and Habitat Use of Arctic Charr

In the Canadian Arctic archipelago there are approximately eight species of freshwater and anadromous fish, half of which are from the family Salmonidae (Power *et al.* 2008). Of all the Salmonidae, the species *Salvelinus*, specifically Arctic charr (*Salvelinus alpinus*, herein referred to as "charr") has demonstrated its ability to thrive in

extreme conditions through evolving in cold, nutrient-poor, highly variable, periglacial environments which make up its circumpolar range (Reist *et al.* 2013). Charr have the most northerly distribution of any freshwater fish with a Holarctic, circumpolar range (Scott and Crossman 1974; Johnson 1980*b*; Magnan *et al.* 2002; Kahilainen and Lehtonen 2002; Klemetsen *et al.* 2003) encompassing many Asian, North American and European countries (Magnan *et al.* 2002).

Charr are well adapted to and tolerant of harsh northern climates; likely due to their ecological plasticity which has allowed them to persist in a wide array of Arctic lacustrine habitats (Beddow *et al.* 1998). This plasticity has allowed charr to exhibit many different life history traits across its range and the evolution of localized adaptations that can be population specific (Johnson 1980*b*). As such, charr have been suggested to be the most variable vertebrate on earth, after man (Klemetsen 2013). As a known colonizing species the charr has evolved impressive sympatric and allopatric intraspecific biodiversity to exploit vacant niches in young Arctic lakes (Kristjánsson *et al.* 2011) where they face little interspecific competition as they are often the only fish species present (Johnson 1980*b*; Klemetsen *et al.* 2003; Kahilainen and Lehtonen 2002). In these circumstances, interspecific effects on the charr's lake ecology become unimportant and the driving factors become intraspecific interactions, biotic and abiotic factors in the environment.

Charr have been observed to occupy a wide range of habitats throughout their life cycle including rivers, lakes, estuaries and marine environments (Johnson 1980*b*; Richardsen *et al.* 2001). Of these environments, freshwater lakes play a critical role in the life cycle of charr; with landlocked forms utilizing lakes exclusively for feeding,

reproduction and overall survival and migratory forms utilizing lakes on a seasonal basis for the purposes of overwintering and reproduction (Johnson 1980*b*). There is significant information available on the mechanisms influencing the distribution of salmonids in different fluvial habitats, but this is not the case for lacustrine habitats (O'Connell and Dempson 1996). Many populations of charr depend on freshwater lacustrine habitats for spawning and overwintering and lakes play an important role in their life cycle (Johnson 1980*b*). Charr have been observed to inhabit all sizes of ponds and lakes; some so small that there is very little water under the winter ice (Klemetsen *et al.* 2003) and some extremely large such as Nettiling Lake on Baffin Island (one of Canada's largest freshwater lakes) (Oliver 1964; Kristofferson *et al.* 1991). In deep large lakes charr have been discovered at depths up to 280m (Klemetsen *et al.* 2003), have been shown to continue to feed and survive at very low water temperatures, and unlike other salmonids, have been found to tolerate low D.O. with no visible effect on growth rates (Johnson 1980*b*). How different forms of charr use lake environments has been studied extensively in some regions (Johnson 1980*b*; Magnan *et al.* 2002; Reist *et al.* 2013), but is poorly defined in the Canadian Arctic.

Life History of Arctic Charr

Although classified as freshwater, charr are anadromous throughout much of their northern range, with anadromy becoming more prevalent in populations north of 60°N latitude (Johnson 1980*b*; Beddow *et al.* 1998). Many populations of charr have access to marine habitats during the open water season and the marine environment offers increased foraging opportunities, which in turn can increase growth and fitness

(Gross *et al.* 1988; Rikardsen *et al.* 2000). Anadromy is thought to occur when the benefits of migration outweigh the costs (Jonsson and Jonsson 1993) and is most prevalent in the northern part of the charr's range (Rikardsen *et al.* 2000). During ice-cover, anadromous charr inhabit freshwater oligotrophic lakes and prior to or upon ice break-up in the spring, anadromous individuals will exit the lake migrating into the marine environment to feed intensively, returning to the lake after 35 to 45 days, as observed in Nauyuk Lake, Nunavut (Klemetsen *et al.* 2003). Following this period of intensive marine feeding anadromous charr will return to lacustrine environments which do not freeze to the bottom to overwinter and/or spawn (every 2-3 years) (Johnson 1980*b*; Beddow *et al.* 1998; Richardsen *et al.* 2001). The lack of annual spawning events is due to the high seasonality of food resources, low water temperatures and short growth season within high-latitude environments (Dutil 1986).

Anadromous migrations by charr are complex compared to fish like salmon, as both sexually mature and immature fish perform seasonal migrations and return to freshwater every year (Klemetsen *et al.* 2003). Lake morphometry has been suggested to influence the degree of anadromy of charr, where Kristoffersen *et al.* (1994) found that anadromous charr were prevalent in shallow lakes and non-anadromous charr commonly occurred in deeper lakes containing large profundal zones. However, numerous lakes throughout the range have been found to contain partially anadromous populations, with both anadromous and non-anadromous (commonly referred to as "lake resident") morphotypes present (Loewen *et al.* 2009). Lake residents have access to the marine environment but choose to abstain from migration and remain in fresh water for their entire life cycle (Johnson 1980*b*). Conversely, many populations of charr

do not have access to the marine environment and remain landlocked. These landlocked waterbodies in the Arctic contain populations that have become isolated due to the rise of land relative to sea level following glaciations (Johnson 1980*b*). Such lakes are found throughout the range of charr, from Atlantic Canada (O'Connell and Dempson 1996) to Iceland (Jónasson *et al.* 1998), to Norway (Jensen *et al.* 1997). Thus, based on life history types, charr can be categorized into three main forms: anadromous (making seasonal migrations between lacustrine and marine environments), resident (having access to the marine environment but choosing to remain in lacustrine environments) and landlocked (have no access to the marine environment). With this being said, this thesis will focus on anadromous and landlocked populations of charr.

Morphology of Arctic Charr

Interactive segregation and resource partitioning has been observed between adults within populations of charr, as the charr's phenotypic plasticity and ability to fill vacant niches allows for resource polymorphism through the expression of alternative phenotypes, differing in size at maturation and resource specialization (Johnson 1980*b*; Riget *et al.* 1986; Jónasson *et al.* 1998; Klemetsen *et al.* 2003; Amundsen *et al.* 2008; Loewen *et al.* 2009). In these populations, resource segregation by body size is widespread, with the smaller form developing as niche specialists and rarely found co-occurring with the larger form (Riget *et al.* 1986; Klemetsen *et al.* 2003; Amundsen *et al.* 2008). Partitioning of resources and habitats between small and large-sized charr may be more pronounced in this region due to the fact that small charr need only be

concerned with competing for resources with and avoiding predation by large charr, as other apex predators and strong competitors are absent. This is in contrast to sympatric populations of charr and Ferox Trout (*Salmo trutta*) in various European lakes where *S. Trutta* are known to feed on charr (Schindler 1957).

Growth of Arctic Charr

Growth rates of charr differ by life history. Examination of length at age data (Johnson 1980*b*; Jonsson and Jonsson 1993; Kristoffersen *et al.* 1994) and direct growth rate comparisons (Rikardsen *et al.* 2000) have shown that anadromous charr grow faster than charr which remain in freshwater throughout their entire life cycle (Reist *et al.* 2013). Within lacustrine systems, piscivory and cannibalism have been shown to increase growth rates in charr (Kerr 1979); and some non-migratory charr forms opt to consume lower quality prey (e.g. benthic invertebrates) and prioritize maturation over growth, remaining small-bodied (dwarfed) (Johnson 1980*b*). Although many factors may affect fish growth, water temperature, fish size, and energy intake (ration size, prey availability) are generally considered the most important variables (Brett *et al.* 1969). In low-productivity Arctic lakes, prey resources can be limited and specialization in a single resource and habitat (niche specialization) is common (Skoglund *et al.* 2015) and it's within these adaptations charr achieve growth and optimize fitness (Jonsson and Jonsson 2001). Additionally, as mentioned previously anadromy is common among Arctic freshwater fish, whereby the individuals exploit the resource-rich marine environment (Johnson 1980*b*; Miller and Brannon 1981).

Niche utilization outside of lacustrine systems to optimize growth is common for charr at high-latitudes (e.g. seasonal migration to the marine environment for short periods of intense feeding) (Johnson 1980*b*). Thus, different feeding strategies of charr may account for variation in growth rates between life histories.

Niche Specialization of Arctic Charr

Niche specialization is believed to occur when organisms improve their ability to exploit their habitat through phenotypic adaptation via natural selection (Guénard *et al.* 2009). Niche specialization may evolve as a direct result from intraspecific competition (Loewen *et al.* 2009) or though the presence of ecological barriers (Jónasson *et al.* 1998). In some landlocked charr populations, multiple morphotypes (as many as four in one Icelandic lake) have been observed in sympatry, ecologically segregated, and having evolved physical characteristics specific to their differing prey consumption (e.g., benthivorous, planktivorous and piscivorous) (Jónasson *et al.* 1998). Few studies within Canadian systems have documented niche specialization in charr, particularly in open-lake systems. In the Canadian high Arctic, Reist *et al.* (1995) identified two morphs (planktivorous and piscivorous) in Lake Hazen on Ellesmere Island and Loewen *et al.* (2008) found morphological variation suggesting lake residency between small-maturing and anadromous charr in three open-lake systems within Cumberland Sound.

Lacustrine Habitat Use – Anadromous Arctic Charr

Following the return from marine to lacustrine environments, spawning of anadromous charr occurs between September and October (Johnson 1980*b*; Johnson

1989) in waters ranging from 0.5m to 6m in depth (Dempson and Green 1985; Johnson 1989). Spawning typically takes place over cobble and gravel substrates (Scott and Crossman 1973), with post-spawning fish remaining in the lake until the following spring (Johnson 1989; Richardsen *et al.* 2001). The eggs of anadromous charr hatch in the spring (late March-April) and the fry will remain in the gravel prior to emerging several weeks later upon ice break-up (Scott and Crossman 1973; Johnson 1980*b*; Johnson 1989). The young-of-the-year (YOY) are thought to remain on the spawning grounds following emergence and then relocate to the littoral zone later in the summer (Johnson 1980*b*; Richardsen *et al.* 2001), seeking refuge among rocks (McPhail and Lindsay 1970). Juvenile charr have been known to migrate into deeper habitats to overwinter (Johnson 1980*b*; Richardsen *et al.* 2001).

Lacustrine Habitat Use – Landlocked Arctic Charr

Landlocked populations of charr usually contain multiple morphotypes in sympatry; often with a small-bodied morph (commonly referred to as a “dwarf”) and another morph being large-bodied in comparison (commonly referred to as “normal” charr). Normal landlocked charr have been observed using all habitats of lacustrine environments at various depths; however, they predominately are found in the pelagic zone feeding on zooplankton during the open water season, shifting to benthic/littoral areas in the fall when food becomes less abundant (Richardsen *et al.* 2001; Klemetsen *et al.* 2003; Amundsen and Knudsen 2009). Multiple studies have observed normal charr to favour boulder, rubble and cobble substrates. In contrast, Dick *et al.* (2009) found that large piscivorous landlocked charr of a small lake in Arctic Canada were

found most often in the deepest water over soft substrates, with small landlocked charr preferring more complex substrates such as boulder, pebbles and gravel to feed on invertebrates and fish. In contrast to normal charr, adult dwarf charr generally inhabit shallow littoral waters at depths of 0-5m. They move into the pelagic habitat during late summer and fall (Klemetsen and Grotnes 1980; Hindar and Jonsson 1982; Bjoru and Sandlund 1995). Dwarf charr spawn at greater depths than large charr (30m) and European populations are believed to spawn in February, much later than the large form (Klemetsen and Grotnes 1980; Hindar and Jonsson 1982; Klemetsen *et al.* 1997).

Diet, Cannibalism and Intraspecific Resource Partitioning

Charr are opportunistic, generalist feeders who are renowned for exploiting a range of aquatic environments throughout their circumpolar range. Diets of charr will differ within and between populations, as niche specialization and alternative feeding strategies has been observed within lacustrine systems. Charr have been observed to feed on algae, plankton, insects and fish (Johnson 1980*b*; Kahilainen and Lehtonen 2002; Klemetsen *et al.* 2003; Richardsen *et al.* 2001). Charr have the ability to adjust their diets to seasonal food availability (Johnson 1980*b*; Klemetsen *et al.* 2003; Svenning *et al.* 2007) and are known to take advantage of transient opportunities for rapid growth (Hammar 2000). Charr that migrate will move from freshwater to saltwater environments during the summer months (Moore 1975*b*). It is in the saltwater environment where charr predominately feed and grow (Moore 1975*b*). In marine environments, charr are opportunistic and have been observed to shift preferred prey

type depending on availability; such as shifting from a primarily zooplankton-based diet to one rich in forage fish (Imrie 2012).

In low-productivity lacustrine environments, piscivory and cannibalism have become important feeding strategies for non-migratory charr to attain and optimize growth. Piscivorous charr are often found in lakes with a low degree of interspecific competition from other piscivorous species and suitable prey species (Jonsson and Jonsson 2001). Piscivory has been found to be an important growth optimization strategy for charr in lacustrine systems (Kerr 1979). Charr have been observed to be cannibalistic within many systems of their Arctic and subarctic home range (Finstad *et al.* 2001; Byström *et al.* 2004; Svenning *et al.* 2007; Klemetsen *et al.* 2003).

Cannibalism is considered an important strategy for survival of landlocked charr in the High Arctic (Hammar 2000); being suggested to have a profound impact on the longevity and reproductive output of larger fish by providing a nutritional benefit in highly impoverished environments with high seasonality in invertebrate and prey availability (Hammar 2000). The seasonality of prey and slow juvenile growth in conjunction with fitness components which favour large body size has been a suggested mechanism for inducing cannibalism (Hammar 2000). Thus, cannibalism will be favoured in species-poor habitats with low food availability for much of the year (Griffiths 1994; Gulseth and Nilssen 2001); with the prevalence of cannibalism increasing with latitude (Griffiths 1994).

Segregation within and between populations is thought to occur as the impact of competition can be reduced by partitioning resources through habitat, diet and temporal segregation (Schoener 1974; Arcifa *et al.* 1991; Alanärä *et al.* 2001). In High Arctic

lakes where charr are cannibalistic, the risk of predation on small charr by larger conspecifics may lead to intraspecific resource partitioning. Small charr may be important food source for larger charr, particularly in landlocked lakes and during ice-covered periods (Svenning *et al.* 2007). Intraspecific resource partitioning has been observed in lacustrine habitat studies of charr in Canadian Arctic and European subarctic lakes, where small charr predominantly inhabited the littoral area (Byström *et al.* 2004; Dick *et al.* 2008) which tends to offer greater refuge from predators (Byström *et al.* 2004; Karlsson and Byström 2005). As previously discussed, large adult charr tend to utilize all habitats, but concentrate the majority of their effort in the pelagic zone which is commonly considered high-risk habitat for smaller individuals at risk of predation.

Arctic Charr in Cumberland Sound, Nunavut

Cumberland Sound is located on south Baffin Island, Nunavut, Canada (Figure 1.1). It is approximately 250km long and 80km wide and is home to numerous freshwater lake systems that contain anadromous and landlocked populations of charr (Martin and Tallman 2013). Anadromous charr use open-water lake systems for the purposes of spawning and overwintering - migrating into Cumberland Sound following ice break up to feed in the marine environment for up to 45 days and spawning thereafter in freshwater (Moore 1975). Landlocked charr on the other hand remain in their respective lakes year round - a direct cause of lack of sufficient migratory pathways from the lake into the marine environment of Cumberland Sound.

Local traditional knowledge states that differences between anadromous and landlocked charr in Cumberland Sound are distinct. Anadromous charr grow larger in size than their landlocked counterparts, making them more desirable for both commercial and subsistence purposes (Pangnirtung Hunters and Trappers Association, personal communication). As well, the two forms are easily distinguishable by sight, with the landlocked form displaying distinct dark colouring; namely orange colouring on the underside, specifically the belly (Pangnirtung Hunters and Trappers Association, personal communication). Landlocked populations of charr in Cumberland Sound are not readily harvested or consumed by the local population, suffering little to no harvest pressure.

Anadromous and partially anadromous populations of charr in Cumberland Sound have been studied in both past and recent years (Moore and Moore 1974; Moore 1975a and b; Loewen 2008, Imrie 2012). However, no studies have examined landlocked populations and none have examined the lake ecology of either form. With this being said, the lake ecology of both anadromous and landlocked charr in Cumberland Sound remains undefined and poorly understood and is the focus of this thesis.

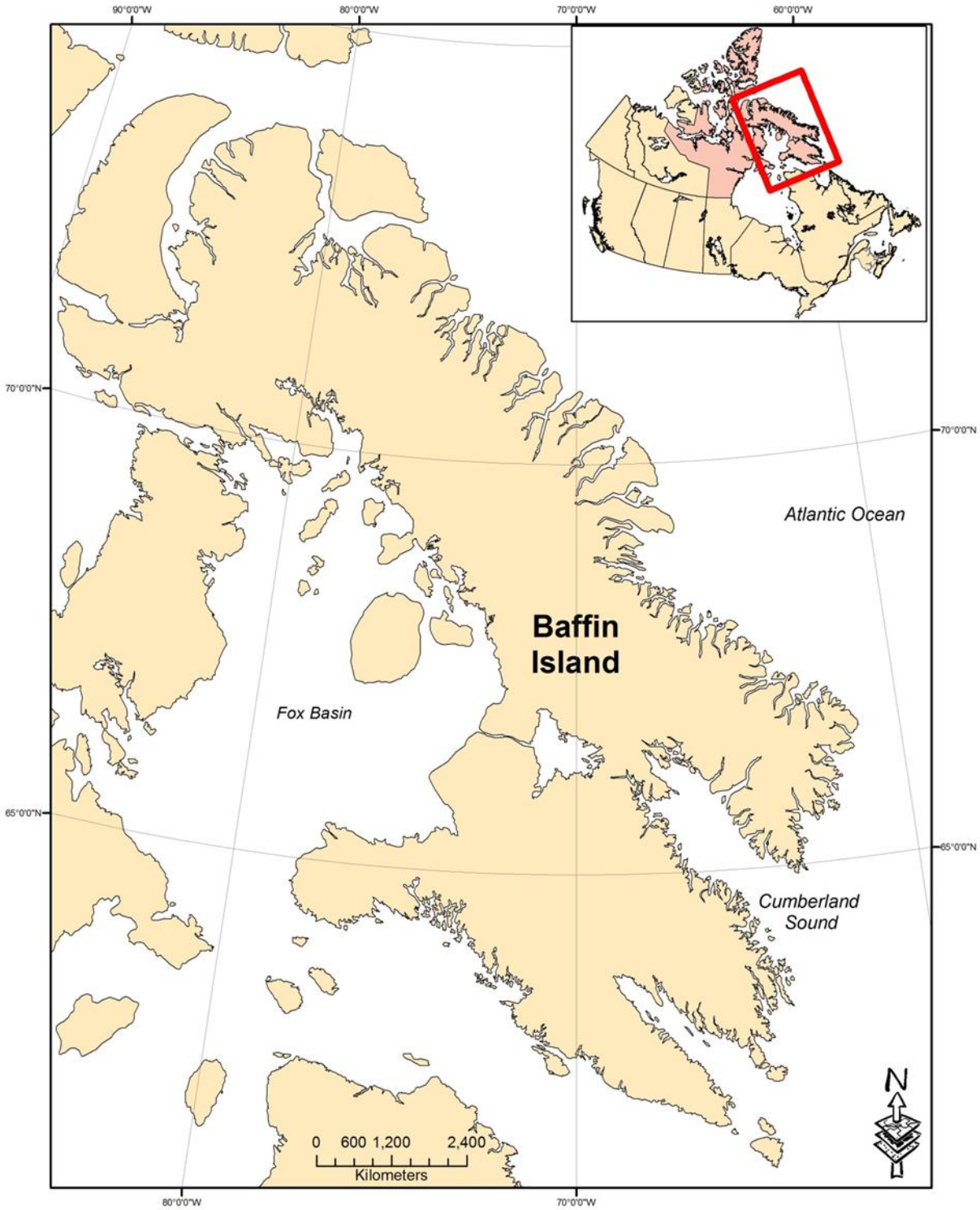


Figure 1.1. Map of southern Baffin Island showing Cumberland Sound, Nunavut, Canada.

Summary

This review of the literature has demonstrated that charr are an adaptable, generalist species that can thrive in a wide range of habitats. Each lacustrine environment throughout the charr's range offers unique and somewhat limiting habitats, with each population facing its own individual challenges. The ability of charr to adapt to their environment such as their high tolerance to cold water temperatures, their ability to opportunistically use all available habitats from marine to lacustrine environments and their ability to fill vacant niches demonstrates that charr are well-suited to life in the Arctic. Thus, my research focused on a comparative examination of the ecology of two differing populations of Arctic charr within different lacustrine systems in the Canadian Arctic. The term "lake ecology" will be used throughout this thesis to describe the ecology of the charr populations within their respective lake systems.

Objectives and Hypotheses

The purpose of this research was to define and compare the lake ecology of two populations of Arctic charr inhabiting different lacustrine systems in Cumberland Sound on South Baffin Island, Nunavut. The charr populations I examined inhabit different lake systems and display different life histories, with one population being anadromous inhabiting an open water system and the other being landlocked, inhabiting a closed water system. To accomplish this I examined seasonal lacustrine habitat use, body morphology, length-age indices, length and age at maturity, diet, condition and growth of charr from each population. The various lacustrine habitat parameters I used to

describe lake habitats included lake zone, and physical and chemical parameters of the water column including depth, water temperature and D.O.

I hypothesized that the lake ecology of the two charr populations would differ from one another given their respective life histories. Accordingly, I expected to observe differences in habitat use, diet, growth, condition and body morphology between the two populations of charr and that these differences would be representative of each population's respective life history.

To achieve my objectives, I sampled charr from littoral, pelagic and benthic habitats within each lake; I profiled the water column and collected bottom substrate samples at each set location during March and September for two consecutive years. I sampled charr for biological, morphological and catch characteristics in both lakes.

Chapter 2: The comparative lake ecology of two allopatric Arctic charr populations with differing life histories in Cumberland Sound, Nunavut.

Introduction

Lacustrine biodiversity is shaped by biotic and abiotic factors. High-latitude lakes are species-poor, oligotrophic environments which can be unpredictable and highly variable; presenting a unique challenge to the species that inhabit them (Power *et al.* 2008). As such, in order to persist in Arctic lacustrine systems species must be highly adaptable; possessing the necessary physiological adaptability to persist in cold, low-production freshwater systems which are ice-covered for most of the year (Power *et al.* 2008). Given the extreme seasonality of feeding opportunities in high-latitude lakes, the ability to optimize available habitats and feeding opportunities - be it through occupying vacant niches or making seasonal migrations to alternative habitats - are important life history characteristics of Arctic fish species.

Adaptation and acclimatization are important factors in shaping within-species biodiversity (Kissinger 2017), particularly in Arctic fishes. A prime example is with the evolution of alternative life history strategies of diadromous fishes such as those observed within the Salmonidae. It is not uncommon to have one population exhibit multiple life history forms, while an allopatric population within the same demographic exhibit different life histories (e.g., differences between stream and lake populations and landlocked and migratory populations, etc.) (Jonsson and Jonsson 2001). Life history strategies of salmonids can be migratory (anadromy) or non-migratory (e.g., freshwater residency and landlocked). Some Salmonidae populations have been observed to have

both anadromous and freshwater resident life histories living in sympatry which are referred to as “partially anadromous” populations (Chapman *et al.* 2012).

Given the short seasonality of food availability in freshwater Arctic systems, migration has become an essential part of the life history of some Arctic fishes. The marine environment offers rich feeding opportunities which surpass those in high-latitude freshwater lakes, which is thought to be the driving force behind the anadromous life history in coastal freshwater fishes (Chapman *et al.* 2012). Nearly all salmonids with access to marine environments possess life histories that use marine or brackish-water ecosystems at some point within the life cycle (Kissinger 2017). Thus, anadromy has evolved as an important life history characteristic for some Arctic Salmonids, specifically charrs (*Salvelinus spp.*) and whitefishes (*Coregoninae spp.*) (Spares *et al.* 2012). These forays to the sea can have significant benefits for species inhabiting low-productivity freshwater systems as it enables the optimization of growth and fecundity (Power *et al.* 2008; Reist *et al.* 2013).

Of the Salmonidae, charr are the northernmost species and their high degree of plasticity has led to the suggestion that they are “the most variable vertebrate on earth, after man” (Klemetsen 2013). Charr display ecological, phenotypic and life history diversity throughout its circumpolar range (Klemetsen 2010). Charr have been observed to differ in overall body size and morphology; size and age at maturity; diet and colouration when living both in sympatry and allopatry (Johnson 1980*b*). Charr utilize a wide array of northern freshwater environments (lakes, streams and rivers) as well as marine environments and have been documented to display niche specialization and polymorphism in many systems throughout their range (Johnson 1980*b*; Jonsson

and Jonsson 2001; Kelmetsen *et al.* 2003; Power *et al.* 2008). Polymorphism and speciation within charr is commonly referred to within the literature as “the charr problem” (Behnke 1972; Jonsson and Jonsson 2001; Kelmetsen *et al.* 2003; Klemetsen 2010). Multiple life history types of charr living in sympatry and allopatry have been documented including anadromous, partially-anadromous and landlocked populations (Johnson 1980*b*; Jonsson and Jonsson 2001; Power *et al.* 2008). Due to this variability in life histories between populations, charr have been exposed to a greater range of natural selection forces (e.g. temperature and nutrient gradients) compared to other northern fish species (Reist *et al.* 2013).

Given the high degree of variability documented between charr populations along environmental gradients in concert with their generalist and adaptable opportunist nature, charr both an intriguing and challenging species to study. Within lakes charr have been found to utilize all habitat types (e.g., pelagic, littoral, profundal zones) (Reist *et al.* 2013). Niche-specific polymorphism has been widely observed within this species, where phenotypically similar morphotypes are often found to occupy similar niches in different lakes (Kristjánsson *et al.* 2011). Charr are opportunistic feeders that demonstrate an ability to adapt to and exploit different environments for feeding through migration, niche specialization and even cannibalism (Power *et al.* 2008). However, the lake ecology of charr is difficult to generalize due to the high variability between populations, life histories and environments. Some charr populations have been extensively studied (e.g., Norway, Iceland) while some populations have not (e.g. the Canadian Arctic). Most charr research has been focused on European non-migratory

charr populations, with little research focused on charr populations in the Canadian Arctic.

The Canadian Arctic contains an abundant amount of freshwater lake systems, many of which contain populations of charr. Coastal lake systems are either open (those that enable seaward migration of fishes) or closed (those offering no migratory pathways, rendering fish populations landlocked), enabling life history variation in charr populations throughout this part of their range. In the Territory of Nunavut, there are many open and closed lake systems in which populations of charr persist with anadromous, lake resident and landlocked life histories (Johnson 1980*b*). Many of these populations of charr are exploited for both subsistence and commercial purposes by local Inuit, with anadromous fish being the preferred choice for human consumption due primarily to their large size, colouring of the meat and lower instance of parasitism (Pangnirtung Hunters and Trappers Association, personal communication). This has led to anadromous charr populations in Nunavut facing significantly higher exploitation rates than landlocked populations in subsistence and commercial charr fisheries (Zoya Martin, Fisheries and Oceans Canada, personal communication).

On Baffin Island in the Territory of Nunavut, charr is the sole salmonid species and top predator present in lacustrine systems (Power *et al.* 2008). Given the lack of interspecific competition and highly variable environment in this northern part of their range, a high degree of variability in size and appearance has been observed by local (Nunavut Inuit) fishers between charr with differing life histories – specifically between anadromous and landlocked populations. A high degree of variability in size has also been documented in the literature between some lake-dwelling charr populations on

Baffin Island ranging from large lake resident fish in Nettiling Lake (Kristofferson *et al.* 1991) to small mature (“dwarf”) lake resident charr in Cumberland Sound (Loewen 2008). Loewen (2008) found that small mature (resident) charr differed morphologically from their anadromous cohorts in partially anadromous populations on Baffin Island. Many populations of non-anadromous charr exhibit morphological characteristics indicative of lacustrine habitat specialization (ecophenotypes) (Reist *et al.* 1995; Jónasson *et al.* 1998; Jonsson and Jonsson 2001; Power *et al.* 2008). Lacustrine habitat specialization has yet to be documented within anadromous charr populations that utilize lake habitats on a seasonal basis (Johnson 1980*b*; Reist *et al.* 1995; Rikardsen *et al.* 2000; Loewen *et al.* 2008); and these findings suggest that non-anadromous charr may use lake habitats differently than anadromous charr.

In this chapter I examine and compare the lake ecology of two populations of charr in the Cumberland Sound area of south Baffin Island, Nunavut. These populations inhabit different lacustrine systems (open versus closed lake systems) and have differing life histories (anadromous versus landlocked). To accomplish this I did the following: 1) described and compared the biological characteristics of each population; 2) described and compared the lacustrine habitat use of both populations during seasons critical to spawning (fall) and winter survival (winter); 3) described and compared the diets of both populations; 4) attempted to identify linkages between habitat variables and biological characteristics of each population; and 5) generally described the seasonal limnological properties of each lake. I expected to observe differences in overall length at age and length and age at maturity between the

populations; differences in the seasonal use of lake habitats use between the populations; and differences in diet (lacustrine feeding) between the populations.

Materials and Methods

Study Sites

My research took place on two different lake systems in south Baffin Island, Nunavut: Iqalugaarjuit and Qinniqtuq. Iqalugaarjuit Lake (herein referred to as “PG027” which represents its commercial waterbody code) is a small open lake system located atop Iqalugaarjuit Fjord in Cumberland Sound ($65^{\circ}44'27''\text{N}$, $64^{\circ}47'5''\text{W}$, Figure 1.2). This lake is approximately 77 ha in size and currently holds a small commercial quota for the harvest of anadromous charr. PG027 has one known life history form of charr - anadromous. Historically, this population of charr has received little to no attention from fisheries scientists and very little is known about this small, open-lake system. Qinniqtuq Lake is a small freshwater landlocked lake located 42km W of Pangnirtung, in Cumberland Sound ($66^{\circ}21'13''\text{N}$, $66^{\circ}28'51''\text{W}$, Figure 1.2). This lake is approximately 150 ha in size and is considered closed system due to the blockage of the outlet leading from the lake to the marine environment by boulders from a rock fall decades ago. This lake contains an unexploited population of landlocked charr which have not been observed by local residents to migrate in or out of the lake due to the outlet barrier (Pangnirtung Hunters and Trappers Association, personal communication).

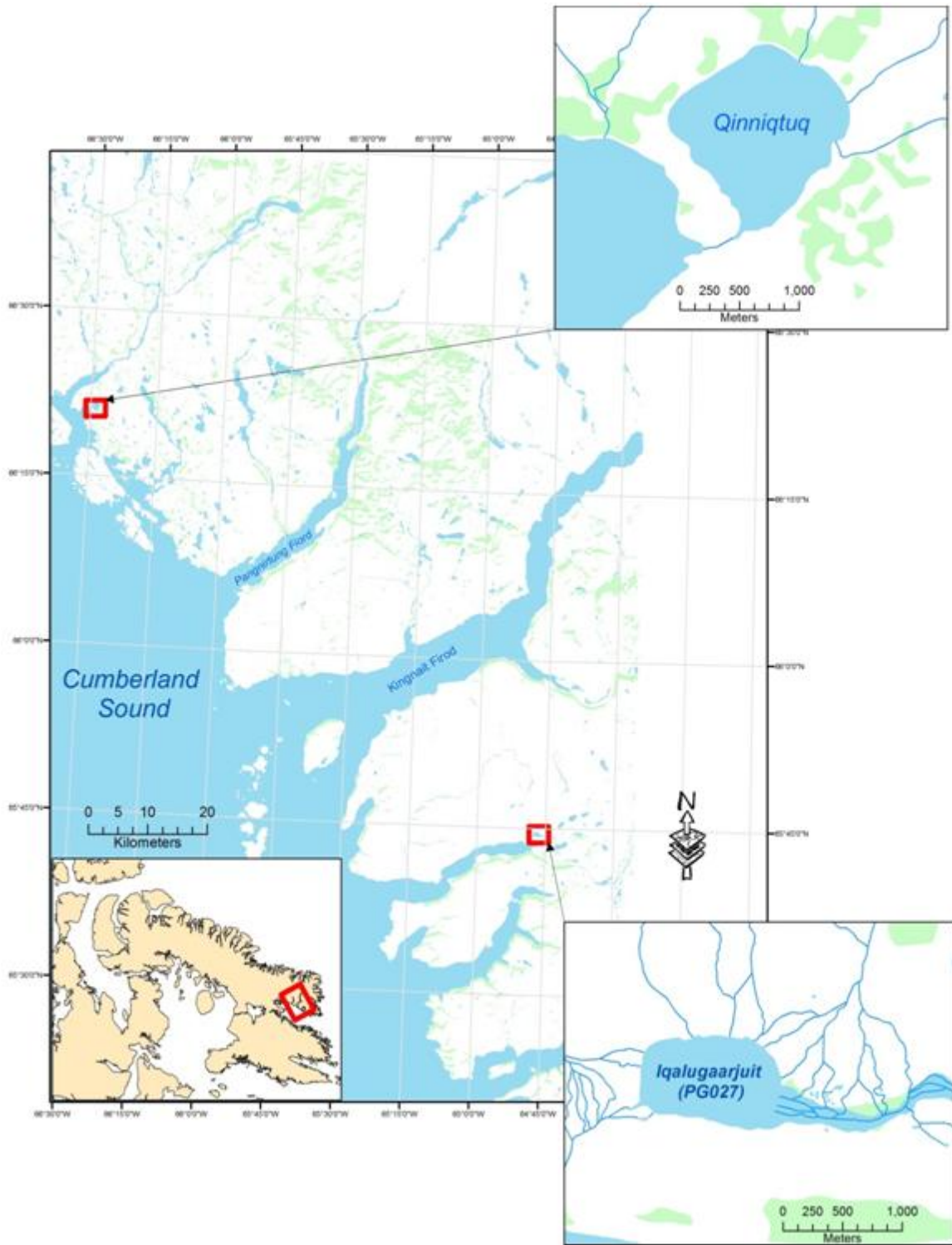


Figure 1.2. Map of the study sites within Cumberland Sound, Baffin Island, Nunavut, Canada. Study sites (lakes) are identified, labeled accordingly Qinniqtuq and Iqalugaarjuit (PG027), and enlarged.

Additionally, the lake is situated approximately 10m above the high tide reach, which would inhibit fish migration.

Field Collection

PG027 was first sampled in September 2011, followed by both lakes subsequently sampled in March and September of 2012, and again in March 2013. Experimental gillnets with panels of 3.8cm (1.5 inch) to 14.0 cm (5.5 inch) stretched mesh sizes were set in each lake at varying depths representative of littoral, pelagic and benthic environments. For the sake of this thesis, littoral habitat will be defined as nearshore habitat; pelagic habitat will be defined as area within the middle and upper water column; and benthic habitat will be defined as up to two meters above the lake bottom. Gillnets set in littoral areas were set perpendicular to the shoreline with the exception of winter when some nets had to be set parallel to the shoreline for logistical reasons and gillnets were rotated and reset in the same location. Nets set in pelagic habitats were set at mid-point in the water column at each set location, and benthic nets were set approximately 1m off of the lake bottom in deep areas. In September, all nets were set in open water using a small boat. Nets set in March were set under the ice using a jigger board. Catch per unit effort (CPUE) was calculated using the following formula and expressed as number of fish/hr:

1.0) **CPUE = # Fish/Net soak time**

Fish Sampling

All fish captured were sampled for fork length to the nearest mm, round weight to the nearest 0.05g, sex, maturity stage, gonad weight to the nearest 0.05g, and aging structures (otoliths). All stomachs containing food items were removed whole and stored in 90% ethanol for subsequent diet analysis.

Limnological Sampling

Limnological habitat sampling occurred at both lakes during each sampling season. All samples were obtained from the end of the gillnet where the second anchor was set. Bottom dredges were obtained in the fall using an Ekman dredge and were preserved in 90% ethanol for laboratory examination. Water chemistry and depth measurements were taken using an OxyGuard dissolved oxygen (D.O.) meter which profiled the water column for temperature and D.O. This was done in all sampling seasons. In March, ice thickness was measured at each set location and subtracted from depth measurements.

Pelagic zooplankton samples were obtained using a Wisconsin plankton net with a mouth diameter of 30cm and 53 μ m mesh. At least five vertical hauls at a towing speed of 0.5-1m sec⁻¹ from just above the lake bottom to the lake surface (Nero and Davies 1982) were performed at each set location in September 2012. Net contents were then washed into a jar; rinsing at least twice from the outside using a plastic squeeze bottle and preserved with 90% ethanol.

Laboratory Analysis

Stomach Contents

Stomachs were opened and contents were examined using a dissecting microscope. Prey items were identified to species, genus or family level and sorted into five functional diet categories: (a) charr; (b) stickleback; (c) digested fish (unidentifiable/unknown); (d) culicidae (eggs, larvae and pupae); and (e) chironomid pupae. With one exception, all stomachs contained only a single functional category of prey item (e.g. culicidae).

Lengths of whole prey items obtained from stomachs were measured using digital calipers to the nearest 0.1mm. When large amounts of invertebrates were present in a single stomach, they were divided into functional groups (e.g., invertebrate egg sacks, culicidae larvae and pupae, chironomid pupae, etc.) and subsamples were measured to obtain an average prey length for each functional group.

Age Estimation

Ages of individual fish were determined by counting the annuli of whole or embedded and sectioned sagittal otoliths (Chilton and Beamish 1982). Whole ageing was predetermined for each population as an appropriate ageing technique for fish ages estimated up to 11 years old for Qinniqtuq and up to 12 years for PG027. This was accomplished through ageing of a sub-sample of otoliths using both the surface-reading technique (whole ageing) and the sectioning technique to determine the maximum surface-reading age cutoff for each population. If the whole ageing technique indicated that a fish was older than the abovementioned age maximum for surface reading or if

the otolith was of poor quality for surface reading, otoliths were then embedded and sectioned for ageing following Chilton and Beamish (1982) and Jenke (2002). With this technique, otoliths were embedded with epoxy resin and sectioned perpendicular to the acusticus sulcus across the nucleus with a Buehler Isomet 1000 sectioning saw and then the otolith section was aged.

Limnological Samples

Benthic samples were examined for macrobenthos. Preserved samples were placed into a 500µm sieve and rinsed with water to remove alcohol and small particles. The sample was then transferred into a tub and weighed to the nearest 0.05 g. A subsample of 10% of the overall sample weight was randomly extracted and transferred into a petri dish to be examined using a high resolution digital microscope. Organisms were identified down to family or genus and counted.

Zooplankton samples were processed for relative density per functional group. A subsample of 5 mL was removed from the fully mixed sample at random using a wide-bore pipette and placed into a ward counting wheel to prevent duplication of counts. Using a dissecting microscope, animals were counted and sorted into functional groups (e.g., copepods, cladocerans, and rotifers). Relative density (D) was calculated using the following formula:

$$1.1) \quad D = \frac{(n)(V_s)}{V_m} \times 100000$$

where n is the average number of organisms in a 5mL sample, V_s is the volume of the plankton sample (mL), and V_m is the volume of lake water sampled (m^3).

Data Analyses

All statistical analyses were conducted using R statistical software (R Development Core Team 2017). Each population was first examined individually, and direct comparisons were made where applicable.

Statistical data exploration was applied following the protocol described in Zuur *et al.* (2010) and Ieno and Zuur (2015) (see Appendix 1.0) before any modeling was employed. Cleveland dotplots were used to inspect the variables for outliers and multi-panel scatterplots were used to visualize relationships. Collinearity (correlation between covariates) was assessed in multiple ways including: multi panel scatterplots, Pearson Correlation Coefficients, boxplots for categorical covariates, and examination of variance inflation factor (VIF) values using a VIF cut-off of 3 (Zuur *et al.* 2007; Zuur *et al.* 2015) (Appendix 1.0). Collinearity increases standard errors of estimated regression parameters which in turn inflates *p*-values (Montgomery and Peck 1992; Zuur *et al.* 2007); thus, collinear covariates were not modeled together. Model fit and meeting of model assumptions were assessed by visual examination of Pearson residuals.

To assess possible differences of length at age by sex for each population, following Ogle (2016) and Gerritsen *et al.* (2006) a multinomial model was applied to age-length keys using the `nnet()` package in R (R Core Development Team 2017). No significant difference between age-length keys by sex was found for either population so sexes were pooled for analysis.

Generalized linear models (GLMs) were used throughout to assess relationships between biological and habitat variables as well as to make predictions. The common generalized linear model formula to assess relationships between variables was:

$$1.2) \quad E(Y_i) = \beta_0 + \beta_1 x_{i1}$$

where E is the link function, Y_i = biological (dependent) variable and x_{i1} is the habitat variable (*water temperature, D.O., depth and lake zone*) (Quinn and Keough 2002). To make predictions, logistic regression (GLMs) were employed using the `glm()` function in R (R Core Development Team 2017). The independent and dependent variables differed for each model, but the common formula used throughout was:

$$1.3) \quad \text{logit}(\pi) = \log\left(\frac{\pi}{1-\pi}\right) = \beta_0 + \beta_1 x_{i1}$$

where β_0 and $\beta_1 x_{i1}$ are the parameters to be estimated and π is the probability that the dependent variable is of class 1, given the independent variables (Quinn and Keough 2002).

Habitat Use

Due to multicollinearity among all habitat variables as well as the variable “season”, multiple linear regressions could not be employed to examine relationships between habitat and biological variables within seasons for each life history type. Thus, sampling years were combined and data were grouped into populations and further grouped by season and GLMs were applied. To identify relationships between measured habitat variables (*water temperature, D.O., depth, and lake zone*) and biological variables (*fork length, sex, sexual maturity*) in the fall and winter, various GLMs were employed using the `glm()` function in R (see Appendix 1.1).

Variable: Fork Length

To assess the occurrence of seasonal size segregated habitat use in either lake, Gaussian GLMs using the identity link were used to model *fork length* against all habitat variables (Equation 1.2).

Variable: Number of fish (abundance)

To examine the relationship between habitat and fish abundance (measured as number of fish per set and its relating habitat variables), Poisson GLMs using the log link were applied to catch data and habitat variables by season (Equation 1.2). For the anadromous population, initial analyses indicated overdispersion; therefore a negative binomial GLM was applied. For the landlocked population, data exploration indicated zero inflation (more than 20% zeros) of the count data; therefore a zero-altered Poisson (ZAP) hurdle model was applied. Zero inflation of Qinniqtuq abundance data is likely due to structural error (habitat is not suitable) and the zeros were assumed to be true negatives (Zuur et al. 2009). Given that abundance sample sizes were small overall ($n = 29$ for anadromous, $n = 50$ for landlocked), both populations were modeled with combined seasons as well as by individual seasons.

Variable: Sexual Maturity

Logistic regressions were estimated by binomial GLMs using the logit link to examine interactions between measured seasonal habitat variables (*water temperature*, *D.O.*, *depth* and *lake zone*) and *sexual maturity* in both systems (Equation 1.3) with probability that the dependent variable is “mature”.

Variable: Sex

Logistic regressions were estimated by binomial GLMs using the logit link were used to examine interactions between measured seasonal habitat variables (*water temperature, D.O., depth and lake zone*) and sex in both systems, with probability that the dependent variable is “male” (Equation 1.3).

Length and Age at First Maturity

Logistic regressions were estimated by binomial GLMs using the logit link to predict the length at first maturity (L50) and age at first maturity (A50) for both populations with probability that the dependent variable is “mature” (Equation 1.3, see Appendix 1.2). Predictions were calculated where 50% of the fish sampled were mature. Predictions were made for males, females, and both sexes combined for both populations.

Diet

Diet was assessed as percent composition of functional prey categories of individual fish. Given the lack of diversity of functional prey categories within landlocked charr stomachs, percent composition was calculated as the number of stomachs containing a single functional category of prey.

Results

General Observations

A total of 409 fish were sampled from PG027 and a total of 69 fish were sampled from Qinniqtuq (2011-2013). Catch rates were noticeably lower in Qinniqtuq than PG027, which limited the number of samples obtained from this system creating a 4:1 difference in sample size between lakes (Table 1.0). A total of 17 fish were harvested from Qinniqtuq in winter 2012, 10 fish were harvested in winter 2013, and 42 were harvested in fall 2013. The large variability in annual seasonal catches made statistical comparisons between habitats by season problematic.

Mean CPUE differed between the two systems, with PG027 yielding the highest overall CPUE of 9.0 ± 2.2 fish/hr and Qinniqtuq yielding a much lower CPUE 0.15 ± 0.03 fish/hr (Table 1.0). CPUEs also differed within each system between seasons, with the fall yielding the highest overall CPUE in both PG027 (15.1 ± 3.4 fish/hr) and Qinniqtuq (0.18 ± 0.07 fish/hr) compared to the winter (3.3 ± 0.5 fish/hr and 0.13 ± 0.04 fish/hr, respectively) (Appendix 1.3).

Charr sampled from PG027 ranged in fork lengths from 178-790mm, while charr from Qinniqtuq fork lengths ranged from 150-507mm. Ages ranged from 4-26 years in PG027 and 5-25 years in Qinniqtuq (Tables 1.1 and 1.2, respectively).

In PG027, no fish were recorded in the size range of 238mm-321mm, causing an absent size class in the length frequency distribution (Figure 1.3). Mean length at age differed between the populations, with anadromous charr achieving greater overall mean length at age (Figure 1.4). Mean length at age of anadromous charr was almost double that of landlocked charr by age 15 (Figure 1.4). Mean lengths between ages 6

and 7 of anadromous charr are noticeably different, with an increase of approximately 200mm (Figure 1.4).

Sex ratios for both systems indicate a higher presence of males in both systems (Tables 1.0, 1.1, and 1.2), with an almost 2:1 ratio of males to females in the landlocked population (Tables 1.0, 1.1, and 1.2). A near 2:1 ratio of mature to immature fish was observed in both PG027 and Qinniqtuq (Tables 1.0, 1.1, and 1.2). Age at first maturity (A50) prediction for the landlocked population was 0.8 years higher than that predicted for the anadromous population (Table 1.3, Appendix 1.4) and length at first maturity (L50) prediction for anadromous charr was 136mm longer than that predicted for landlocked charr (Table 1.3, Appendix 1.4)

Size frequency distributions differed between the populations with PG027 displaying a left-tailed unimodal distribution and Qinniqtuq displaying an apparent bimodal distribution (Figure 1.3). Mean length at ages for both populations is displayed in Figure 1.4.

Habitat Distribution

PG027

Charr were caught in all lake zones in all sampling seasons, with every net set yielding fish. Percent composition of anadromous charr by habitat was relatively consistent in both seasons, with the littoral zone yielding the highest amount of fish and the pelagic zone yielding the lowest amount for both seasons, years pooled (Figure 1.5). In combined years of fall sampling data, the shallowest depth in which charr were caught was <1m and the deepest depth was 26m. In winter, the shallowest depth in which charr were caught was 2m and the deepest depth was 13m, years pooled. In the

fall, the lowest water temperature charr were caught in was 7.3° and the highest was 9.4°; and the lowest D.O. level was 8.8ppm and the highest was 15.4ppm, years pooled. In the winter the lowest water temperature charr were caught in was 0.3° and the highest was 2.2°; and the lowest D.O. level being 10.9ppm and the highest being 14.1ppm, years pooled (Table 1.2).

Results of general linear models of habitat and biological variables (*fork length*, *sex* and *sexual maturity*) for anadromous charr are displayed in Table 1.4, (See Appendix 1.1 for example R code and Appendix 1.5 for figures associated with habitat models yielding statistically significant results). Given the large number of individual GLMs performed to assess the relationships between habitat variables and biological variables, details are provided only for those models which yielded statistically significant results. For the biological variable *sex*, results from data collected in the fall indicated statistically significant relationships with habitat variables *D.O.* and *water temperature* and from data collected in the winter indicated statistically significant relationships with habitat variables *water temperature* and *lake zone* (specifically, the pelagic zone). For the biological variable *fork length*, results from data collected in the winter indicated a statistically significant relationship with the habitat variable *D.O.* No statistically significant relationships were found between *maturity* and any habitat variable in either season.

The GLMs used to assess the relationship between habitat variables and the abundance of fish in combined seasons found a statistically significant negative

Table 1.0. Comparative lake ecology data of anadromous (PG027) and landlocked (Qinniqtuq) charr populations in Cumberland Sound.

	Lake Size (ha)	Max Depth (m)	Life History	Number of Fish Sampled	Mean CPUE	Length Range (mm)	Age Range (yr)	Sex Ratio M:F
<i>PG027</i>	77	25	Anadromous	409	9.0 ± 2.2	160-790	4-26	1.25
<i>Qinniqtuq</i>	150	50+	Landlocked	69	0.15 ± 0.03	178-507	5-25	1.39

Table 1.1. Summary table of biological and habitat variables associated with anadromous charr sampled from PG027. Sex and maturity ratio column totals expressed as decimals.

	No. of Fish Sampled	Mean CPUE	Fork Length Range (mm)	Weight Range (g)	Age Range (yr)	Sex Ratio M:F	Maturity Ratio M:I	Depth Range (m)	Temperature Range (°C)	D.O. Range (ppm)
2011										
Fall	84	21.5	344-790	800-4490	7-26	0.68	9.50	0.85-17	7.3-8.2	13.47-15.4
Littoral	52	9.4	344-720	405-4010	7-26	21:31	45:7	0.85-2	8.0-8.2	13.47-14.9
Benthic	21	40.0	431-732	800-4031	7-13	10:11	20:1	17	7.8	14.72
Pelagic	11	15.1	451-790	1000-4490	7-12	3:8	11:0	17	7.3	15.4
2012										
Winter	107	3.0	178-756	273-4229	5-20	1.23	5.69	2-10	0.4-2.9	10.3-14.1
Littoral	60	3.9	178-755	273-3456	5-20	1:1	51:9	2	0.4-2.2	12.5-14.1
Benthic	29	2.8	399-705	485-3534	8-18	15:14	26:3	10	1.3-2.9	10.3-10.4
Pelagic	18	2.2	386-756	569-4229	8-17	7:2	7:2	6	2.2	11.1
2012										
Fall	128	13.7	384-756	560-4316	7-15	1.44	32	0.85-26	8.0-9.4	8.8-12.8
Littoral	76	25.9	384-756	642-4316	7-15	21:19	19:1	0.85-2	8.5-9.2	11.5-11.6
Benthic	41	10.1	386-741	560-4178	7-15	49:27	47:1	11-26	8.0-9.4	8.8-12.6
Pelagic	11	5.1	410-703	776-2704	8-15	5:6	11:0	7	8.6	12.8
2013										
Winter	90	3.3	160-764	30-4140	4-18	2	1.51	2-13	0.3-2.4	10.9-15.0
Littoral	39	4.0	160-740	30-3407	4-14	23:16	17:21	2	0.3-1.3	10.9-11.2
Benthic	31	3.3	378-764	454-4140	7-15	20:11	24:7	11-13	2.3-2.4	14.6-15.0
Pelagic	20	2.5	184-715	51-3408	4-18	17:3	12:7	5-7	1.5-1.9	11.8-12.2
Total	409	8.99	178-790	30-4490	4-26	1.26	2.55	0.85-26	0.4-9.4	8.8-15.4

Table 1.2. Summary table of biological and habitat variables associated with landlocked charr sampled from Qinniqtuq. Sex and maturity ratio column totals expressed as decimals

	Number of fish	Mean CPUE	Fork Length Range (mm)	Weight Range (g)	Age Range (yr)	Sex Ratio M:F	Maturity Ratio M:I	Depth Range (m)	Temp Range (°C)	D.O. Range (ppm)
2012										
<i>Winter</i>	17	0.2	178-472	45-656	6-25	2.75	1.5	2-48	0.8-3.9	5.5-16.6
Littoral	6	0.1	178-275	45-140	6-25	4:1	2:3	2-3	0.9-1.2	15.1-16.6
Benthic	7	0.3	191-461	64-656	5-12	3:1	5:2	23-48	2.5-3.9	5.5-14.2
Pelagic	4	0.2	185-472	185-472	6-21	2:1	2:1	6-11	0.8-1.4	15.2-15.4
2012										
<i>Fall</i>	42	0.2	150-507	51-1177	5-23	1.21	2	2-29	4.1-10.9	11.6-13.5
Littoral	40	0.3	180-507	51-1177	5-23	21:19	13:7	2	10.3-10.9	11.6-11.9
Benthic	2	0.05	418-480	579-932	20-21	2:0	2:0	29	4.1	13.5
Pelagic	-	-	-	-	-	-	-	-	-	-
2013										
<i>Winter</i>	10	0.1	193-495	63-1142	5-17	2.33	0.67	1-46	0.3-2.4	12.3-17.5
Littoral	7	0.1	193-495	63-1142	5-17	4:3	2:5	1	0.3-0.6	15.3-17.5
Benthic	3	0.04	253-368	128-385	10-12	3:0	2:1	12-46	2.2-2.4	12.3-14.3
Pelagic	-	-	-	-	-	-	-	-	-	-
Total	69	0.15	150-507	45-1142	5-25	1.58	2.0	1-48	0.3-10.9	5.5-17.5

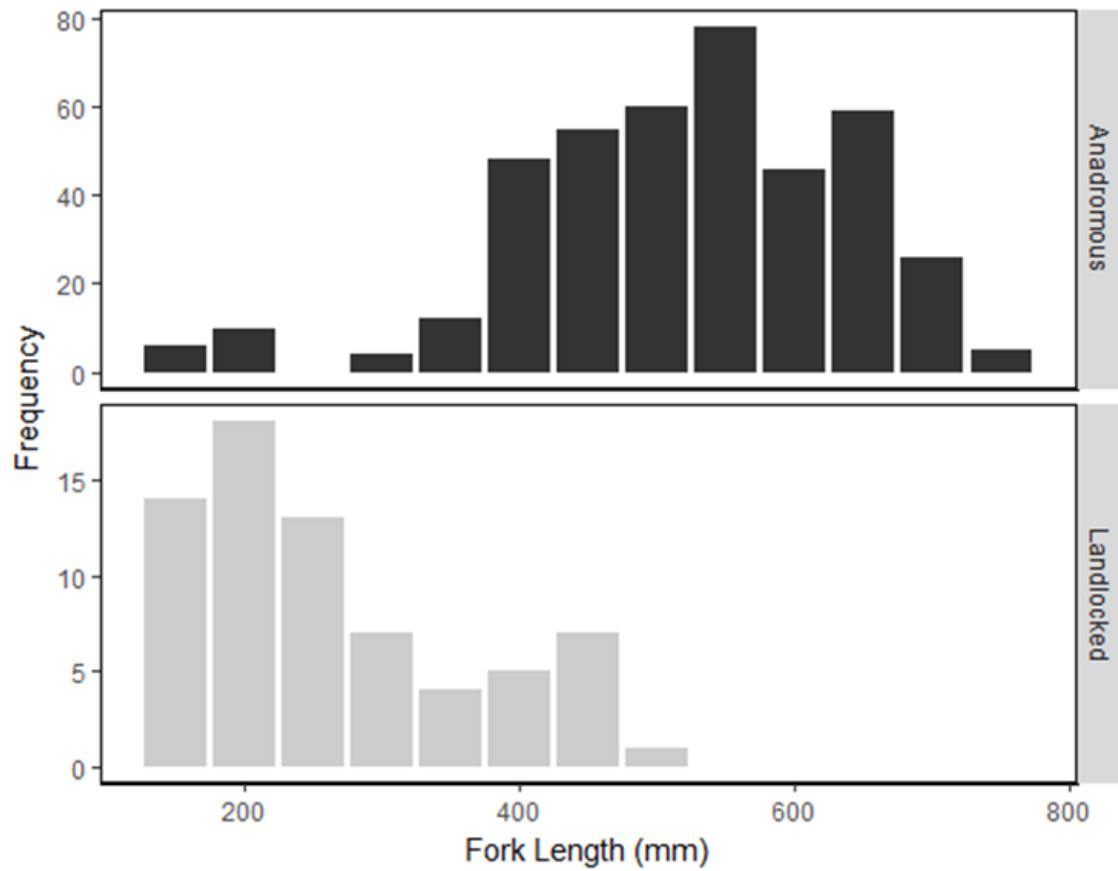


Figure 1.3. Length frequency distributions of anadromous and landlocked charr. Note that the y-axis scales are different.

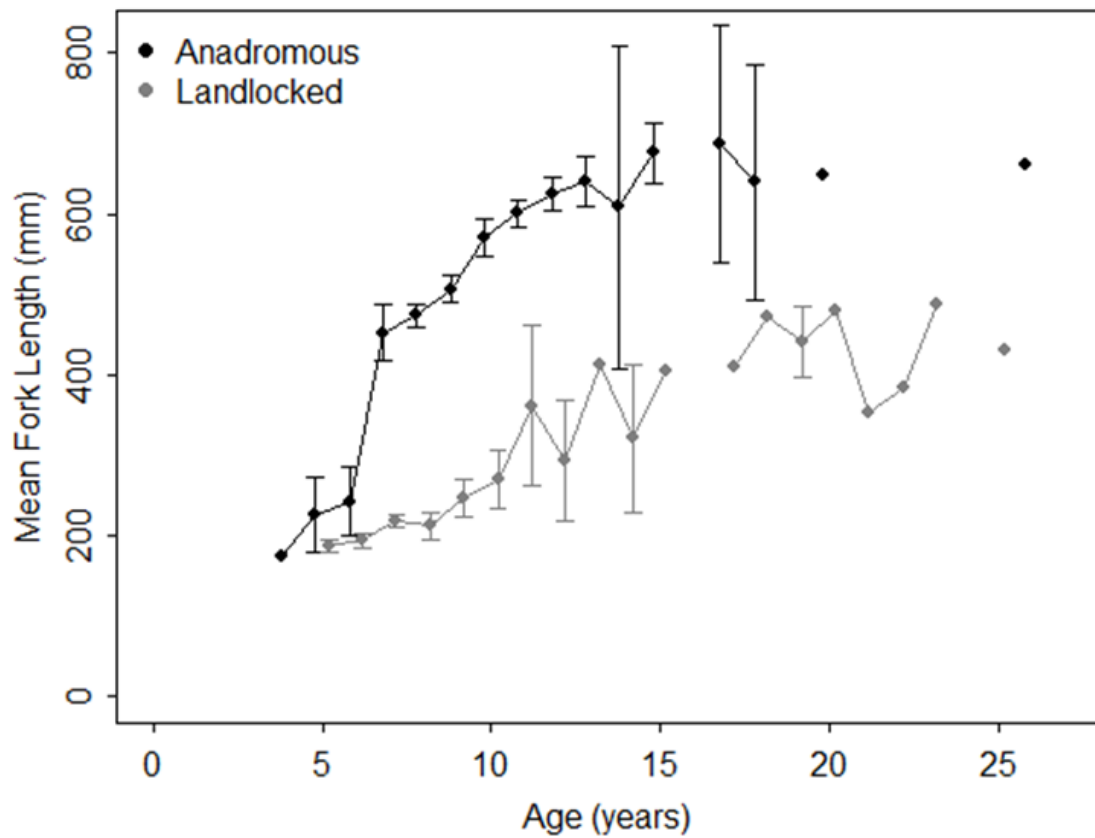


Figure 1.4. Mean length at age of anadromous (black) and landlocked (grey) charr. Error bars represent 95% confidence intervals, standard error included.

Table 1.3. Summary table of length and age ranges and estimates of age at first maturity (A50) and length at first maturity (L50). Mean length and mean age include standard error.

Life History	Sex	Length Range (mm)	Mean Length (mm)	Age Range (yr)	Mean Age (yr)	A50 (yr)	L50 (mm)
Anadromous	Male	160-790	526 ± 9	4-20	10.2 ± 0.2	6.49	356.32
	Female	193-675	523 ± 7	5-26	10.1 ± 0.2	6.77	418.36
	Both	160-790	545 ± 6	4-26	10.1 ± 0.1	6.6	387.5
Landlocked	Male	180-507	314 ± 16	5-23	11.8 ± 0.8	7.56	231.68
	Female	183-483	251 ± 15	5-25	10.15 ± 1.1	8.08	217.95
	Both	180-507	289 ± 12	5-25	11.1 ± 0.6	7.4	220.5

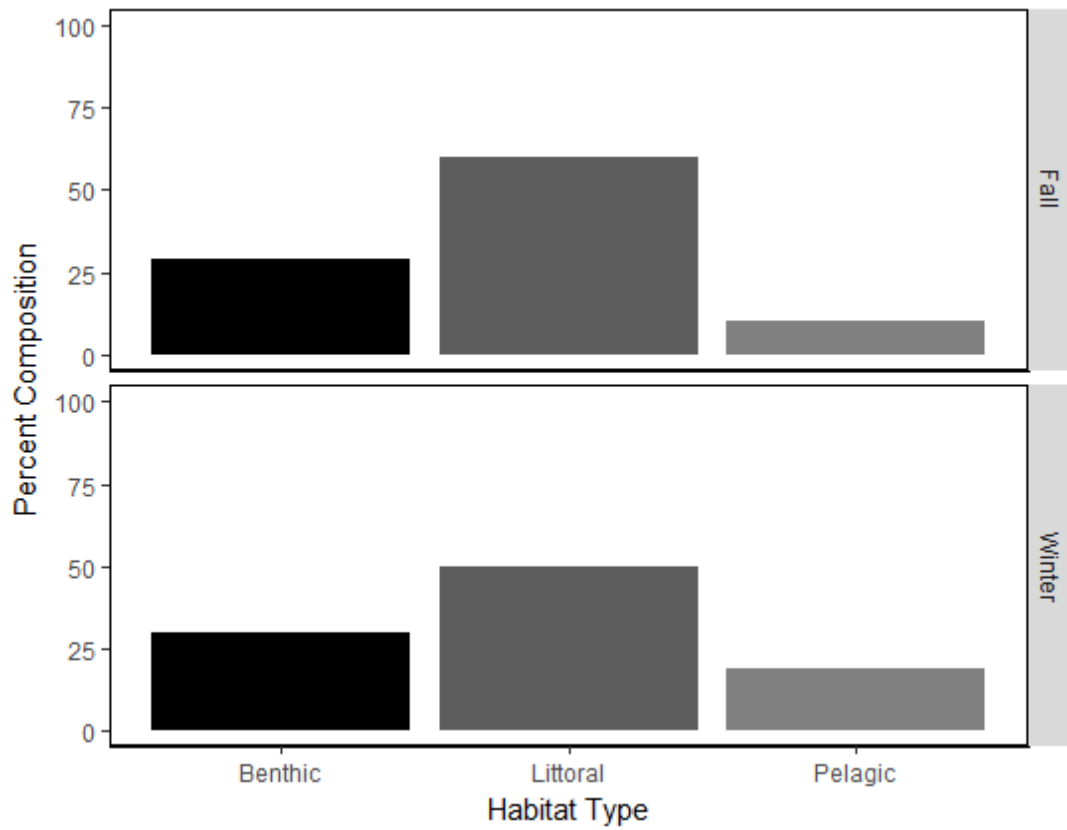


Figure 1.5. Percent composition for catches of anadromous charr by habitat for each sampling season for PG027, years pooled.

Table 1.4. GLM results for the anadromous population in fall (n=212) and winter (n=197) for biological variables (*fork length, sex, and maturity*) and habitat variables (*D.O., water temperature, depth and lake zone*). Details are presented only for models with statistically significant results. Dashed lines represent non-significant results.

Biological Variable	Season	Habitat Variable	Model Coefficients	Estimate	Std. Error	z-value	p-value
Fork Length	Fall	All	Intercept	-	-	-	>0.05
			Slope	-	-	-	>0.05
	Winter	Dissolved Oxygen	Intercept	702.836	72.300	9.721	<0.05
			Slope	-13.012	5.691	-2.287	<0.05
Sex	Fall	Dissolved Oxygen	Intercept	2.84885	1.010	2.820	<0.05
			Slope	-0.22011	0.078	-2.805	<0.05
	Water Temperature	Intercept	-4.7304	2.3582	-2.006	<0.05	
		Slope	0.5749	0.2834	2.029	<0.05	
	Winter	Lake Zone - Pelagic	Intercept	0.3365	0.2619	1.285	0.199
			Slope	1.1188	0.4947	2.261	<0.05
Water Temperature	Intercept	-0.4114	0.2957	-1.391	0.164		
	Slope	0.5637	0.18	3.132	<0.05		
Maturity	Fall	All	Intercept	-	-	-	>0.05
			Slope	-	-	-	>0.05
	Winter	All	Intercept	-	-	-	>0.05
			Slope	-	-	-	>0.05

relationship between pelagic habitat and fish abundance for anadromous charr in the fall (Slope=-0.748, intercept=2.741, SE=0.372, $p < 0.05$). No statistically significant relationships were detected between habitat variables and fish abundance in the winter or in combined seasons.

Qinniqtug

Charr were caught in all habitat types; however, just over half of the nets yielded no fish. Nets containing no fish were prevalent in all three habitat types. Pelagic habitat sets yielded no fish in the fall or winter of 2013. In the fall the majority of catches occurred in the littoral zone, with the benthic zone yielding a small amount of fish. For combined years of winter sampling, the largest amount of fish was harvested from the littoral, followed by the benthic zone. A small percentage of fish was harvested from the pelagic zone in the winter 2013 sampling season (Figure 1.6).

In the fall the shallowest depth that charr were caught in was 2m and the deepest depth was 29m. In combined years in the winter, the shallowest depth that charr were caught in was 1m and the deepest depth was 48m. In the fall, the lowest water temperature charr were caught in was 4.1° and the highest was 10.9°; and the lowest D.O. level being 11.6ppm and the highest being 13.5ppm. In the winter the lowest water temperature charr were caught in was 0.3° and the highest was 3.9°; and the lowest D.O. level being 5.5ppm and the highest being 17.5ppm (Table 1.2).

The GLMs used to assess relationships between habitat variables and biological variables of landlocked charr (*fork length*, *sex*, *sexual maturity*) found a statistically significant relationship between littoral habitat and *fork length* for combined seasons (Slope=-96.35, intercept=364.92, SE=29.81, $p < 0.05$, $n=69$) (Figure 1.7; Appendix 1.5).

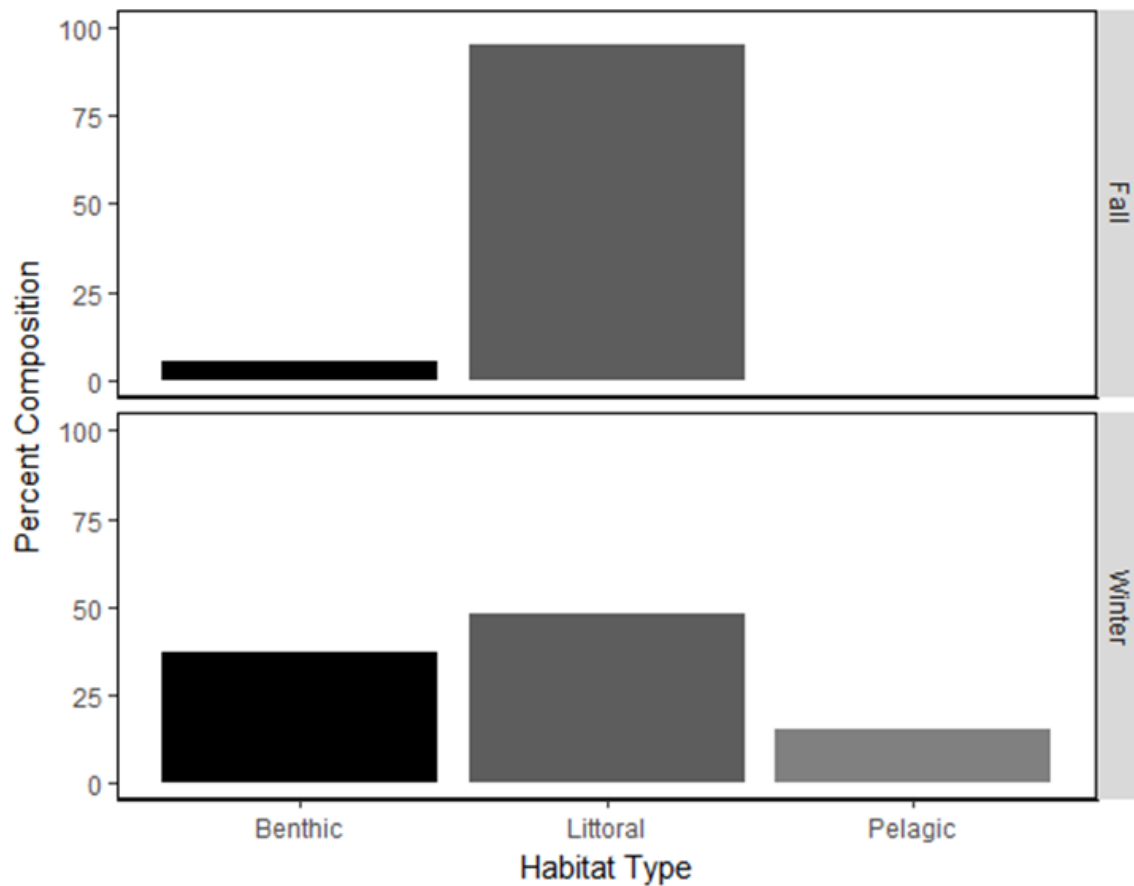


Figure 1.6. Percent composition for catches of landlocked charr by season for combined years. Fall data represents a single sampling season (fall 2012) where winter data is from combined field seasons (winter 2012 and 2013).

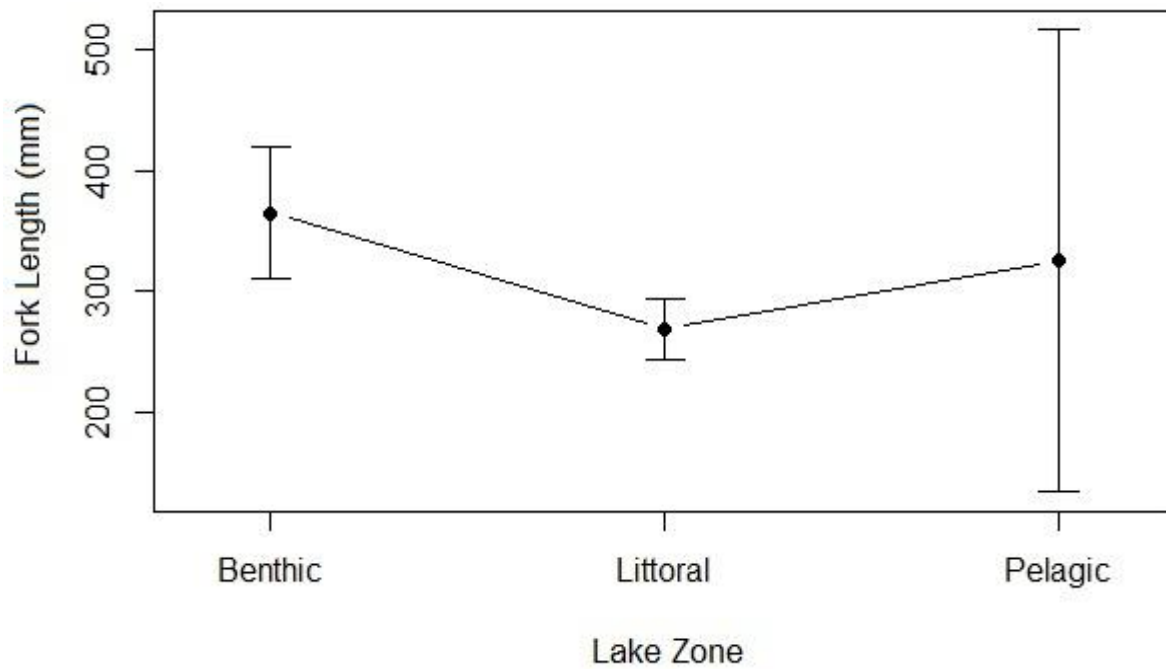


Figure 1.7. GLM predictions for length of landlocked charr by lake zone for combined seasons with associated confidence intervals.

The GLMs used to assess the relationship between habitat variables and the abundance of fish in combined seasons found a statistically significant relationship between *D.O.* and fish abundance for landlocked charr in the winter (slope=0.771, intercept=-11.850, SE=0.390, $p<0.05$). No statistically significant relationships were detected between habitat and fish abundance in the fall or in combined seasons.

Stomach Contents

Only a single fish from PG027 was found to have food in its stomach. The contents were identified as fish carrion that was likely scavenged. In Qinniqtuq, a total of 34 fish (or 43% of fish sampled) had food in their stomachs between all seasons. Stomach contents included various species of invertebrates including culicidae (mosquito) pupae and culicidae egg sacks as well as chironomid (midge) larvae. A total of two species of fish were found within the stomachs: gasterosteidae (sticklebacks) and juvenile charr; in addition to fish eggs. No zooplankton species were found in any landlocked charr stomachs. Given the lack of food in the stomachs of anadromous charr, stomach contents are only discussed for the landlocked population.

Fall

In the fall, 57% of landlocked fish sampled had food in their stomachs. During this season, stomachs contained either invertebrates or fish, with only one stomach found to contain both prey types. Invertebrates were the dominant prey item in the fall with 80% of stomachs containing this prey item. Sticklebacks or partially digested, unidentifiable fish species were less common, with only 20% of stomachs containing

this prey type (Figure 1.8). No charr were identified as prey in any stomach samples obtained in the fall.

Winter

From all winter samples a total of 10 landlocked fish had stomachs containing food. Prey consisted of fish and invertebrates, with only one prey type present per stomach with the exception of one fish in which both prey types were present. Fish comprised 75% of prey items; 50% of which were identified as juvenile charr. Chironomids comprised the remaining 25% of identified prey items (Figure 1.8).

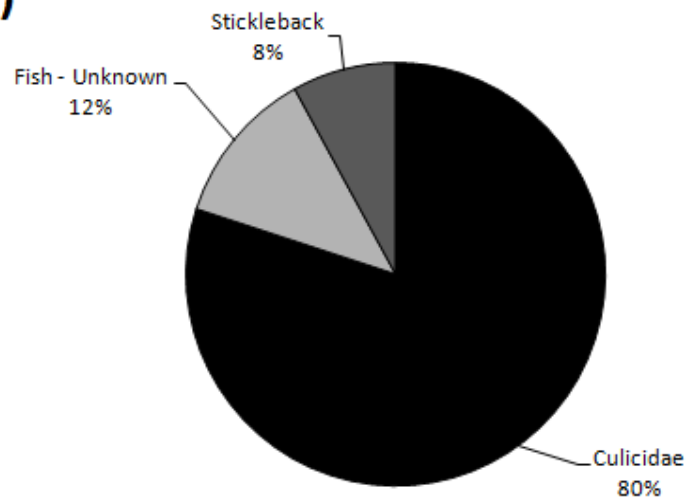
Combined Seasons

In combined seasons, invertebrates were the most common prey item for fish caught in the littoral zone (73%). Conversely, fish were the most common prey item for charr caught in the benthic zone (80%). The pelagic zone yielded fish with stomachs containing equal amounts of either fish (50%) or invertebrates (50%).

Zooplankton and Benthic Communities

Zooplankton communities and relative densities differed between waterbodies. The zooplankton community in PG027 was comprised of primarily cladocerans with some copepods. Relative density of zooplankton for this waterbody was estimated to be 87 organisms/m³. Conversely, the zooplankton community for Qinniqtuq was comprised mainly of copepods, cladocerans and rotifers, with copepods being the most predominant species followed by cladocerans. Relative density of zooplankton for this waterbody was estimated to be 400 organisms/m³.

A.)



B.)

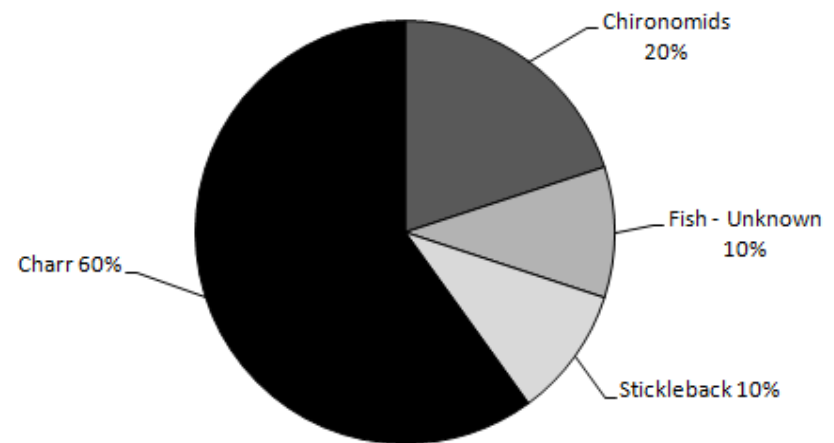


Figure 1.8. Percent composition of stomachs containing functional categories of prey items for landlocked charr in A.) Fall and B.) Winter, from Qinniqtuq in Cumberland Sound, Nunavut

Bottom substrate samples from both lakes consisted of mostly silty sand or silty clay deposits. Little to no vegetation was found within the samples. Benthic communities between the lakes were different. PG027 benthic samples were comprised solely of chironomidae larvae, with an average of 0.6 animals/g of sediment. Qinniqtuq on the other hand consisted of chironomidae; ceratopgonidae; and tipulidae species larvae. Chironomids made up the majority of the species composition, followed by ceratopgonidae and tipulidae, respectively, with an average of 0.9 animals/g of sediment.

Discussion

This research presents differences in the diet, biological characteristics and general lake ecology of two populations of charr with contrasting life histories. The difference in seasonal CPUE between the populations suggests a possible difference in population size. Despite Qinniqtuq being twice the size of PG027 and appearing to be more productive in regards to prey availability (zooplankton and benthic invertebrates), the considerably lower overall CPUE(s) may be indicative of a small population or possibly that the vast majority of fish in this system congregate in smaller, specialized habitats that were not accessed during sampling.

Anadromous charr attained greater overall length at age than landlocked charr, with size at age of anadromous charr double that of landlocked charr in the older size classes. Following age 5 fork lengths differed noticeably between the populations with a noticeable increase in mean length at age of anadromous charr between ages 6 and 7, which is likely the cause of the absent size class in the length ranges 238mm-321mm. This may be an indication of the timing of first migration and the growth

achieved therein, as the marine environment offers a greater diversity in high-lipid prey than freshwater environments (Imrie 2012) and the majority of growth in anadromous charr occurs at sea during annual summer feeding periods (Johnson 1980*b*). Mean length at age data suggest that a small amount of fish in this system make their first migration at age 5, with 14% of fish in that year class being over 300mm. By age 6, 20% of fish were over 300mm. By age 7, 100% of fish were over 300mm. This suggests that age 6 might be the most common age that fish in this system make their first migration to sea, with all charr having migrated by age 7. Similar findings of age at first migration have been reported by Gulseth and Nilssen (2001) where in the Dieset watercourse in Svalbard, 91.8% of first-time migrant charr in a partially anadromous population were 6 years of age or older and Loewen (2016) used otolith strontium analysis to determine that populations of Nunavut charr make their first migrations between ages 5-7 years. The marine environment offers rich feeding opportunities which have been shown to improve growth in anadromous fishes (Chapman *et al.* 2012*b*), making a drastic increase in growth between ages 6 and 7 a plausible indication of age at first migration for anadromous charr in PG027. Further, size and fecundity are directly related (Murua *et al.* 2003) and a large increase in growth prior to achieving sexual maturity would likely set the stage for the animal's lifetime fecundity potential. Age at first migration of anadromous charr will be discussed in further detail in Chapter 3 of this thesis.

Mean length at age of landlocked charr showed little variability between ages 5-9 years. Some variation becomes apparent at age 10 and onwards, with distinct variation in mean length at age apparent by age 12. Similar to the anadromous population, this initial change in length at age may also be attributable to an ontogenetic diet shift (e.g.

the shift from invertebrate feeding to piscivory). However, no significant increases in growth between age classes is evident in the landlocked population, suggesting that a possible change in freshwater feeding alone may not have the same noticeable influence as short periods of marine feeding on length at age as observed in the anadromous population.

A larger proportion of landlocked charr appear to attain older ages than anadromous charr, with 28% of landlocked charr aged 13 years or older and only 10% of anadromous charr aged 13 years or older. Landlocked charr also appear to mature at an older age and smaller size than anadromous charr. Given the presence of three small (<200mm), older, sexually mature charr captured in Qinniqtuq, this may be evidence of both fast and slow growing charr in this system; an occurrence that has been observed in other landlocked systems in Nunavut (van der Veldon *et al.* 2012), but further research is required to validate this. Conversely, no small mature fish were detected in PG027 and a lack of any small mature fish historically sampled from this system suggests that this population exhibits a singular, anadromous life history. This is surprising as many populations of charr in Cumberland Sound are suspected to be partially anadromous due to the documented presence of small mature (resident) charr in many populations (Dr. Tracey Loewen, Fisheries and Oceans Canada, personal communication).

Disproportionate sex ratios were observed in the landlocked population with an almost 2:1 ratio of males to females. Sex ratios can often be skewed within and between spawning aggregations and cohorts (Fryxell *et al.* 2015). Possible causal mechanisms of sexual asynchrony in this population are discussed later in this thesis.

The appearance of a bimodal size structure of the landlocked population is of particular interest. Bimodality is not uncommon in this species as size frequency distributions of charr commonly exhibit one or more bell shaped catch curves reflective of population structures that can be described as unimodal, bimodal and even trimodal (Johnson 1975, 1976, Hammar 2000). Each mode exhibits a well-defined modal value which is unique to each system (Hammar 2000). Causes of bimodal size structures can include cannibalism (Svenning & Borgstrøm 1995), with larger-sized fish actively suppressing smaller-sized fish thereby prohibiting their recruitment to the dominant size-classes (Johnson 1976; Power *et al.* 2008); or more so in the case of Qinniqtuq, through the interaction between mortality and growth schedules over a long lifespan, as in single-species lakes such as these it is not uncommon for populations to exhibit many small and large-sized fish but few medium-sized fish (Power *et al.* 2009). The left-tailed unimodal structure of PG027 charr reflects a high frequency of larger fish in this system. The low frequency of smaller sized (<400mm) fish sampled in PG027 may be related to gear selectivity; however, given that multi-mesh panel gillnets were used a more likely cause may be that small charr in this system may use more specialized habitats (such as the river) during the open water season. This may be the case given that the majority of the smaller sized charr sampled in PG027 were caught in a single set in the winter. Further investigation is required to adequately address this observation.

Diet and Feeding

Feeding differed between the populations; anadromous charr had no food in their stomachs in any season. This observation is likely due to the fact that anadromous fish do little to no feeding in the freshwater environment following the return from migration

(McDowell 2009; Rikardsen *et al.* 2003). In contrast, landlocked fish were found to actively feed in both fall and winter, with majority of feeding occurring in the fall (73% of all stomachs contained prey items in the fall). Fish and invertebrates comprised the two classes of prey found within stomachs. Despite the large abundance of zooplankton availability in Qinniqtuq, no evidence of zooplankton feeding was observed.

Landlocked charr appear to use seasonal opportunistic feeding strategies. In the fall when aquatic invertebrates are readily available in various life stages, landlocked charr appear to feed heavily on culicidae pupae likely because they float on the water's surface (Walker and Merritt 1991) and are easily accessible in large numbers.

Sticklebacks are likely more active in the open water season due to spawning activity (Scott and Crossman 1973) which would make them a more readily available food source for an opportunistic piscivore like charr. The presence of juvenile charr in the stomachs of larger fish is indicative of cannibalistic feeding within this population. The fact that cannibalism was only detected in fish sampled in the winter months suggests that landlocked charr may adopt seasonal alternative feeding strategies when food sources are limited, such as during the ice-covered season.

Habitat Use

Differences in habitat use between the populations is likely attributable to feeding and habitat availability within different lacustrine systems. Non-migratory populations of charr have been documented to actively feed in both the fall (Amundsen *et al.* 2008) and the winter (Amundsen and Knudsen 2009). Since their only feeding opportunities occur within the lake, different lake habitats may be utilized to maximize feeding. This is apparent in the fall where the littoral zone yielded all sizes of fish, many of which were

found to have full stomachs. The littoral zone is optimal habitat for forage fish and juvenile charr as these habitats are often considered refugia for small and young fish (Karlsson and Byström 2005). The littoral zone also offers ideal habitat for aquatic invertebrates as microhabitats are important for egg-laying to support the development of various life stages (Danks 2007). This implies that the littoral zone in Qinniqtuq is important habitat for both invertebrate and piscivorous feeding of all sizes of this population of landlocked charr.

The lakes differed drastically in morphometry (size, shape and depth), productivity and thermal structure; thus each lake offers different habitats and available niches. For instance, Qinniqtuq is a deep, bowl-shaped lake with a maximum depth of approximately 50m with obvious thermal stratification. PG027 on the other hand is a small, shallow lake which displayed no apparent thermal stratification in any season and no profundal zone. The shorelines (and subsequent littoral zones) of both lakes differed noticeably, as PG027's shoreline was primarily a mixture of sand and pebbles, where Qinniqtuq's shoreline was rocky and far more structured providing greater habitat availability for small fish (Karlsson and Byström 2005). The differences in depths between the systems also allowed for differences in water temperature and D.O. availability; with Qinniqtuq having a wider range of both. Since lake morphometry (Kristoffersen *et al.* 1994; Riget *et al.* 2000) and physical watercourse parameters (Kristoffersen 1994) have been shown to influence the level of anadromy in Arctic charr, the lack of resident charr in PG027 is likely a combination of lake morphometry and poor habitat and prey availability. Water column profiles indicated that PG027 lacked a profundal zone (Appendix 1.6) which encourages lake residency (Kristoffersen *et al.* 1994) and was found to contain a relatively low abundance of zooplankton and

benthic species which would be necessary to provide adequate food resources for a small, lake-dwelling morphotype specializing in these resources.

The littoral zone appears to be important habitat for small fish in both systems. Small fish appear to use the littoral in both seasons in Qinniqtuq; while, in PG027 they primarily use the littoral in the winter. This observation suggests that size-segregated habitat use takes place in both lakes and may be a seasonal behavior in PG027. This would not be surprising given that large (migratory) charr leave the lake for most of the short summer season to feed at sea allowing the younger (small), non-migratory fish to access other habitats normally dominated by large fish (Byström *et al.* 2003). In PG027 in the fall, once the migrants have returned from sea, few small charr were caught in any habitat and large fish were observed congregating in shallow littoral areas which is likely a display of pre-spawning behavior (Johnson 1980*b*). The lack of smaller fish caught in PG027 in the fall suggests that young charr were likely driven into lower quality lake habitats by the migratory charr (such as the small deep lake pocket) or that they were possibly utilizing the river habitat during the open water season, as small and young charr are commonly thought to use riverine and littoral habitats (Johnson 1980*b*).

In Qinniqtuq, the littoral zone appears to be important habitat for feeding for all size classes of charr. This is no surprise given the littoral zone provides optimal habitat for juvenile charr and forage fish species as well as for aquatic invertebrates (Karlsson and Byström 2005). Low catch rates in pelagic habitats in both lakes is likely related to a lack of zooplankton feeding within both populations and suggests that this habitat type is the least important lacustrine habitat type for charr in these systems.

Although some of the habitat GLMs yielded statistically significant results (see Table 1.4), the resulting interpretation is not simplistic. Statistically significant results

suggest that there is a seasonal, ecological relationship between some biological variables (*fork length, sex and maturity*) and habitat variables (*lake zone, water temperature, depth and D.O*) in both systems. Multicollinearity (lack of independence among exploratory variables) is problematic in regression models (Montgomery and Peck 1992; Zuur *et al.* 2007). In aquatic habitats, linear relationships between habitat variables have been widely observed with the negatively correlated relationship between water temperature and D.O. as one of the most common examples (Wetzel 2001). Although the issue of multicollinearity of habitat variables was addressed in this research through conducting numerous univariate regression models as opposed to few multivariate regression models, the resulting significant terms of model outputs still come into question. For instance, individual models found statistically significant relationships between the biological variable *sex* and habitat variables *water temperature* and *D.O.* for anadromous fish in the fall. However, given the close linear relationship between these two habitat variables, one cannot say with any certainty which of the two habitat variables is the driving force influencing the distribution of male and female charr within those habitats or if they work in concert to influence sex distributions. Further, given the non-significant habitat variables regressed against *sex* (*lake zone* and *depth*), both of these variables are also closely linked with *water temperature* and *D.O.* and univariate analyses cannot take into account the confounding effects of all habitat variables to identify the “driving” variable(s) behind charr sex distribution in this system. Thus, interpretation of statistical significance of the model results is problematic in addressing the relationship between species-related biological variables and freshwater habitat variables of landlocked and anadromous charr populations in Cumberland Sound. Consequently, the overarching conclusion of these

analyses is simply the existence of seasonal relationships between biological variables related to charr and freshwater habitat variables in these two systems, with the driving force related to habitat variables not clearly defined from these analyses. Alternative statistical approaches to explore this question in future research include Principal Components Regression (PCR) to examine relationships between biological variables and habitat variables, as this is a restricted type of ordinary least squares (OLS) which reduces the confounding effects of multicollinearity in regression analyses (Zuur *et al.* 2007). Factor Analysis of Mixed Data (FAMD) is a method for consideration to extrapolate relationships between all variables, as this is a principal component method that allows for analysis of both qualitative and quantitative data (Feuillet *et al.* 2011).

Conclusion

In summary, this comparison of the lake ecology of these two differing populations of charr is a prime example of the extreme variability that exists within this species, and how their lacustrine environment influences this variability. Anadromous charr appear to use freshwater habitats differently than landlocked charr by depending on their lacustrine environment only for spawning and overwintering once they become migratory. Anadromous charr feed annually at sea; and there is no evidence of feeding occurring within freshwater post-migration. This research found no indication of freshwater seasonal habitat preference by anadromous fish. Anadromy appears to facilitate sexual maturation at a larger size and a younger age compared to charr that remain in freshwater for the entirety of their life cycle.

Unlike their anadromous counterparts, landlocked charr use their freshwater habitat for all aspects of their life cycle and as such, appear to use lake habitats more

opportunistically with feeding as an apparent selection influence. Landlocked charr appear to feed year round; adopting a cannibalistic feeding strategy in the winter when food resources are scarce and an opportunistic feeding strategy in the fall when a variety of prey items are readily available, which is common within many high Arctic charr populations (Svenning and Borgstrøm 2005). The littoral zone appears to be an important habitat for smaller fish in both systems, particularly Qinniqtuq. Although not clearly defined by this research, it is apparent that some kind of seasonal, ecological relationship exists between lake habitat variables and charr *fork length*, *sex* and *maturity* within both populations. Sexual asynchrony was observed in landlocked charr with an almost 2:1 sex ratio of males to females.

In closing, this research demonstrates the obvious differences that environment can play in shaping the biology, life history and lake ecology of a plastic species such as charr. Whether the life history is selected (e.g. anadromy) or dictated based on environment (e.g. landlocked), charr appear to exploit their environments advantageously in a climate that is highly variable with narrow windows of feeding opportunity. The life history variation of these two allopatric charr populations in the Canadian Arctic is indicative of the difficulty in generalizing the lake ecology of this species which may have consequences regarding population management as well as predicting the impacts of climate change on this species. Further research into describing the lake environments of charr populations with different life histories in the Canadian Arctic is required to better understand the extent of within-species variability and accompanying habitat needs of populations throughout its Northern range.

Chapter 3: Niche shift and life history variation in Arctic charr: the effects of diet and migration on the growth, condition and body morphology of two Arctic charr populations in Cumberland Sound, Nunavut.

Introduction

Diet and feeding ecology play an important role in an organism's growth and development throughout its life and may contribute to shaping an organism's life history. The dietary needs of animals expand during ontogeny (Laegdsgaard and Johnson 2001) and the quality and quantity of prey consumed will determine an animal's overall growth and fecundity potential. Often with dietary shifts there is a need or advantage for habitat shifts to coincide (Kimirei *et al.* 2013). Ontogenetic niche shifts (e.g., changes in feeding, habitat use, morphology, etc.) are extremely common in species with variable life histories (Werner and Gilliam 1984; Fryxell and Sinclair 1988; Post 2003; Kimirei *et al.* 2013). These shifts are related to behavioral or morphological changes during ontogeny, are often correlated with discrete growth periods in the life history (Werner and Gilliam 1984) and may be dramatic or subtle (Werner and Gilliam 1984). Examples of dramatic habitat shifts are metamorphosis in amphibians and holometabolous insects. Examples of less dramatic habitat shifts include diet shifts in fishes, where species progress from carnivore to herbivore or vice versa (Werner and Gilliam 1984; Olson 1996).

It is theorized that organisms select foraging strategies that optimize individual fitness (Pyke 1984). As fish grow their ability to access certain habitats and prey change and may result in clear distinct prey and habitat shifts. Larger fish are able to consume larger prey (Karachle and Stergiou 2012) and access different habitats which often optimize their energy gains (Werner and Gilliam 1984). For instance, the

piscivorous largemouth bass (*Micropterus salmoides*) will undergo 3-4 marked ontogenetic shifts in diet as it grows to optimize its energetic return (Olson 1996). These ontogenetic shifts in habitat and prey may be finite and non-reversible where individuals move through stages throughout their life cycle.

In contrast to strict niche shifts with ontogenetic change, some species of fish have adapted habitat and prey expansion with growth e.g., seasonal resource shifts with growth. As fish grow larger they are able to access new habitats and new prey, while still using their original habitat and/or prey (Gulseth and Nilssen 1999). This is a common trait found in fish that live in extreme environments like the Arctic. Habitats and resources within the Arctic are only available for specific, short periods of time and many Arctic fish species have evolved to take advantage of their availability at some point during their lifecycle (Brannon 1981; Miller and Brannon 1981). For example many Arctic salmonids have been documented undertaking seasonal migrations from freshwater to saltwater for feeding in summer months (anadromy). Such ontogenetic shifts in diet provide high energetic return allowing the individual to optimize growth attaining a larger size; potentially reducing the risk of predation and increasing fitness (Hendry and Stearns 2004).

In low-diversity Arctic lakes, feeding strategies of fishes are commonly focused on exploitation of a singular resource such as benthos, zooplankton or fish. Given that changes in prey are commonly associated with changes in habitat (Werner and Gilliam 1984), niche shifts throughout ontogeny are commonly observed in high-latitude freshwater fishes for the purpose of maximizing fitness (Eloranta *et al.* 2010). A common example of prey shift in freshwater fishes includes a general shift in main prey type (e.g. shift from an invertebrate-based to piscivory) (Werner & Gilliam 1984).

Within Arctic fish populations that have evolved some sort of ontogenetic shift in feeding, not all individuals in the population necessarily make the same shift resulting in ecotype polymorphism. Ecotype polymorphism has been documented in some high-latitude salmonids, which is the occurrence of intraspecific morphs or ecophenotypes within a single lacustrine system who use different niches (e.g., planktivores, benthivores, piscivores, etc.). This phenomenon is ubiquitous in the Salmonidae literature, with some of the most noted examples of resource polymorphism documented in lake trout (Chavarie *et al.* 2016) and charr (Johnson 1980*b*; Riget *et al.* 1986; Jónasson *et al.* 1998; Klemetsen *et al.* 2003; Amundsen *et al.* 2008). It is not uncommon to observe some populations having multiple life histories existing allopatrically or sympatrically, including anadromous, partially anadromous and resident populations (Hendry and Stearns 2004). Of these life histories, anadromy has the most marked effect on overall growth and fecundity given the benefits attained with a shift from freshwater feeding to a seasonal marine-based diet (Chapman *et al.* 2012). The productivity offered by the ocean in temperate and northern climates far exceeds that of freshwater, thus oceanic feeding enables higher growth rates, larger size at age, and greater energy stores in anadromous salmonids (Gross 1987; Hendry and Stearns 2004). A study on anadromous charr from the Dieset watercourse in Svalbard found that charr more than doubled their body weight with marine feeding (Gulseth and Nilssen 2001). Size differences between migratory and non-migratory life history types are ubiquitous in the literature, where comparisons of size at age data have shown that searun fish grow faster than lake-resident fish (Johnson, 1980; Jonsson and Jonsson 1993; Kristoffersen *et al.* 1994; Rikardsen *et al.* 2000); with freshwater resident fish remaining smaller with lower overall growth rates (Chapman *et al.* 2012).

Charr are an ideal species to examine ecological and dietary-morphological differences between migratory and non-migratory populations for a multitude of reasons. The charr is renowned for its evolution of not only multiple life histories throughout its circumpolar range (anadromous, semi-anadromous, lake resident and landlocked) but also multiple phenotypes (Jonsson and Jonsson 2001). Charr are renowned for their plasticity (Johnson 1980*b*) with various examples of polymorphism in populations throughout their circumpolar range (Jónasson *et al.* 1998). Resident ecotypes are documented having lower growth rates and attaining maturity at a younger age and smaller size than their anadromous cohorts (Loewen 2008, Reist *et al.* 2012). Morphological variation has been documented between sympatric life history types, with difference in diet as the proposed underlying cause (Loewen *et al.* 2009).

Charr populations have been shown to differ morphologically within and between systems throughout their range with most studies in the literature focusing on European populations (e.g., Henricson and Nyman 1976; Klemetsen and Grotnes 1980; Hindar and Jonsson 1982; Snorrason *et al.* 1994; Pavlov 1997; Jonsson and Jonsson 2001; Klemetsen *et al.* 2003; Klemetsen 2010). There is little research looking into the diet, growth and morphological characteristics of charr populations in the Canadian high Arctic (Moore and Moore 1974; Johnson 1980*b*; Reist *et al.* 1995; Loewen *et al.* 2009; Imrie 2012), and to my knowledge there is no research comparing the growth, morphological traits and diets of charr between different life history populations (anadromous versus land locked). In this chapter I attempt to address this knowledge gap by examining the differences in growth, condition and body morphology between two populations of charr with differing life histories in Nunavut, Canada (anadromous and landlocked), while factoring the role of ontogenetic shifts in diet. My objectives

were to: (i) Determine if growth, seasonal condition and morphology differ between the two populations/life histories; and (ii) Determine if any differences in growth, condition and morphology can be associated with ontogenetic diet/niche shifts. I hypothesized that growth and seasonal condition would differ between the populations and that morphology would differ both within and between the populations. I expected that differences in growth, seasonal condition and between-population morphological variation could be associated with differences in diet; and within-population morphological variation could be associated with ontogenetic diet shifts.

Materials and Methods

Information on the study site, field collection and laboratory methods are provided in Chapter 2.

Fish Sampling

Morphology

Fish were sampled for morphological measurements adapted from Loewen (2008), Cadrin (2005) and Reist *et al.* (1995). Measurements were made from the left side of each fish to the nearest 0.01mm with digital calipers and included: snout length; eye diameter; upper jaw length; pectoral fin length; pelvic fin length; body depth; caudal peduncle width; fork length (F_L); standard length (S_L); and fork depth (Figure 1.9). Fork depth was calculated by subtracting fork length from standard length. This group of morphological characters has been used in previous charr studies to discriminate

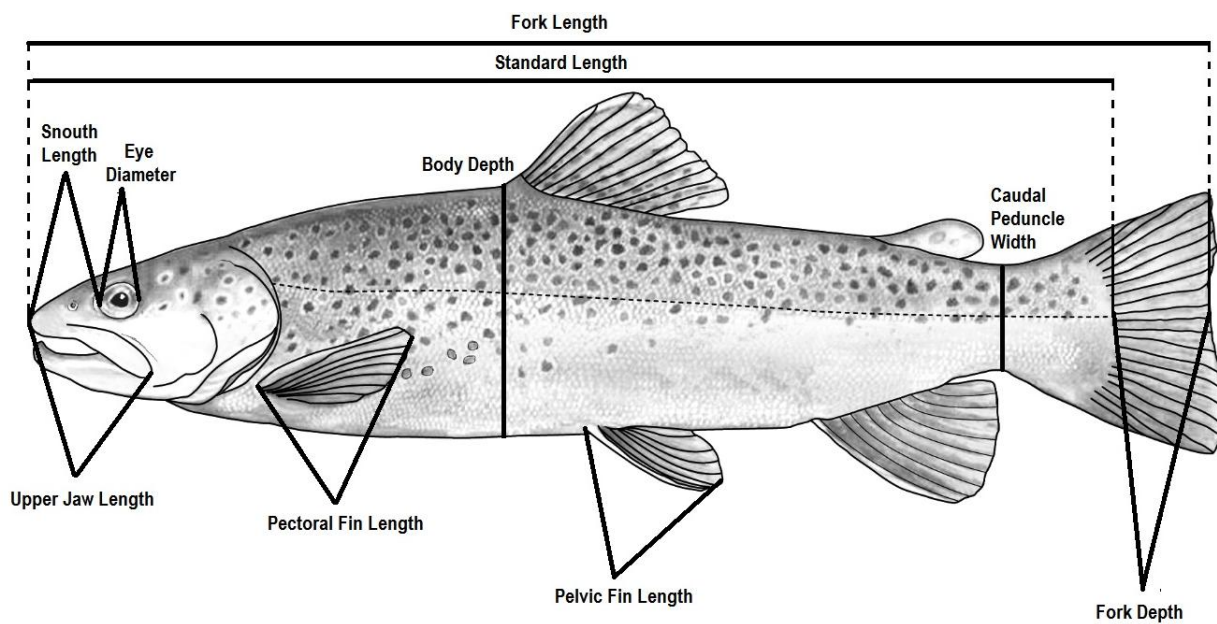


Figure 1.9. Morphological characteristics measured: snout length; eye diameter; upper jaw length; pectoral fin length; pelvic fin length; body depth; caudal peduncle width; fork length (F_L); standard length (S_L); and fork depth (diagram courtesy of the Government of Nunavut).

between phenotypic groups with multi- and univariate analyses (Reist *et al.* 1995; Adams and Huntingford 2002; Alekseyev *et al.* 2002; Kristofferson 2002; Loewen 2008).

Data Analyses

Growth

Growth curves and growth comparisons between populations based on length at age data were calculated with the non-linear Gompertz growth model using the FSA() package and GompertzFuns() function in R (see Appendix 1.7; Ogle 2016). The model equation was:

$$2.0) \quad E(L_t) = L_{\infty} e^{-e^{-g_i(t-t_i)}}$$

where L_{∞} is the mean asymptotic length, t_i is the age at the inflection point and g_i is the instantaneous growth rate at the inflection point (Ogle *et al.* 2017). Differences in parameters from the Gompertz model between populations were assessed by fitting a family of models where each parameter, two parameters, one parameter, or no parameters differed between populations (Ogle 2016; Ogle *et al.* 2017). The most parsimonious significant model from this family of models was then selected through the sequential application of extra sums-of-squares tests (Ogle 2016; Ogle *et al.* 2017).

Condition

Length-weight relationships were assessed as a measure of condition within and between the populations using the lm() and anova() functions in R (see Appendix 1.8; Ogle 2016). Sexes were pooled for analysis and somatic weight (round weight - gonad

weight) was used to avoid seasonal, spawning-related weight bias caused by differences in maturity stage. A GLM with continuous and dichotomous (dummy) predictors was used to assess condition within and between the populations by season.

The initial linear model was:

$$2.1) \quad Y_i = \beta_0 + \beta_1 x_{i1} + \beta_2 x_{i2} + \beta_3 x_{i3} + \beta_4 (x_{i1} * x_{i2}) + \beta_5 (x_{i2} * x_{i3}) + \beta_6 (x_{i1} * x_{i2} * x_{i3}) + \xi_i$$

where $Y_i = \log(\text{somatic weight})$, $x_{i1} = \log(\text{fork length})$, $x_{i2} = \text{form}$ (anadromous/landlocked), $x_{i3} = \text{season}$ (fall/winter) and $\xi_i = \text{normally distributed error}$ (Quinn and Keough 2002). Following an extra sum of squares test on the full model, the model was then re-fit using only significant terms. The final model was:

$$2.2) \quad Y_i = \beta_0 + \beta_1 x_{i1} + \beta_2 x_{i2} + \beta_3 x_{i3} + \beta_4 (x_{i2} * x_{i3}) + \xi_i$$

where $Y_i = (\log)\text{somatic weight}$, $x_{i1} = (\log)\text{fork length}$, $x_{i2} = \text{form}$ (anadromous/landlocked), $x_{i3} = \text{season}$ (Fall/winter) and $\xi_i = \text{normally distributed error}$ (Quinn and Keough 2002). Because the final model indicated that the slope of the $\log(\text{somatic weight}) - \log(\text{fork length})$ relationship did not differ among any groups, the intercepts could be compared to determine if the mean $\log(\text{somatic weight})$ while holding $\log(\text{fork length})$ constant differed among groups. Therefore, a group with a significantly larger intercept weighed more at a given length and was, thus, in better “condition” than the comparison group. Intercepts from this model were compared using Tukey-adjusted p -values using the `FSA()` package and `compIntercepts()` function in R (Ogle 2016).

Morphometrics

Morphometric data was analyzed using Factor Analysis (FA) (Loewen 2008). FA is a similar technique to Principle Component Analysis (PCA) but operates on the reduced covariance matrix (Field *et al.* 2012; Everitt 2007). FA derives a mathematical model from which factors are estimated, whereas PCA simply reduces the original data into a set of linear variates. FA estimates the underlying factors where PCA is only concerned with establishing which linear components exist within the data and how a particular variable might contribute to that component (Field *et al.* 2012). Unlike PCA, FA does not account for all observed variance; rather, it accounts for variance that is shared through common factors (Loewen 2008; Everitt 2007). FA was chosen over PCA because it has a specific statistical model associated with its functional use; has a formal hypothesis testing procedure for the number of factors used within the model; and uses a maximum likelihood approach to calculate factor scores (Loewen 2008; Crawley 2007; Field *et al.* 2012).

In performing FA, once factors have been extracted it is necessary to calculate the loading of the variable on each factor; and for this a factor rotation was used to discriminate between factors. Orthogonal rotation was chosen as it keeps factors independent during rotation. Of the four methods of orthogonal rotation (varimax, quartimax, BentlerQ and geominQ), varimax was chosen as it attempts to maximize the dispersions of loadings within factors, resulting in more interpretable clusters of factors (Field *et al.* 2012).

FA was performed on both populations to identify morphological differences within and between the anadromous and landlocked charr populations. Since most size standardizing techniques are considered statistically problematic due to their inability to

remove size from shape analysis (Rohlf 1990; Freckleton 2002; Jensen 2003; Parsons *et al.* 2003), comparisons between populations were only made between fish of like sizes (Loewen 2008). Any fish from PG027 longer than 525 mm were not included in this analysis as the largest charr caught in Qinniqtuq was 507mm. Sexes were pooled for all analyses.

To account for size within the shape analysis, standard length was included in the analysis. The stats library package in R was used for the FA and FA rotation, specifically the `factanal()` and `rotation()` functions (see Appendix 1.9; Everitt 2007; Field *et al.* 2012). An orthogonal (varimax) rotation was applied to the principal factor scores. Factors loaded highest on either score 1 or 2; therefore only two factors were maintained in the FA. The factor which loaded highly on standard length (>0.700) was considered to be size-related and not used for further analysis. The remaining factor was then assumed to be representative of variation in body morphology unrelated to size. For FA performed between populations, univariate analyses were performed using the `lm()` function in R on the morphological traits loading highly on the factor retained for analysis. The linear univariate model was:

$$2.3) \quad Y_i = \beta_0 + \beta_1 x_{i1} + \beta_2 x_{i2} + \beta_3 (x_{i1} * x_{i2}) + \xi_i$$

where Y_i = morphological character, x_{i1} = standard length, x_{i2} = form (anadromous/landlocked), $x_{i3} = (x_{i1} * x_{i2})$, and ξ_i = normally distributed error (see Appendix 1.10; Quinn and Keough 2002). A Bonferroni correction was applied to univariate statistics so as to avoid a type 1 statistical error. The Bonferroni correction factor for the univariate analysis was 4; this is based on the number of morphological

traits that were identified in the FA as not related to body size making the Bonferroni corrected level of significance $p < 0.01$.

For FA performed within populations, all fish were used in the Qinniqtuq FA and only fish $\leq 525\text{mm}$ were utilized in the PG027 FA. FA plots were visually examined for evidence of morphologically unique groups within each population by overlaying individual ages of fish on the FA plot to identify patterns (clusters) that may be indicative of discrete groups. Multiple Discriminant Analysis (MDA) was then performed when more than two groups were identified by the FA to further discriminate between morphological groups within each system using the `lda()` function from the MASS package in R (See Appendix 1.11; Field *et al.* 2012). MDA is a method of linear modeling which discriminates between *a priori* defined groups (Zuur *et al.* 2007) and is similar to multivariate analysis of variance (MANOVA), with the difference being that MDA aims to maximally distinguish natural groups of individuals. It is a canonical method which tests for differences in the explanatory variables among the predefined groups and then finds linear combinations (discriminant functions) of the explanatory variables that best discriminate among the groups while minimizing the variation within each group (Legendre and Legendre 1998).

Length at age was examined for each of the three morphologically distinct size classes of landlocked charr using simple linear regression models. For each size class, the linear univariate model was:

$$2.4) \quad Y_i = \beta_0 + \beta_1 x_{i1} + \xi_i$$

where Y_i = fork length, x_{i1} = age, and ξ_i = normally distributed error (Quinn and Keough 2002).

Diet

Diet analysis was only conducted on landlocked charr given that of the two populations examined, they were the only population found to have stomachs containing food items. Percent composition of functional prey categories (fish or invertebrates) was calculated as the number of stomachs containing a single functional category of prey.

A simple linear regression model was used to examine prey choice as a function of body size using the `lm()` function in R (see Appendix 1.12). Prey length was modeled against charr fork length to examine if prey size increases with fish length. Following model equation 2.4, prey as a function of body size was modeled where Y_i = fork length, x_{i1} = prey length and ξ_i = normally distributed error (Quinn and Keough 2002).

A logistic regression model was used to predict length at which landlocked charr switch from an invertebrate-based diet to a fish-based diet using the `glm()` function in R (see Appendix 1.13). Given that only one fish had stomach contents containing both fish and invertebrates, any charr with fish in its stomach was considered piscivorous. Logistic regression was estimated by a binomial GLM using the logit link with the `glm()` function in R (R Core Development Team 2017). The model equation was:

$$2.5) \quad \text{logit}(\pi) = \log\left(\frac{\pi}{1-\pi}\right) = \beta_0 + \beta_1 x_{i1}$$

where X_{i1} = fork length and π = the probability of piscivory (Quinn and Keough 2002).

Length at piscivory predictions from the logistic regression model were overlain on the MDA plot to examine the extent of the overlap of piscivory by size class of landlocked charr. Percent stomach content was graphically examined in relation to class size and season.

Results

Growth

Overall growth between the two populations varied over the lifespan (Figure 1.10). The most parsimonious significant growth model showed that the L_{∞} and g_i parameters but not the t_i parameter differed among populations ($p=0.00008573$). Note that the wide confidence intervals for the landlocked population indicate that the model is poorly estimated for landlocked charr (Table 1.5).

Condition

The $\log(\text{somatic weight})$ and $\log(\text{fork length})$ were significantly related ($p < 0.05$), but the $\log(\text{somatic weight})$ - $\log(\text{fork length})$ relationship did not differ among any groups (all difference in slope $p > 0.05$). Because slope did not differ among groups, differences in intercepts could be used as a proxy for condition e.g., comparison of mean $\log(\text{somatic weight})$ among groups at a constant value of $\log(\text{fork length})$. Model results are presented in Table 1.6 and Figure 1.11. Statistically significant differences in intercepts were found between Form and Season combinations, indicating differences in condition due to form (anadromous/landlocked) and season. Statistical comparison

of intercepts indicated no statistical difference between intercepts for landlocked fish in the fall and winter ($p=0.9755$). However, a statistically significant relationship was found between anadromous charr in the fall and winter ($p<0.05$), with charr in the fall having a higher intercept. A statistically significant difference was found between intercepts of anadromous charr in the fall and landlocked charr in the fall ($p=0.05$) and winter ($p=0.05$), with the anadromous fish having a higher intercept. A statistically significant difference was found between intercepts of anadromous charr in the winter and landlocked fish in the fall ($p=0.0418$) and winter ($p=0.04561$), with the anadromous fish having a higher intercept. These data show that anadromous charr have an overall higher intercept in the fall than all other groups.

Morphometrics

Between Populations

Between-population comparison of morphological traits identified four morphological characteristics that were independent of body size. Uniqueness scores represent the variability in x_i of the FA which is not shared with other variables (Everitt 2007). Morphological traits identified to be ecologically significant by the FA were pectoral fin length, pelvic fin length, snout length and upper jaw length (Table 1.7). Univariate analysis showed statistically significant differences between anadromous and landlocked charr in all of the abovementioned morphological traits (Table 1.8; Figure 1.12). Landlocked charr were found to have relatively longer pectoral and pelvic fins and longer snout and upper jaw lengths than anadromous charr.

Table 1.5. Gompertz model parameters and associated confidence intervals for anadromous (n=409) and landlocked (n=69) charr. L_{∞} is expressed as length in mm and t_i is expressed as age in years.

	Anadromous	Landlocked
L_{∞}	678.93 (652.19-712.06)	503.66 (434.87-692.46)
g_i	0.37 (0.30-0.44)	0.13 (0.07-0.19)
t_i	5.34 (5.0-5.63)	5.70 (4.42-8.98)

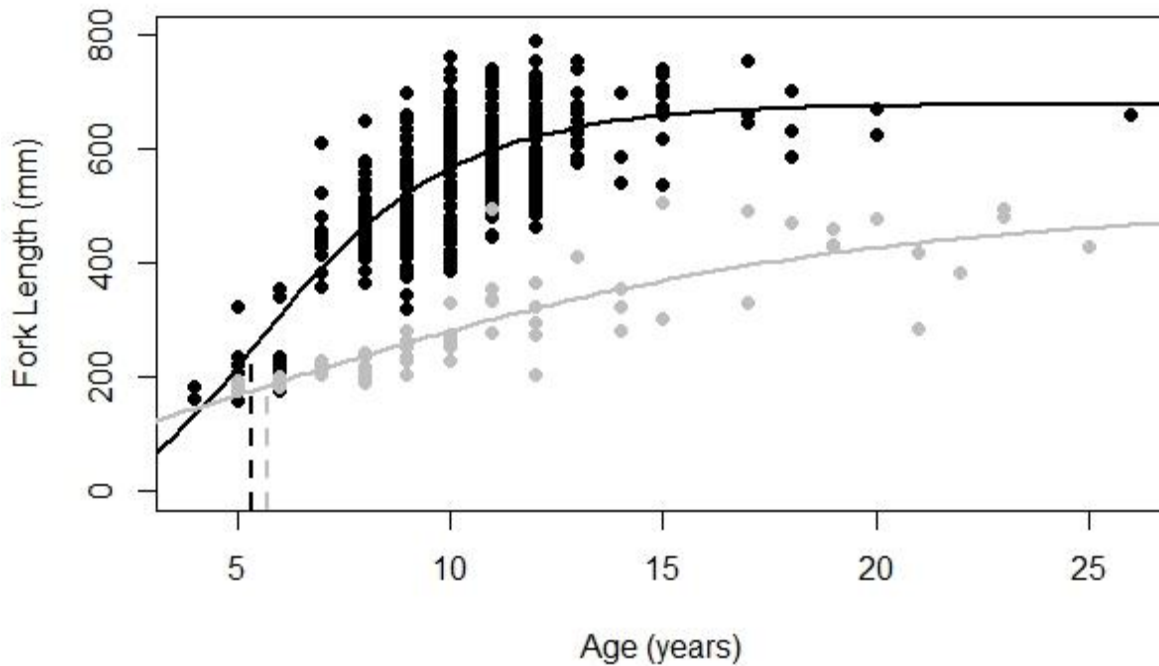


Figure 1.10. Plot of the Gompertz growth curves for anadromous (black) and landlocked charr (grey). Vertical dotted lines represent estimated inflection points in the growth curves for anadromous charr (5.34 years) and landlocked charr (5.70 years).

Table 1.6. Table of coefficients and confidence intervals for linear regression of seasonal condition for anadromous (n=409) and landlocked charr (n=69).

	Coefficients	CI - 2.5%	CI - 97.5%
Intercept	-11.773	-12.131	-11.414
log(Fork Length)	3.039	2.982	3.096
FormLandlocked	-0.174	-0.243	-0.106
SeasonWinter	-0.099	-0.132	-0.067
FormLandlocked:SeasonWinter	-0.083	-0.005	0.170

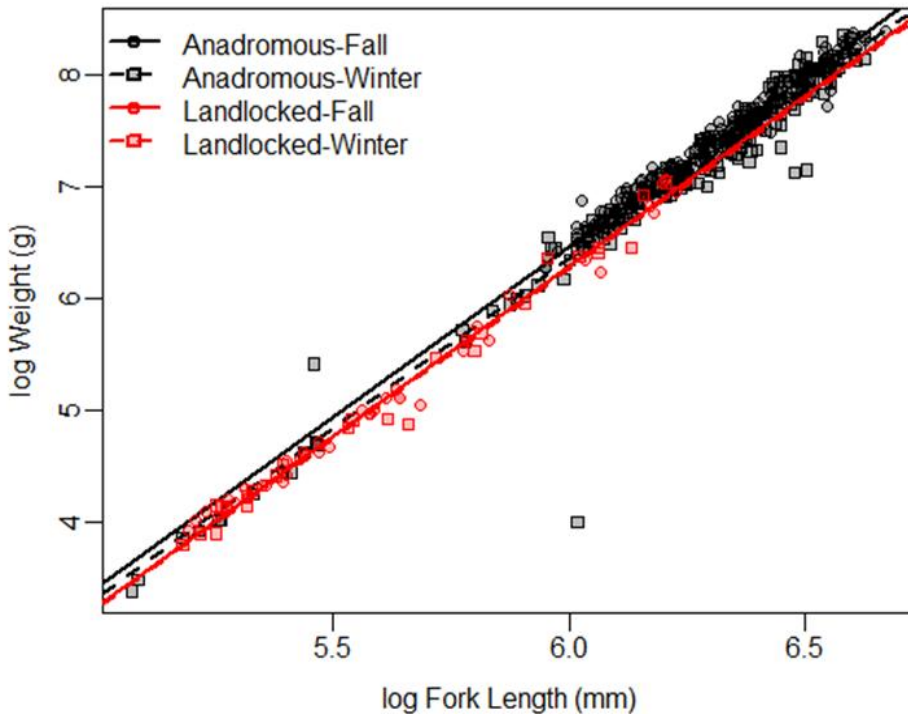


Figure 1.11. The linear regression model fit for weight-length relationship as a matter of condition for anadromous charr in the fall (solid black line, black circles) and winter (dashed black line, black squares), and landlocked charr in the fall (solid red line, red circles) and winter (dashed red line, red squares).

Within Populations

Individual lengths and ages of fish were examined on the FA plot to aid in delineating groups with differing morphology with discrete length and age ranges. In PG027, two distinct groups were identified by this process. The closed circles denote the first group (*Small*), comprised of charr measuring 160mm-237mm and aged 4-6 years. The open circles denote the second group (*Large*), comprised of charr measuring 322mm-790mm and aged 7-26 years (Figure 1.13). Morphological traits identified to be different were pectoral fin length; pelvic fin length; snout length; and upper jaw length (Table 1.9).

In Qinniqtuq, three groups were identified by examination of FA plots by overlaying lengths, ages and stomach contents of individual fish and groups were delineated based on patterns of length and age classes identified within clusters of the FA plots. Stomach contents of individual fish were subsequently overlain on the FA plot to aid in determining the diet of each size class.

Triangles denote the first size grouping (*Small*), comprised of charr measuring 178mm-264mm and aged 5-12 years. Closed circles denote the second size grouping (*Medium*), comprised of charr measuring 253mm-368mm and aged 9-21 years. Open circles denote the third size grouping (*Large*), comprised of charr measuring 385mm-507mm and aged 11-25 years (Figure 1.14). Morphological traits identified by the FA as different were fork depth, pectoral fin length; pelvic fin length; snout length; and upper jaw length (Table 1.10).

The discriminant analysis of the morphological traits for the landlocked population defined two discriminant functions. The first explained 96.6% of the variance, whereas the second explained only 3.4% of the variance. The discriminant

Table 1.7. FA and uniqueness scores for anadromous (n=409) and landlocked (n=69) charr. Morphological scores that loaded high (>0.700) on factor 1 scores are highlighted and considered to be ecologically significant.

Morphological Characteristic	Factor 1	Factor 2	Uniqueness
Body Depth	0.551	0.799	0.057
Caudle Peduncle Width	0.574	0.794	0.040
Eye Diameter	0.646	0.479	0.354
Fork Depth	0.657	0.656	0.138
Pectoral Fin Length	0.768	0.616	0.030
Pelvic Fin Length	0.769	0.607	0.040
Snout Length	0.710	0.652	0.072
Standard Length	0.625	0.760	0.032
Upper Jaw Length	0.790	0.592	0.025

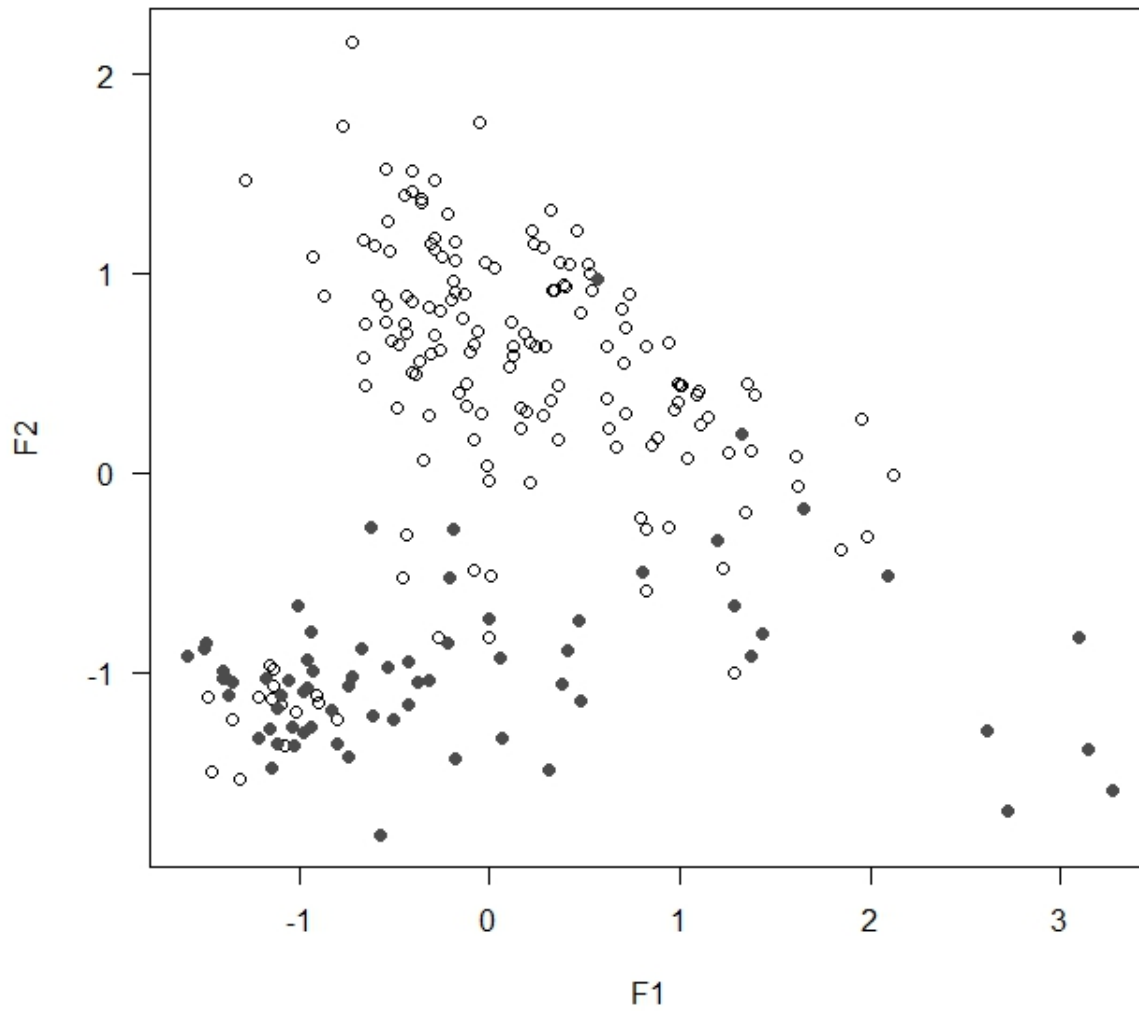


Figure 1.12. FA plot of factor scores for morphological characteristics of anadromous and landlocked charr. Open circles represent anadromous charr and closed circles represent landlocked charr

Table 1.8. Univariate statistical analysis of anadromous (n=409) and landlocked charr (n=69). Morphological scores that loaded high (>0.700) on factor 1 scores are considered to be ecologically significant. The star symbol denotes the Bonferroni corrected level of significance at $p < 0.01$.

Morphological Characteristic	Model Coefficients	Estimate	Std. Error	t-value	p-value
Pectoral Fin Length	Intercept	-3.472	1.945	-1.785	<0.01*
	S. Length	0.151	0.005	32.040	<0.01*
	Form	-3.623	2.642	-1.371	0.172
	St. Length:Form	0.028	0.008	3.603	<0.01*
Pelvic Fin Length	Intercept	-3.066	1.723	-1.780	<0.01*
	S. Length	0.120	0.004	28.906	<0.01*
	Form	-4.173	2.325	-1.795	<0.01*
	St. Length:Form	0.024	0.007	3.527	<0.01*
Snout Length	Intercept	-6.036	1.484	-4.068	<0.01*
	S. Length	0.118	0.004	32.821	<0.01*
	Form	-6.409	2.002	-3.201	<0.01*
	St. Length:Form	0.035	0.006	5.975	<0.01*
Upper Jaw Length	Intercept	-2.943	1.093	-2.692	<0.01*
	S. Length	0.071	0.003	26.738	<0.01*
	Form	-3.275	1.476	-2.219	<0.01*
	St. Length:Form	0.012	0.004	2.719	<0.01*

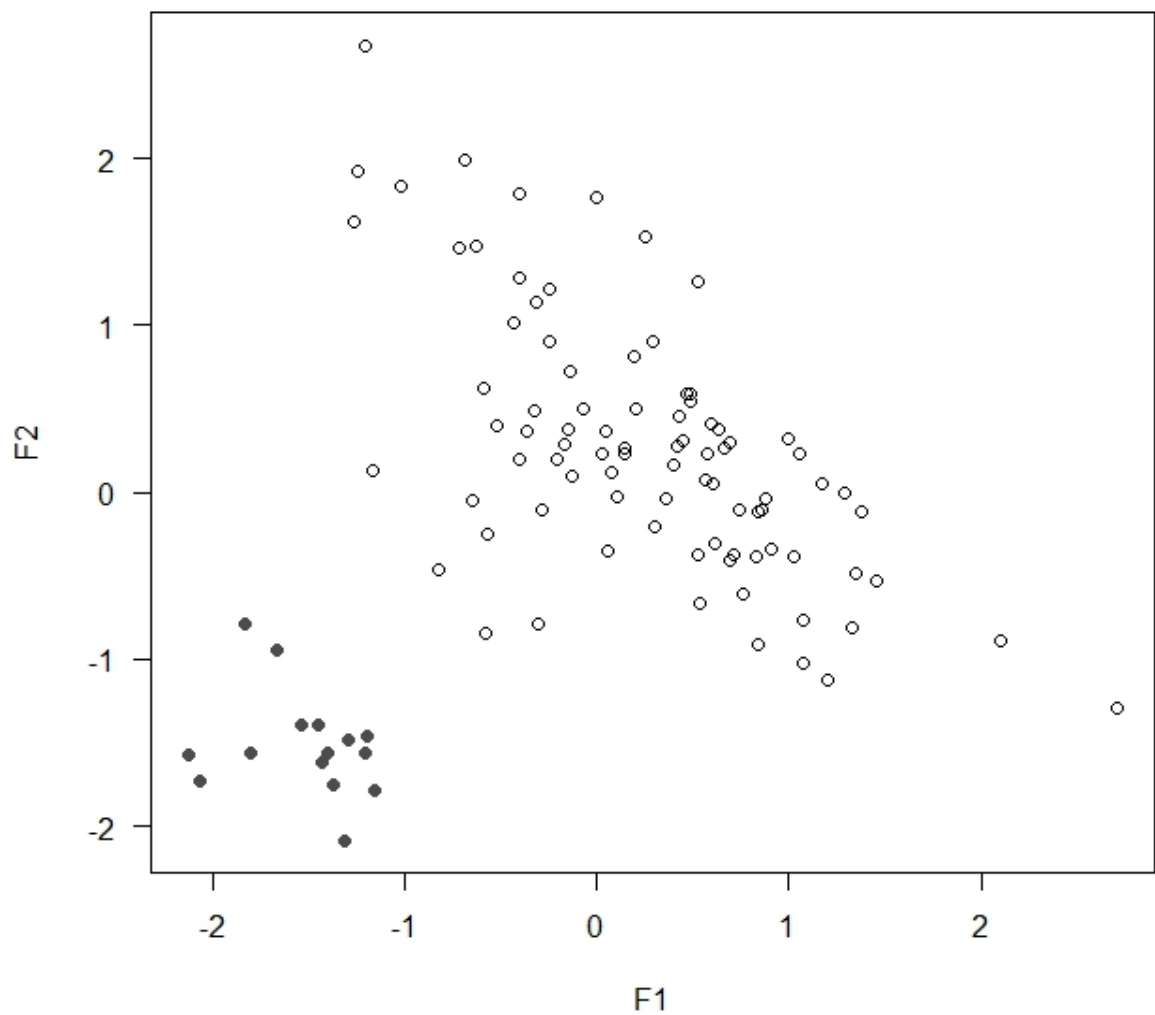


Figure 1.13. FA plot of factor scores for morphological characteristics of anadromous charr. Size classes of charr were determined by length-age categories. Closed circles represent *Small* charr and open circles represent *Large* charr.

Table 1.9. FA and uniqueness scores for anadromous charr (n=409). Morphological scores that loaded highly (>0.700) on factor 2 scores are highlighted and considered to be ecologically significant.

Morphological Characteristic	Factor 1	Factor 2	Uniqueness
Body Depth	0.708	0.641	0.089
Caudle Peduncle Width	0.784	0.580	0.049
Eye Diameter	0.751	0.479	0.207
Fork Depth	0.740	0.563	0.136
Pectoral Fin Length	0.639	0.720	0.073
Pelvic Fin Length	0.632	0.722	0.079
Snout Length	0.642	0.722	0.066
Standard Length	0.711	0.666	0.051
Upper Jaw Length	0.535	0.842	0.005

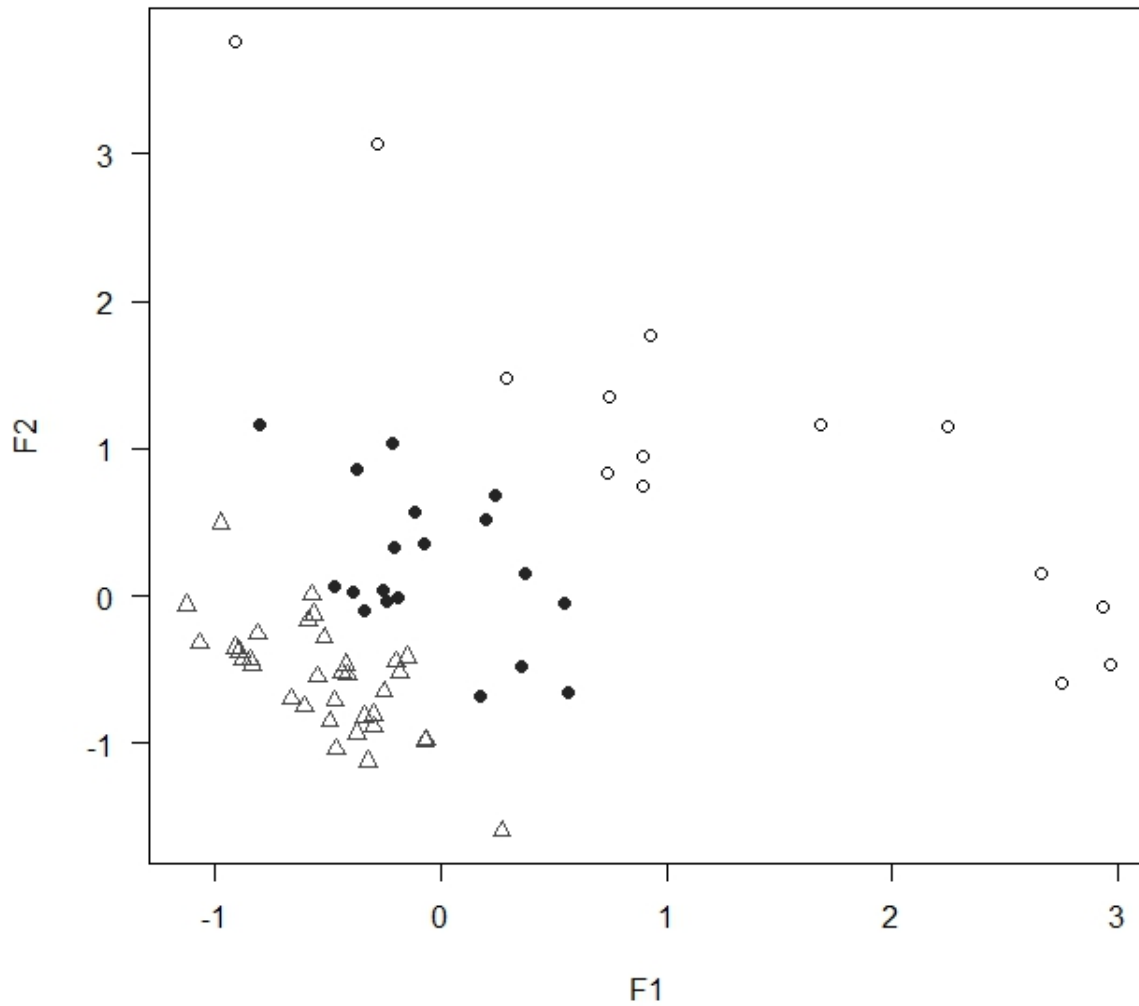


Figure 1.14. FA plot of factor scores for landlocked charr. Triangles denote Small charr, closed circles denote Medium charr and open circles denote Large charr.

Table 1.10. FA and uniqueness scores for landlocked charr (n=69). Morphological scores that loaded high (>0.700) on factor 1 scores are highlighted and considered to be ecologically significant.

Morphological Characteristic	Factor 1	Factor 2	Uniqueness
Body Depth	0.595	0.774	0.046
Caudle Peduncle Width	0.632	0.756	0.029
Eye Diameter	0.644	0.596	0.230
Fork Depth	0.799	0.568	0.039
Pectoral Fin Length	0.748	0.648	0.020
Pelvic Fin Length	0.750	0.638	0.030
Snout Length	0.748	0.643	0.027
Standard Length	0.677	0.728	0.012
Upper Jaw Length	0.786	0.614	0.005

function plot showed that the first function discriminated all size classes and coefficients of the discriminant functions are displayed (Appendix 1.14)

Length-age regressions for each size class are displayed in Figure 1.15. A statistically significant relationship was found between length and age for *Small* charr (slope = 0.0478, intercept = -2.946, SE = 0.0103, $p = <0.05$, $R^2 = 0.419$). No statistically significant relationship was found for length and age of *Medium* charr (slope = 0.0150, intercept = 7.590, SE = 0.0199, $p = 0.461$, $R^2 = 0.0325$) or *Large* charr (slope = -0.0241, intercept = 30.009, SE = 0.0328, $p = 0.4796$, $R^2 = 0.0512$).

Diet

To examine prey size as a function of body length, the linear regression model indicates that the log(length) of prey increased with the log(length) of charr (slope=3.8213, intercept=-19.3901 SE=0.6518, $p<0.05$, $R^2 = 0.5266$, Figure 1.16).

The logistic regression model predicted that 50% (LP50) of landlocked charr were piscivorous by 322mm (Figure 1.17). Piscivory predictions for individual fish were overlain in the MDA plot of morphological characters to examine the extent of the overlap of piscivorous feeding (Figure 1.18).

Seasonal stomach contents of the three size classes of charr were divided into functional groups ("fish" and "invertebrates") and displayed in Figure 1.19. Invertebrates comprised the main prey in both fall and winter for *Small* charr (93% and 67%, respectively); whereas for *Medium* and *Large* size classes, equal proportions of fish and invertebrates were found in stomachs in the fall but fish were the only prey item in stomachs in the winter for these two size classes.

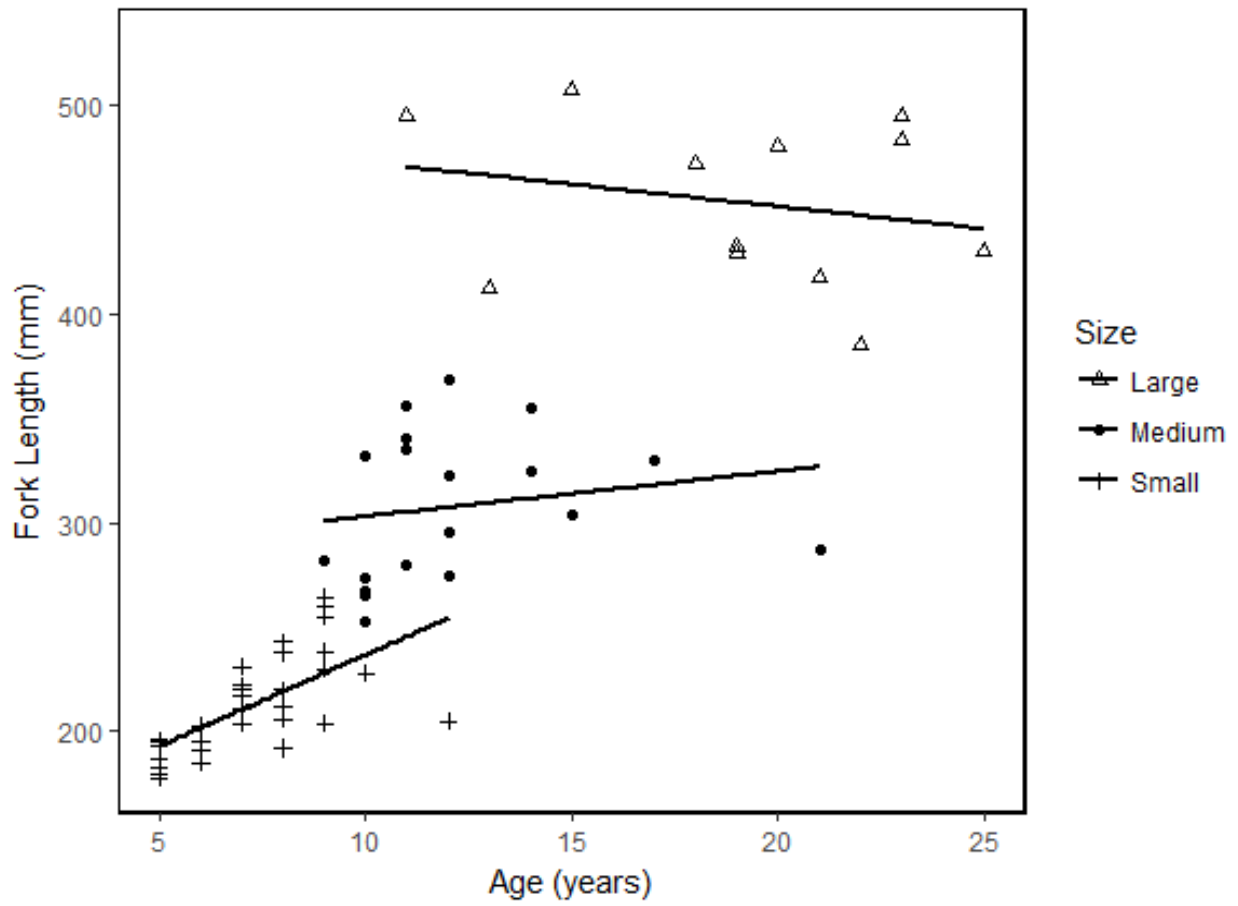


Figure 1.15. Length-age relationships for morphologically distinct size classes of landlocked charr (*Small, Medium and Large*).

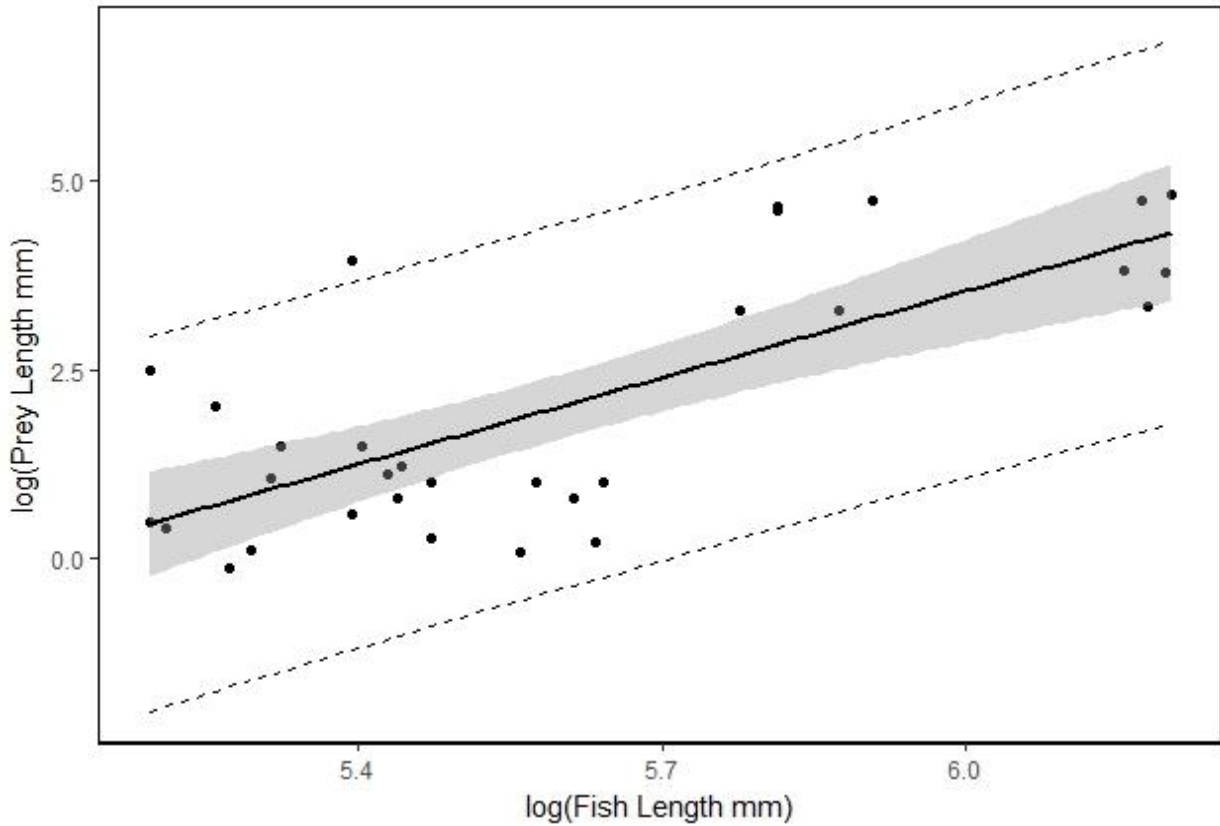


Figure 1.16. The linear regression model fit for prey as a function of body size for landlocked charr (black circles) with associated confidence intervals (black dashed lines) standard error (grey shaded area).

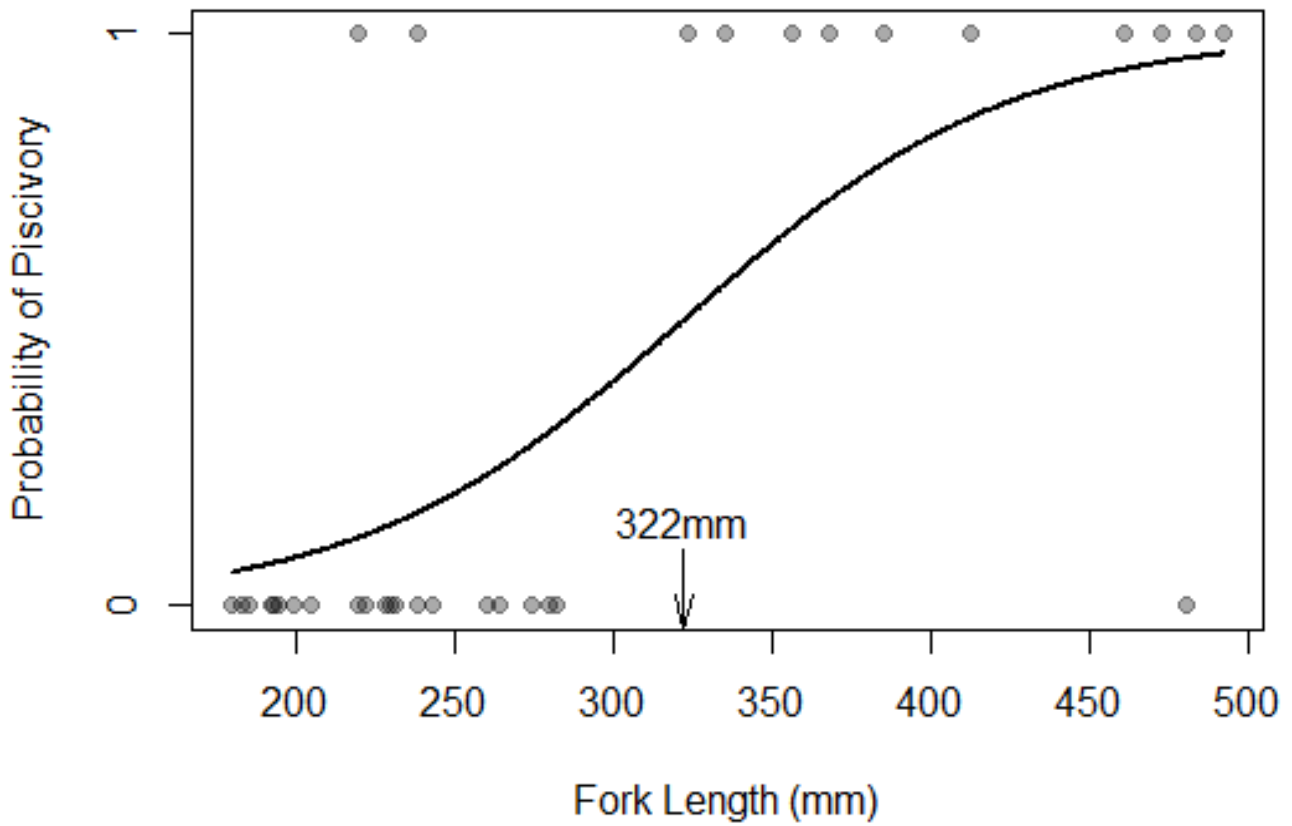


Figure 1.17. The logistic regression fit for probability of piscivory based on fork length of landlocked charr. Length at piscivory was predicted to be 322mm.

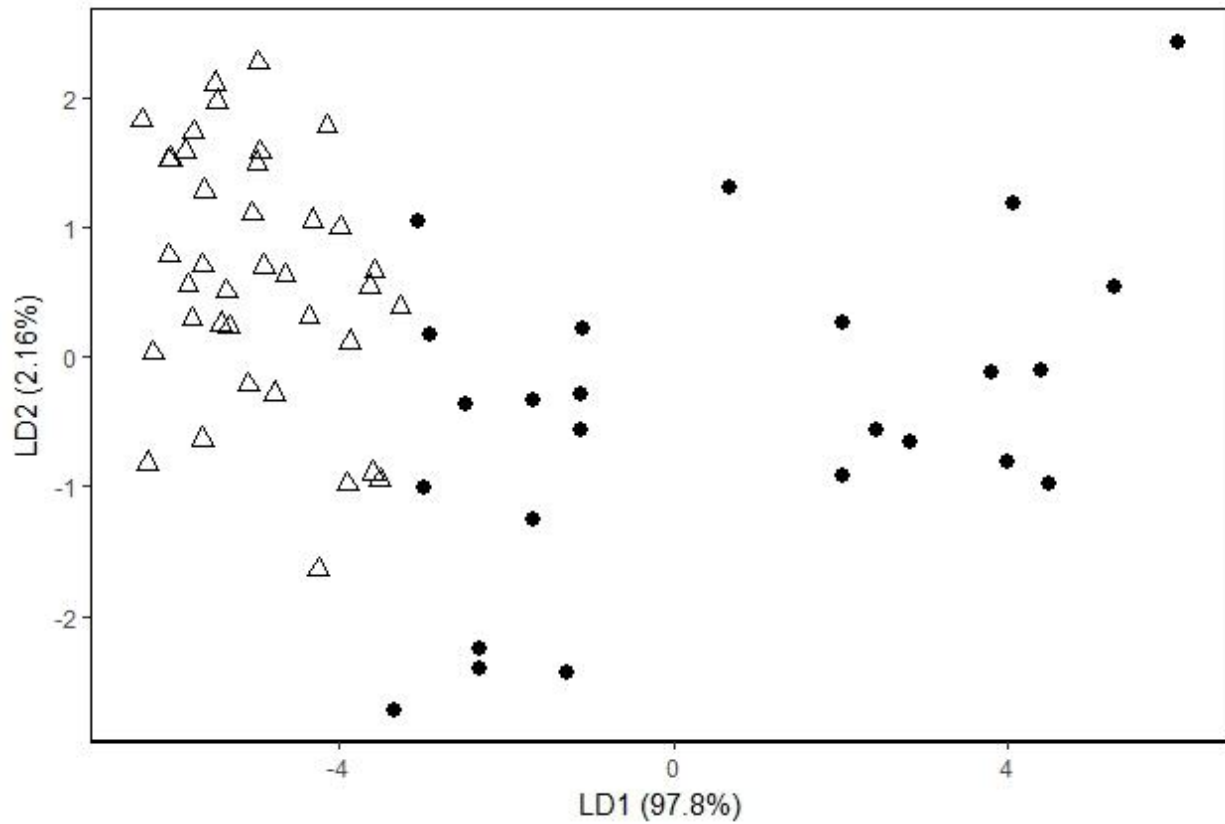


Figure 1.18. Plot of MDA scores for size classes of landlocked charr with logistic regression predictions of probability of piscivory. Triangles represent charr that are “Not Piscivorous” and circles denote “Piscivorous” charr.

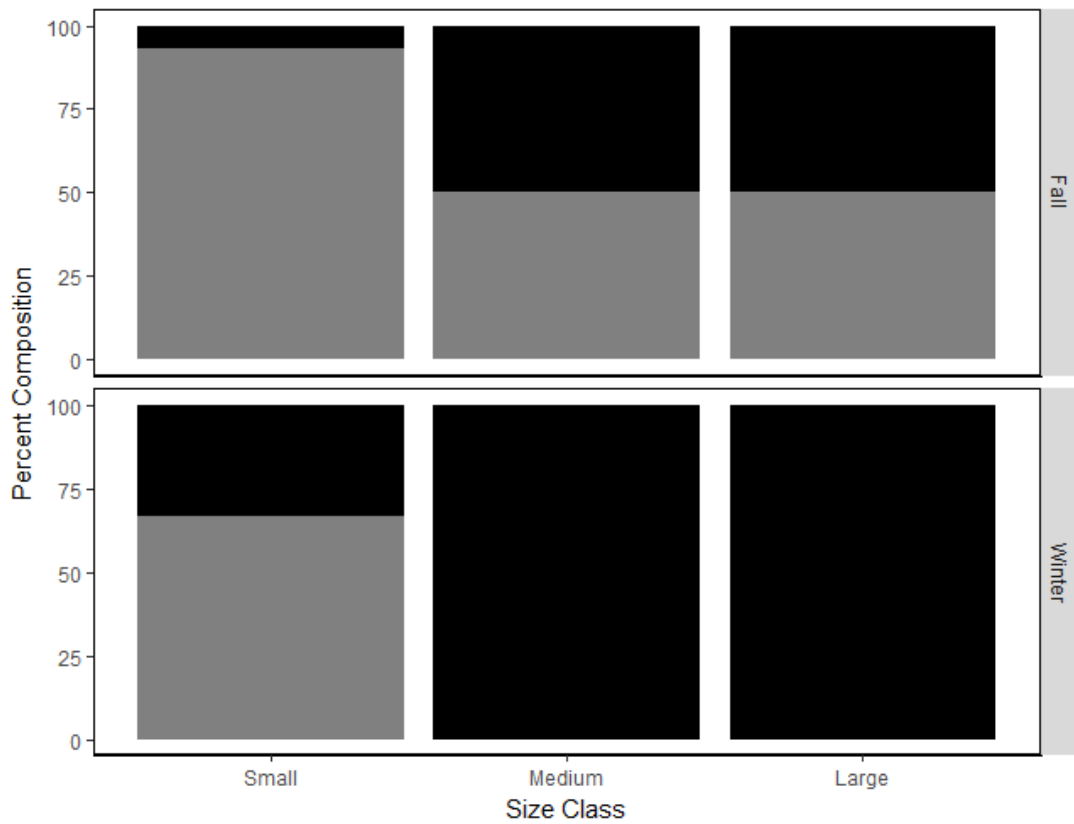


Figure 1.19. Percent composition of stomachs of landlocked charr containing prey items categorized by two functional categories (fish and invertebrates) by season and size class. Black bars denote “fish”, and grey bars denote “invertebrates”.

Discussion

These data fill some of the knowledge gaps on the effect of diet and life history on the growth, condition and body morphology of high-latitude populations of charr. Additionally, this research shows that there is large variation among the life histories of charr within the Canadian Arctic, notably between landlocked and anadromous populations, and some of the variation can be attributed to ontogenetic diet shifts.

As stated in the Chapter 2 of this thesis, charr in the anadromous population are suspected to make their first migration to sea between ages 5-7 with the majority of charr suspected to migrate at age 6 given the large difference in mean length at age between ages 6-7. This postulation may be further supported given the estimated inflection point in the growth curve of the anadromous population at age 5.34 years. The Gompertz model also indicated difference in mean asymptotic lengths between the populations which is evident given that anadromous charr achieved lengths almost double those of landlocked charr by age 12. Multiple studies have shown that anadromous charr grow faster than charr that remain in fresh water throughout their entire life cycle (Johnson 1980*b*; Jonsson and Jonsson 1993; Kristoffersen *et al.* 1994; Rikardsen *et al.* 2000). The marine environment offers greater food diversity and availability than freshwater habitats, allowing anadromous charr to experience faster growth rates during periods of marine feeding (Chapman *et al.* 2012).

Results from the weight-length linear regression model indicate that condition is higher overall for anadromous charr, particularly in the fall following their annual period of marine feeding. This is not surprising as marine feeding offers abundant food supply and once anadromous charr make the ontogenetic shift to marine feeding growth rates increase (Jonsson and Jonsson 2001). It is theorized that in concert with this shift in

diet anadromous charr cease feeding while overwintering in freshwater lakes. This is supported by local Traditional Knowledge (Pangnirtung Hunters and Trappers Organization, personal communication) and the abundance of empty stomachs found in most anadromous Cumberland Sound charr sampled in the winter (Zoya Martin, Fisheries and Oceans Canada, personal communication). Thus, it appears that the feeding strategy of PG027 anadromous charr is that of short period intense marine feeding (<45 days) followed by a long period of starvation. Although resources in high-latitude lacustrine environments are less diverse and abundant than those of the marine environment (Gulseth and Nilssen 2001), the strategy of feeding continually throughout the year as opposed to a single annual intense feeding period provides the opportunity for maintaining a stable weight-length relationship. Although landlocked charr were found to feed more intensely in the fall than in the winter, almost all food consumed in the winter was fish (young charr) with invertebrates making up the majority of the fall diet. This suggests a trade-off with the seasonal opportunistic feeding strategies of large landlocked charr which influences condition - where eating a large amount of low-lipid prey in the fall is balanced out by eating lesser amounts of higher-lipid prey in the winter (Imrie 2012).

As generalists, charr display a high degree of dietary variability; much of it associated with morphological variation (Reist *et al.* 2013). Accordingly, differences in body morphology were identified within and between the populations. Between-population morphological features that had significant covariation and were considered ecologically significant were pectoral fin length, pelvic fin length, snout length and upper jaw length; with landlocked charr having overall longer pectoral and pelvic fins and longer snout and upper jaw lengths. Of these, pectoral fin length showed the highest

relative degree of variation between the populations, suggesting that longer pectoral fins in landlocked charr may be a key discriminatory variable in the morphological variation between the two populations. Length of paired fins has also been identified in other Canadian charr studies as a key discriminatory morphometric variable within multivariate analyses (Reist *et al.* 1995; Kristofferson 2002; Loewen 2008). Comparison of morphological characteristics between lake-resident and anadromous charr in Cumberland Sound by Loewen *et al.* (2009) found that pectoral fin length differed between the life history types, with lake-resident charr having longer overall pectoral fins. Pectoral fin length has been shown to be a significant morphological character in examining locomotor abilities in salmonids (Robinson and Parsons 2002; Andersson 2003; Drucker and Lauder 2003; Peres-Neto and Magnan 2004; Loewen *et al.* 2009), with benefits of longer pectoral fins in lacustrine charr thought to be an adaptation to improve short fast swimming maneuvers in slow flowing water, thereby increasing predator avoidance and prey capture (Loewen *et al.* 2009). Pectoral fin length and other phenotypic characters relating to swimming demands are considered highly plastic in early ontogeny and are known to respond to environmental constraints such as water velocity (Grünbaum *et al.* 2007, Peres-Neto 2004); with longer pectoral fins associated with low water velocity (Loewen *et al.* 2008), such as lacustrine environments. Morphological variation within each population was also identified by the multivariate analysis. Factor score plots displayed distinct morphological difference in anadromous charr in the form of two discrete groups – one group (*Small*) with ages ranging from 4-6 years (mode = 6) and the other group (*Large*) with ages ranging from 7-26 years (mode = 9). The *Small* group had noticeably shorter fork lengths (160mm-237mm), while the *Large* group had longer fork lengths overall (322mm-790mm). Morphological

characters identified in the FA as significant were pectoral fin length, pelvic fin length, snout length and upper jaw length. Of these, upper jaw length showed the highest amount of variation in relative size between groups, with *Large* charr having more elongate upper jaws. The morphological difference found between these two groups is theorized to be a result of differences in feeding ecology, as charr aged 7-26 are suspected to be migrant based on the large increase in growth observed between ages 6-7.

Examination of factor score and discriminant analysis plots allowed for identification of three morphologically distinct size classes of landlocked charr in Qinniqtuq, subsequently categorized as *Small*, *Medium* and *Large* based on size and age ranges within each cluster. Size classes were relatively discrete in length at age, diet and in some cases habitat use. The charr classified as *Small* had the shortest overall fork lengths (180-265 mm) and were younger overall with age ranges from 5-9 years (mode = 5), with the exception of two fish ages 10 and 12 years. The majority of these fish were found to be feeding primarily on invertebrates in both seasons. Charr classified as *Medium* were larger than the *Small* charr with fork lengths ranging from 253-355mm and had a larger range of ages which were older overall (9-21 years, modal age = 10 years). *Medium* charr were observed to feed on both fish and invertebrates in both seasons, with fish being the dominant food source (50%), followed by invertebrates (33%) and then a combination of both prey types (16%). Charr classified as *Large* were larger (385-507mm) and older (13-25 years, mode = 19) overall than the other two size classes. Length-age regressions of each size class display an obvious difference in length-at-age between size classes, with R^2 values for *Medium* and *Large* charr indicating a high degree of variability (a weak relationship) between length and age of

charr within these size classes. Differences in slope between all three size classes suggest a difference in growth rates between size classes.

All *Large* charr observed to feed primarily on fish (80%). Morphological characters identified in the FA as significant were pectoral fin length, pelvic fin length, snout length, upper jaw length and fork depth. Between-size class comparison of standardized data of these morphological variables found that upper jaw showed the most variation between *Small* and *Medium* charr as well as *Medium* and *Large* charr. *Large* charr also displayed considerable variation in pelvic and pectoral fin lengths as compared to all size classes, although not as pronounced as that of upper jaw. The presence of discrete morphological size classes are likely related to the introduction of fish into the diet (piscivory). The piscivory hypothesis suggests that individuals switching to a mainly fish-based diet will experience accelerated growth rates as a result of prey metamorphosis (Kerr 1979; Power and Dempson 2013). Ontogenetic shifts from an invertebrate-based diet to piscivory at a particular length have been observed in other salmonid populations, with mouth gape as the main limiting factor (Jensen *et al.* 2008; Keeley and Grant 2001). Length at piscivory (LP50) for this population was predicted to be 322mm, which coincides with the length range of the *Medium* size class as well as with the findings of Keeley and Grant (2001) which suggest that salmonids become predominantly piscivorous at 31cm (310mm). Accordingly, charr in the *Medium* size class were observed to have stomach contents containing almost equal proportions of both prey types, where charr in the *Small* size class were found to have predominantly invertebrates in their stomachs. This suggests that dietary-morphological change begins to manifest within the *Medium* size class in concert with an ontogenetic, piscivorous shift in diet. Morphological changes appear to continue with allometric

growth as charr achieve longer lengths and establish a primarily fish-based diet, which is apparent in the *Large* size class. The shift to piscivory in larger individuals is likely related to the fact that charr are facultative (or secondary) piscivores; and facultative species become piscivorous at larger sizes than piscivorous species (L'Abée-Lund *et al.* 1992).

Elongation of the upper jaw in larger size classes was apparent in both populations when examining within-population morphological variation. This similarity within the populations coincides with the ontogenetic diet shift observed in each population – piscivory for landlocked charr and marine feeding for anadromous charr. The variation in upper jaw length between *Small* and *Large* anadromous charr and between all three size classes of landlocked charr is suggestive of within-population dietary-morphological relationships. Both the ontogenetic diet shifts and morphological adaption of a longer upper jaw are indicative of an expansion of prey resources. My results are similar to those of Loewen (2009) who found that lake-resident charr in Cumberland Sound had longer overall upper jaw lengths than those of small immature anadromous charr. Loewen (2009) speculated that upper jaw length may be indicative of mouth position, suggesting that lake-resident charr had sub-terminal mouths specialized for feeding on benthos and anadromous charr had terminal mouths for generalized feeding. Anadromous charr in Cumberland Sound have been documented to feed heavily on invertebrates (particularly amphipods), copepods and fish when at sea (Moore and Moore 1974; Imrie 2012). Given the larger overall sizes of migratory charr, mouth morphometry would undoubtedly differ between a marine-feeding generalist and their pre-migrant, freshwater counterparts, as larger mouth size is required to consume large prey (Keeley and Grant 2001). A similar explanation can be

given in regards to the variation in upper jaw lengths between both populations, as differences in diet between searun and lake-dwelling fish would likely manifest in the mouth morphology of a plastic species such as charr. Landlocked charr of similar size to anadromous charr have a piscivorous diet, where anadromous charr have a more generalist diet with prey preference seemingly dependent on opportunism as documented by Imrie (2012), who found that the diet of anadromous charr in Cumberland Sound shifted from one dominated by amphipods to one rich in forage fish (*Mallotus villosus* or capelin) in years when capelin were available in large numbers. Since mouth size has been shown to be the limiting factor of piscivorous fishes (Keeley and Grant 2001), it seems likely that a large mouth size would be advantageous to a specialized predator such as a piscivore than in an anadromous marine generalist.

The variation in relative upper jaw lengths between all three size classes of landlocked charr size is also suggestive of dietary-morphological variation. Difference in upper jaw lengths between *Small* charr and the piscivorous size classes is likely related to the predominance of fish in the diet, as with the introduction of piscivory in the *Medium* size class the length of upper jaw will increase with allometric growth as the diet becomes more piscivorous and the fish increases in length. The noticeable variation in both relative lengths of paired fins and upper jaw in *Large* charr from the other two size classes may be a direct relation to a primarily piscivorous diet of *Large* charr, as these morphological traits are considered important to the acquisition and consumption of piscivorous prey (Ward-Campbell and Beamish 2004). Accordingly, the results of the linear regression found that prey size increased with fork length in landlocked charr, further suggesting that as charr grow larger they consume larger prey

(such as fish) while also demonstrating allometric growth patterns in morphology with the introduction of fish into the diet.

In summary, this research shows that growth, seasonal condition and morphology differed between the two allopatric populations of charr with contrasting life histories. These results suggest that these differences are related to ontogenetic shifts in diet, with a shift to marine feeding for the anadromous population and a shift to piscivory for the landlocked population. Growth differed noticeably between the populations, with anadromous charr having growth rates two times those of landlocked charr by 12 years of age. Anadromous charr had the highest overall condition in the fall compared to all seasons and life histories. Morphological differences were apparent within and between both populations, with each population containing morphologically distinct groups, all of which were attributed to dietary-morphological relationships. Both populations displayed a shift in diet at certain points in ontogeny, with these diet shifts thought to attribute to differences in growth, condition and morphology within and between the populations.

These findings are indicative of the obvious dietary-morphological variation that plastic, high-latitude fishes can experience. It is apparent that ontogenetic niche shifts in freshwater species at high-latitudes is a necessary strategy to optimize growth and condition in low-production lacustrine habitats. High-latitude charr appear to feed heavily and opportunistically when resources are abundant. These results demonstrate that adaptations to optimize capture of new prey items throughout ontogeny can be pronounced morphologically in charr. Further research into the morphological variation governing ontogenetic resource shifts in high-latitude salmonids with differing life histories is warranted.

Chapter 4: Discussion

Summary of Objectives

The scope of this research was to examine and compare the lake ecology of two allopatric, high-latitude populations of charr with differing life histories. This research is novel; representing the first study to examine and compare the lake ecology of landlocked and anadromous charr populations in the Canadian Arctic. The findings of this study conclude that allopatric charr populations in the Canadian Arctic are highly variable and exhibit noticeable variation in lake ecology and life history. Landlocked and anadromous charr populations showed distinct variation in important life history characteristics including differences in growth, seasonal condition, length at maturity and age at maturity. Additional differences between the two populations include body morphology, diet and seasonal habitat use. Shared similarities between the populations include ontogenetic niche shifts at critical stages in the lifecycle to improve growth as well as the importance of littoral habitats for smaller fish. Differences in life history and lake ecology were attributable to differences in diet, with migration shown to be an important feeding strategy for anadromous charr and piscivory and important feeding strategy for landlocked charr. This research demonstrates the role that diet and lacustrine environment play in shaping the life history variation of a plastic species at high-latitudes.

General Summary

These data demonstrate the potential influence that life history and diet have on the growth, morphology and use of lacustrine habitats of a plastic, high-latitude

salmonid. In high-latitude Arctic environments where food resources are highly seasonal and lacustrine environments are low-production and ice-covered for much of the year, niche shifts throughout ontogeny are a necessary occurrence in the life history of freshwater fishes. In the case of charr, these data demonstrate the importance of adopting feeding strategies at certain points in ontogeny to optimize growth, condition, and (ultimately) fitness in a highly variable Arctic environment. Differences in life history of charr populations in Cumberland Sound appear to be synonymous with the lacustrine habitats each life history type inhabits. Charr in a small, low-production, open-water system use migration and seasonal marine feeding to achieve large growth while landlocked charr in a larger, closed-water lake use piscivory and cannibalism to achieve growth. The alternative feeding strategies demonstrated by the two populations have led to obvious differences in life history, with each strategy having associated costs and benefits as well as influence on the morphometry of each population.

Different diet and feeding strategies come with associated benefits and risks. The feeding strategy of anadromous charr appears to be that of accumulating lipid reserves during periods of high food availability (summer fattening) and mobilizing them during periods of low food availability (winter emaciation) (Vijayan *et al.* 2006). This is exemplified in Arctic anadromous fish due to the short period of marine feeding in summer (35-45 days) wherein body mass doubles and lipid stores increase dramatically (Jørgensen *et al.* 1997) followed by a freshwater residency for the remainder of the year where lipid reserves are mobilized to cope with energy demands (Aas-Hansen *et al.* 2005; Jobling *et al.* 1998; Jørgensen *et al.* 1997). Anadromy comes with significant benefits for growth and condition; which is likely why condition was found to be higher in the fall for the anadromous population following the brief period of

marine feeding. However, the risks associated with migration can offset the benefits. Common risks of migration include; increased predation, energy expenditure associated with migration distance and rigor to physiological changes required to acclimatize to saltwater (Chapman *et al.* 2012).

Additional costs associated with migration for high-latitude charr with anadromous life histories may include reduced longevity. A noticeable decline in numbers of age classes of anadromous charr was observed after age 12 and continued to decline, with a significant decline evident by age 15. A similar occurrence has also been observed in the Dieset watercourse in Svalbard, where only 5.7% of mature anadromous spawning charr were older than 15 years (Gulseth and Nilssen 2001). This suggests that the costs associated with anadromy may lead to fewer anadromous fish living to older ages, with age 15 as a possible cutoff. This same trend in age frequencies was also observed in populations of Nunavut charr outlined in Johnson (1980*b*), making this observation not necessarily specific to Cumberland Sound charr but to many anadromous charr populations in Nunavut. When looking comparatively between PG027 and Qinniqtuq, only 2% of anadromous charr in PG027 were estimated to be older than 15 years but 19% of Qinniqtuq charr were estimated to be over age 15. These findings are contrary to Tallman and Saurette (1996) who found that migratory charr live longer than non-migratory charr. Further, Jonsson *et al.* (1991) suggests that longevity may decrease with increasing growth rate. Given the higher growth rate of anadromous charr and lower instance of older individuals, the high growth rate associated with an anadromous life history may cause anadromous charr to have a shorter overall life expectancy than the landlocked charr. It must also be considered that the anadromous population is subject to commercial harvest, wherein larger (and

likely older) individuals are targeted by the larger gillnet mesh sizes used in the commercial fishery. This may lead to the removal of older individuals from the population and may play a role in the lack of individuals that are older than 15 years. Overall, these findings suggest that there may be a cost associated with commercial harvest as well as a migratory life history for the age structure of anadromous charr populations in Nunavut, which may be indicative of populations with few older individuals and/or individuals with shorter overall life spans than their allopatric landlocked counterparts.

Anadromy appears to influence the age at maturity of PG027 charr. Charr reach sexual maturity anywhere from ages 4-10 years (Johnson 1980*b*) or older in some cases, with age at first maturity (A50) for the anadromous population estimated to be 6.6 years. Tallman and Saurette (1996) suggest that selection has favoured a delay in maturity so as to increase the size of spawning migrants to reduce the relative expense of migration, with those that return from sea at an earlier age (and smaller size) being selected against. Dempson and Green (1985) estimated migrant Cumberland Sound charr have an A50 of 11 years, with Moore (1975a) estimating anadromous Cumberland Sound charr to have an A50 of 11-19 years and an L50 of 400-600mm. However, the PG027 population appears to favour maturation at a far younger age and smaller length (6.6 years and 403mm) than those documented in the literature for Cumberland Sound and my findings appear to contradict Tallman and Saurette (1996). With that said, the apparent exponential growth experienced by PG027 charr may be an evolutionary consequence to offset the cost of migration by reaching sexual maturity at a larger size for a fish of that age, and to avoid associated consequences of natural selection for smaller and younger migrants being selected against. It must also be considered that

fishing pressure on this commercially harvested stock may also play a role in changing the dynamics of the population structure, where important life history traits such as length and age at maturity may be altered over time.

Changes in age at age at maturity have a significant impact on fitness and juvenile survival within various life history types. Organisms that mature early have a higher overall probability of surviving to maturity given they spend less time as juveniles coupled with the fact that offspring born sooner start reproducing earlier (Stearns 1992). However, delaying maturity also comes with fitness benefits such as both higher initial and later fecundity through larger growth as well as lower instantaneous juvenile death rates (Stearns 1992). Thus, life history theory postulates that long-lived species with high annual survival (e.g. charr) will delay maturity so as to attain larger growth prior to sexual maturity. Forseth *et al.* (1994) suggests that age and length at maturity is influenced by trade-offs between energy intake and costs. Where adult energy surplus is large (e.g. high energy intake) compared to juveniles resulting in high adult growth, maturity may be delayed (Forseth *et al.* 1994). Conversely, where energy surplus is lower for adults than juveniles, decreased age and size at maturity may maximize lifetime reproductive success (Forseth *et al.* 1994). In the case of the anadromous population, adult energy surplus is higher than that of juveniles once migration and marine feeding become prevalent; yet their age at maturity is lower than that of the landlocked population who do not experience the benefits associated with marine feeding. On the other hand, landlocked charr likely have a higher juvenile energy surplus given the low cost of an invertebrate-based diet and the allocation of resources into growth as opposed to sexual maturity for immature fish within the *Small* size class. However, the length at maturity of landlocked charr is considerably lower than that of

the anadromous population yet the age at maturity is slightly older, which is likely attributable to the lower (and thus slower) overall growth rate of landlocked charr compared to that of the anadromous population. This between-population life history variability demonstrates the influential role that intake of different food resources at certain points in ontogeny can play on important life history characteristics such as length and age at maturity in a plastic species such as charr.

The inflection point of 5.34 years identified in the growth model for anadromous charr may be indicative of a large increase in growth around that age, which is additional support of my postulation that the first migration to sea occurs between ages 5-7 for this population, with the majority of charr likely migrating between ages 6-7. A consideration for the observed growth increase experienced with the first trip to sea by the anadromous population may be a year class effect in the form of new prey availability in the Cumberland Sound marine environment. Imrie (2012) found that the diet of anadromous charr in Cumberland Sound shifted in the last decade with the increased availability of capelin in the marine environment. Imrie (2012) found that Cumberland Sound charr had shifted from a marine diet of zooplankton to a diet comprised primarily of capelin within a 10 year period. Capelin are a high-lipid prey item which may provide benefits to charr in terms of growth and condition (Michaud *et al.* 2010). However, Imrie (2012) found no difference in condition between years but results suggest possible growth increase with the shift in diet. However, examination of additional years of stock assessment data for this population (2010-2014, Appendix 1.15) for mean length at age shows the same possible high rate of growth between ages 6-7, reducing the likelihood of a year class effect. What this may in fact suggest is that with the availability of newly abundant high lipid prey (capelin) in Cumberland

Sound, charr may be attaining a younger age at maturity than observed by Dempson and Green (1985) and Moore (1975a). It is obvious that regardless of the motivation and preferred prey type, seasonal marine feeding opportunities maximize the length and age at which sexual maturity is achieved and has an obvious growth benefit for this species.

Landlocked charr do not have the opportunity to shift niches from freshwater feeding to marine feeding, so alternative approaches to achieve growth must be adopted within the lake habitat at certain points in ontogeny. These may include shifting from invertebrate feeding to piscivory and cannibalism. This shift in niche may lead to age and size-specific changes in the life history and will influence population size structure. Similar to this study, Hammar (2000) found life history changes at age 10-15 and size of 200-300mm in bimodal landlocked charr populations in Svalbard, with discrete ontogenetic niche shifts from invertebrate-based feeding to cannibalism. Similar to these results, Hammar (2000) found that charr in the first mode were small-sized, sexually mature, slow-growing individuals with the second mode comprised of large-sized, fast-growing cannibals. Sex ratios were also skewed in these populations, with females dominating the first mode of smaller-sized individuals and males dominating the second mode of large individuals (Hammar 2000, Appendix 1.16). In contrast to Hammar's (2000) findings the sex ratios in the first mode of my data (the *Small* size class) were not skewed nor was the ratio of mature to immature individuals, but similar to Hammar (2000) males dominated the second mode (the *Large* size class). This suggests that differences in timing of ontogenetic niche shifts between sexes in bimodal populations can affect the pace in which one sex moves from the first mode

into the second mode, with males appearing to move into the second mode faster than females in the landlocked population.

The lack of females in the piscivorous size classes of the landlocked population indicates that females are not being recruited into the larger size classes. This finding suggests that some form of intraspecific competition may be occurring while charr are shifting to a piscivorous diet. Although only two females were documented in the *Large* size class, those fish were the oldest fish documented in this system (23 and 25 years). This indicates that some females in this system will become piscivorous and achieve large growth, but growth rates may differ between sexes following the adoption of a piscivorous diet. This may be the result of males adopting a seasonal cannibalistic diet which would aid in accelerating growth rates, allowing males to achieve large sizes at younger ages. Hammar (2000) suggests that lake-resident male charr of cannibalistic populations are more prone to take risks while feeding, which may be another consideration as to the high proportion of larger-sized males in Qinniqtuq. Although the causal mechanism of the lack of females in the piscivorous size classes is not clear from these data, it is apparent that there is sexual asynchrony in the ontogeny of Qinniqtuq charr.

Explanations of skewed sex ratios have included inbreeding and local competition for mates (Hamilton 1967), different mortality rates for males and females (Arendt *et al.* 2014), endocrine-disrupting environmental pollutants (Mills and Chichester 2005), and adaptive maternal effects that allow unequal investment in male or female offspring (Kahn *et al.* 2013). Given the possibility of high female mortality past the 300mm mark as shown in this research, different mortality rates between the sexes may be the underlying cause with the cause of mortality remaining unclear. Walker *et al.*

(2010) postulates that skewed sex ratios may be indicative of an Allee effect (negative density-dependence), which occurs when some component of per capita fitness deteriorates as population size or density decreases toward zero resulting in a negative density-dependent relationship. More research is warranted into the disproportionate sex ratios within this system to adequately address this question.

The appearance of a bimodal size structure in the landlocked population may have several explanations. Given the small sample size obtained from this system (n=69), it is not conclusive that the length frequency distribution is in fact bimodal. However, if the population structure of landlocked charr is in fact bimodal, it could likely be the product of a dietary-morphological relationship. Size bimodality has been documented in several species of the Salmonidae as well as other freshwater teleosts such as largemouth bass (*Micropterus salmoides*), walleye (*Stizostedion vitreum*), pike (*Esox lucius*) and perch (*Perca fluviatilis*) Griffiths (1994). In lacustrine charr, bimodality is not uncommon. Several hypotheses have been proposed to explain bimodality such as allopatric and sympatric speciation, genetic inertia, piscivory, interspecific competition, intraspecific competition and alternative life styles (Griffiths 1994). Bimodality in population structure is commonly observed in freshwater resident charr populations (Borgstrøm *et al.* 2015), particularly in the northern reaches of their range as the frequency of bimodality has shown to increase with latitude (Griffiths 1994). Bimodality in charr is commonly associated with some form of polymorphism, be it trophic polymorphism or size polymorphism (Reist *et al.* 2013). In trophic polymorphism, the presence of individuals use different niches leads to bimodality in population structure (Parker and Johnson 1991; Griffiths 1994), as diet and prey size will have a direct effect on growth rates. Bimodality resulting from size polymorphism

arises through variation in year-class strength and the piling up of slowly growing cohorts (Johnson 1976), resulting in slow-growing and fast-growing individuals (Reist *et al.* 2013). Size polymorphism is commonly associated with piscivory (Reist *et al.* 2013) and has been suggested to be the result of seasonality of food supply coupled with feeding size thresholds (Griffiths 1994). Feeding size thresholds result in larger members of a cohort having the ability to maintain growth rates on seasonally abundant prey items where the smaller individuals who are unable to catch these items form a second mode of slower-growing fish (Griffiths 1994). Griffiths (1994) found that bimodal populations tended to be observed in large, deep lakes in which charr were cannibalistic, which is the case of Qinniqtuq.

Given that there was no clear indication of trophic polymorphism in this system, the cause of the bimodality of the landlocked population may be attributable some form of size polymorphism or simply differences in growth between individuals based on the individual's ability to exploit resources. Variation in length at age was apparent; particularly in the *Large* size class. This variability of large fish is a possible indication of some fast-growing charr in this system, as characteristic modes of large fish have been documented in the northern reaches of the charr's range which typically consist of old, sexually mature fish of both sexes with relatively uniform sizes but highly differing ages (Gullestad and Klemetsen 1997). There was some evidence of slow-growing individuals, as three small, older female charr were documented; aged 10, 12 and 21 years and all less than 300mm in length. Most bimodal population structures involve a large amount of small and large fish, and few intermediate sized fish (Power *et al.* 2008). However, this is not the case in Qinniqtuq as there was still a considerable amount of intermediate-sized fish in the *Medium* size class (28%). The lack of a clear

indication of slow and fast-growing morphs in this system suggests that size-at-age variability is likely related to an individual's ability to exploit seasonal feeding opportunities in a highly variable environment.

Conclusion

This research represents the first known examination of the seasonal lacustrine habitat use of an anadromous high Arctic charr population. These data demonstrate how differences in diet and life history of a plastic, high-latitude freshwater salmonid can influence habitat use, growth, condition and morphology and also emphasize the costs and benefits associated with each life history. This research demonstrates that Arctic charr with different life histories from two allopatric populations differ in how they use the lacustrine environment, differ in what prey they forage and when they feed resulting in difference in biological parameters such as growth, condition and age at maturity. In contrast this research shows that the two populations of charr both underwent at least one ontogenetic shift within their life cycle and that ontogenetic shift was correlated to a shift in diet. This all comes together to re-enforce the notion that Arctic charr are a “plastic” species that allows individual populations to adapt to each microenvironment, resulting in these fish exploiting and thriving in a low-productive, variable and harsh climate – the Arctic.

Future Research

These data demonstrate how differences in diet and life history of a plastic, high-latitude freshwater salmonid can influence habitat use, growth, condition and morphology and also emphasize the costs and benefits associated with each life

history. Although these findings do not overwhelmingly suggest that anadromous or landlocked populations of charr in Cumberland Sound have narrow habitat seasonal requirements, further research should be conducted to examine the possible consequences that climate change may have on the freshwater seasonal habitat needs of high Arctic charr populations. Specifically, an alternative technique such as acoustic telemetry could be utilized to obtain continuous, seasonal habitat use information for both populations. Additional research regarding the cause of the skewed sex ratios of Qinniqtuq is warranted as this population may be at risk of extinction within this waterbody, with suggested research to examine the fecundity potential of each sex for this population. These findings also indicate that future research is necessary to better answer additional questions regarding the dietary-morphological relationships of landlocked charr, particularly those regarding a niche shift to piscivory and the role that sex plays in regards to recruitment of fish into the larger, piscivorous size classes. The shift from an invertebrate-based diet to piscivory in landlocked charr can be more thoroughly examined through additional methodologies such as measuring mouth gape and utilizing meristic counts such as the number of gill rakers to better aid in determining diet between size classes. Further, stable isotope analysis could be utilized to investigate diet of size classes in both landlocked and anadromous charr, as stable isotopes are now firmly established in the field of trophic ecology and can reveal information on diet source and trophic position (Imrie 2012). Thus, stable isotope analysis may be useful in addressing the question of cannibalism being sex-specific in Qinniqtuq. Growth and anadromy should be further examined using otolith strontium analysis, as this can help to confirm if the *Small* anadromous charr have not yet been to sea as well as confirming if the suspected large increase in growth observed between

ages 6-7 is in fact a product of the first migration. Lastly, further examination of the possible relationship between changes in diet and the age at maturity (A50) in the last decade of anadromous Cumberland Sound charr stocks is suggested, as there may be a direct relationship to climate change with regards to range expansion of prey species which requires consideration by fisheries managers.

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Appendix 1.0. Example R code for initial data exploration employed with linear models with example outputs.

```
setwd("C:/Users/Quester/Desktop/Both")
source("C:/Users/Quester/Desktop/Both/HighstatLibV6.R")
Both<-read.csv("C:/Users/Quester/Desktop/Both/Both.Lakes.R.csv")
Lock<-filterD(Both,Form=="Landlocked")

#####Fork Length

####Step 1.) Look for possible outliers
#dotplots side by side
SelX<-c("Dep", "Temp", "DO", "FL")
dotplot(as.matrix(Lock_Fall[,SelX]),groups=FALSE,layout=c(4,1),strip=strip.custom(bg
='white',par.strip.text=list(cex=1.2)),scales=list(x=list(relation="free",draw=TRUE),y=list(r
elation="free",draw=FALSE)),col=1,cex=0.05,pch=16,xlab=list(label=c("Value of the
variable"),cex=1.5),ylab=list(label=c("Order of the data from .csv file"),cex=1.5))
identify(y=Lock_Fall$Num,x=Lock_Fall$Dep)

#boxplot and dotplot side by side
##FL
par(mfrow=c(1,2),mar=c(5,4,1,1))
dotchart(Lock_Fall$FL,ylab="order of data",xlab="range of data")
boxplot(Lock_Fall$FL)
##DO
par(mfrow=c(1,2),mar=c(5,4,1,1))
dotchart(Lock_Fall$DO,ylab="order of data",xlab="range of data")
boxplot(Lock_Fall$DO)
##Temp
par(mfrow=c(1,2),mar=c(5,4,1,1))
dotchart(Lock_Fall$Temp,ylab="order of data",xlab="range of data")
boxplot(Lock_Fall$Temp)
identify(y=Lock_Fall$Num_Fish,x=Lock_Fall$Temp) #outlier
##Dep
par(mfrow=c(1,2),mar=c(5,4,1,1))
dotchart(Lock_Fall$Dep,ylab="order of data",xlab="range of data")
boxplot(Lock_Fall$Dep)

#Conditional Boxplots for habitat
boxplot(FL~Hab,xlab="Fork Length",ylab="Habitat
Type",data=Lock_Fall,main=expression(italic("Fall Landlocked")))
identify(y=Lock_Fall$FL,x=Lock_Fall$Hab)

####Step 2.) Look for collinearity
#pairplots w/ Pearson correlation
attach(Lock_Fall)
```

```

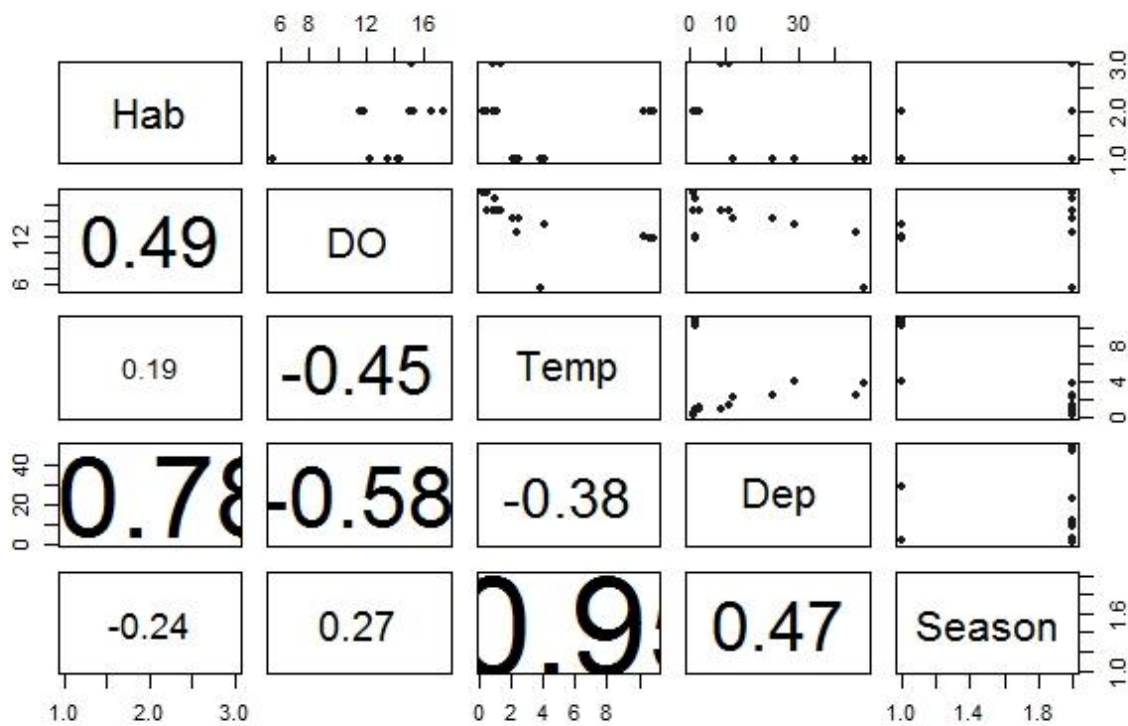
names(Lock_Fall)
Z<-Lock_Fall[,c("FL","Dep","DO","Temp","Hab")]
pairs(Z)
pairs(Z, upper.panel=panel.smooth2,lower.panel=panel.cor,cex.labels=1.5)

#VIF
vif(glm_1)

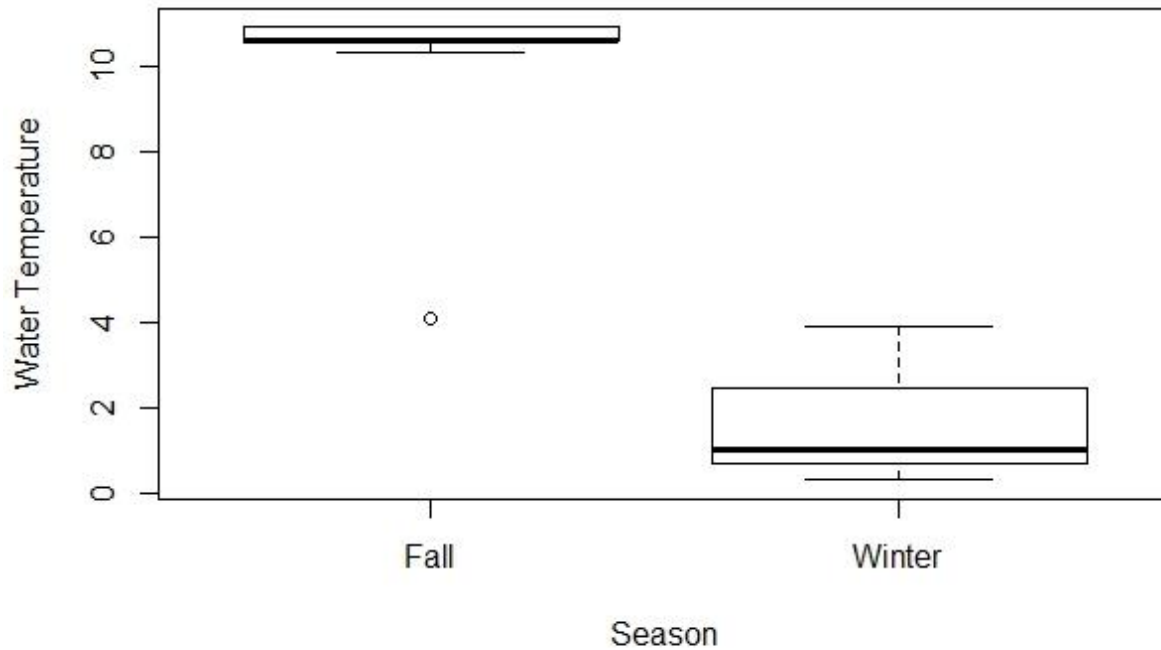
```

Collinearity Example for Habitat Variables the Landlocked Population

Multi panel scatterplots with Pearson Correlation Coefficients (note that the larger the number, the greater the degree of collinearity between variables):



Boxplot to examine collinearity between categorical variable "Season" and continuous variable "Water Temperature":



Variance inflation factors for all habitat variables in the landlocked lake (note all VIF scores are >3):

Variance inflation factors

	GVIF	Df	GVIF ^(1/2Df)
Hab	12.75779	2	1.889922
DO	11.47733	1	3.387820
Temp	34.40939	1	5.865952
Dep	23.21279	1	4.817965
Season	19.26203	1	4.388853

Appendix 1.1. Example R code for generalized linear and logistic regression models of habitat data following initial exploratory data analysis.

```
library(FSA)
library(dplyr)
library(car)
setwd("C:/Users/Quester/Desktop/Both")
Both <- read.csv("Both.Lakes.R.csv")
Anad<-filterD(Both,Form=="Anadromous")
Anad_Mat<-filterD(Anad,Mat%in%c("Immature","Mature"))
Anad_Fall<-filterD(Anad_Mat,Season=="Fall")
Anad_Wint<-filterD(Anad_Mat,Season=="Winter")

#####
##### Fall

#Hab
FL1<-glm(FL~Hab,data=Anad_Fall,family="gaussian")
summary(FL1)
#check residuals
residPlot2(FL1)

#DO
FL2<-glm(FL~DO,data=Anad_Fall,family="gaussian")
summary(FL2)
#check residuals
residPlot2(FL2)

#Dep
FL3<-glm(FL~Dep,data=Anad_Fall,family="gaussian")
summary(FL3)
#check residuals
residPlot2(FL3)

#Temp
FL4<-glm(FL~Temp,data=Anad_Fall,family="gaussian")
summary(FL4)
#check residuals
residPlot2(FL4)

#####

#Logistic regression

#####
##### Fall
```

```
#Hab
Mat1<-glm(Mat~Hab*FL,family="binomial",data=Anad_Fall)
summary(Mat1)
#check residuals
```

```
#Dep
Mat2<-glm(Mat~Dep*FL,family="binomial",data=Anad_Fall)
summary(Mat2)
#check residuals
```

```
#DO
Mat3<-glm(Mat~DO*FL,family="binomial",data=Anad_Fall)
summary(Mat3)
#check residuals
```

```
#Temp
Mat4<-glm(Mat~Temp*FL,family="binomial",data=Anad_Fall)
summary(Mat4)
```

Appendix 1.2. Example R code for logistic regression of length and age at first maturity.

```
library(FSA)
library(dplyr)
library(car)
setwd("C:/Users/Quester/Desktop/Both")
Both<-read.csv("Both.Lakes.R.csv") %>% mutate(logFL=log(FL),logGWT=log(GWT))
str(Both)
Lock<-filterD(Both,Form=="Landlocked")
Lock_M<-filterD(Lock,Sex=="Male")
Lock_F<-filterD(Lock,Sex=="Female")
Anad<-filterD(Both,Form=="Anadromous")
Anad_M<-filterD(Anad,Sex=="Male")
Anad_F<-filterD(Anad,Sex=="Female")
#####
#Length and Age at First Maturity

####Anadromous

####Length
#Both sexes
Anad_LAFM<- glm(Mat~FL,data=Anad,family=binomial)
# Compute length where 100P% of fish are mature
lrPerc <- function(cf,p) (log(p/(1-p))-cf[[1]])/cf[[2]]
lrPerc(coef(Anad_LAFM),0.5) # 50% mature

#Males Only
Anad_M_LAFM<- glm(Mat~FL,data=Anad_M,family=binomial)
# Compute length where 100P% of fish are mature
lrPerc <- function(cf,p) (log(p/(1-p))-cf[[1]])/cf[[2]]
lrPerc(coef(Anad_M_LAFM),0.5) # 50% mature

#Females Only
Anad_F_LAFM<- glm(Mat~FL,data=Anad_F,family=binomial)
# Compute length where 100P% of fish are mature
lrPerc <- function(cf,p) (log(p/(1-p))-cf[[1]])/cf
lrPerc(coef(Anad_F_LAFM),0.5) # 50% mature

####Age
#Both sexes
Anad_AAFM<- glm(Mat~Age,data=Anad,family=binomial)
# Compute length where 100P% of fish are mature
lrPerc <- function(cf,p) (log(p/(1-p))-cf[[1]])/cf[[2]]
lrPerc(coef(Anad_AAFM),0.5) # 50% mature
```

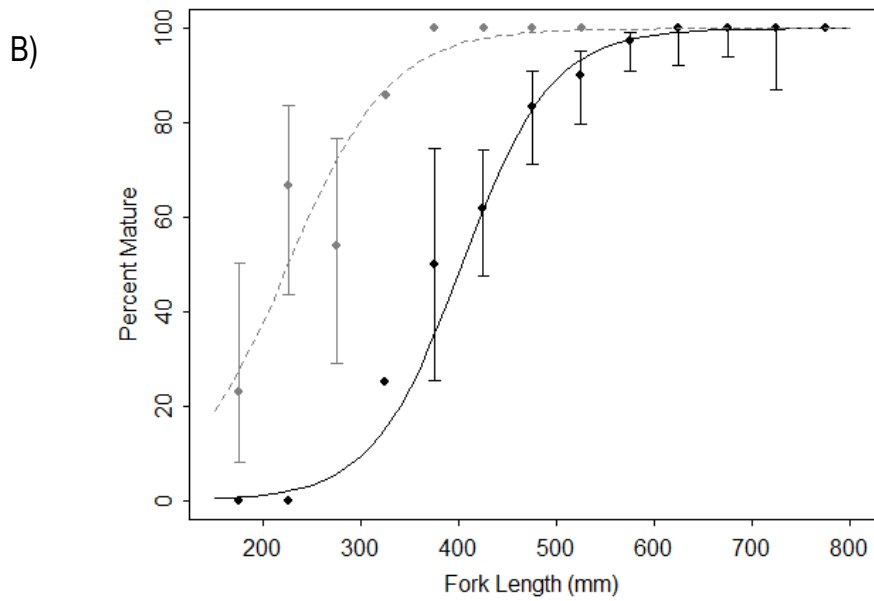
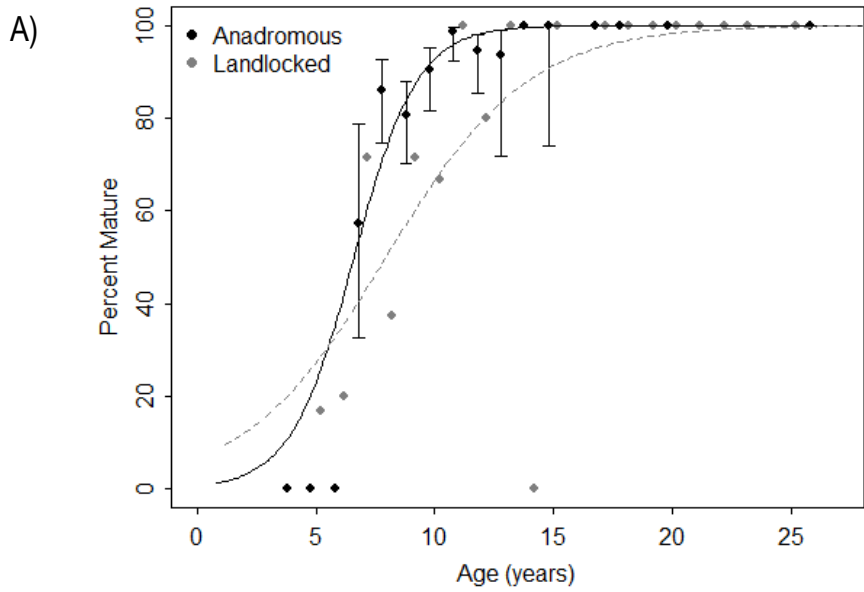
```
#Males Only
Anad_M_AAFM<- glm(Mat~Age,data=Anad_M,family=binomial)
# Compute length where 100P% of fish are mature
lrPerc <- function(cf,p) (log(p/(1-p))-cf[[1]])/cf[[2]]
lrPerc(coef(Anad_M_AAFM),0.5) # 50% mature
```

```
#Females Only
Anad_F_AAFM<- glm(Mat~Age,data=Anad_F,family=binomial)
# Compute length where 100P% of fish are mature
lrPerc <- function(cf,p) (log(p/(1-p))-cf[[1]])/cf
lrPerc(coef(Anad_F_AAFM),0.5) # 50% mature
```

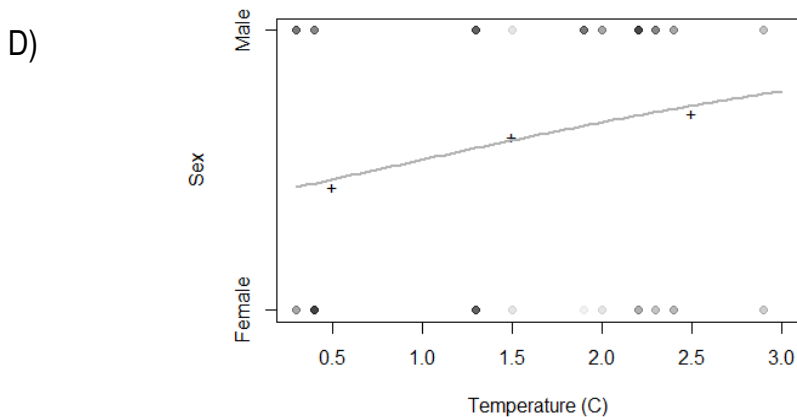
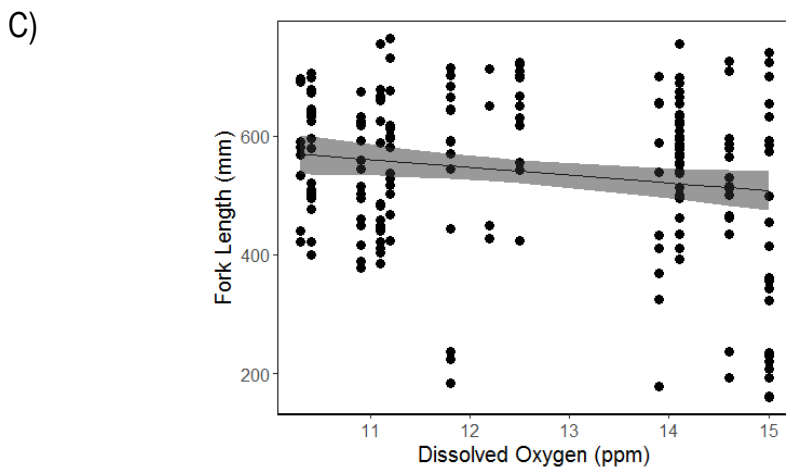
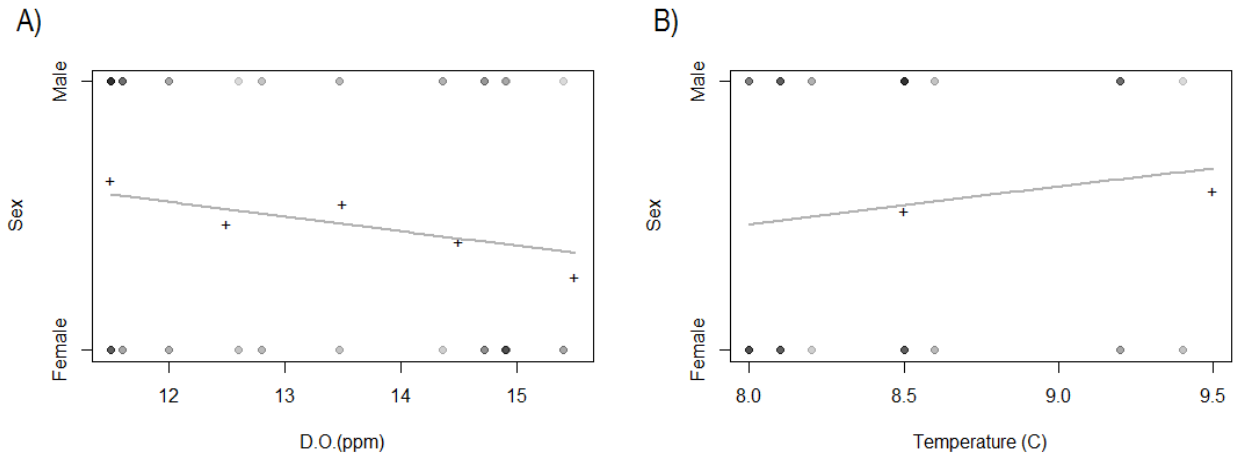
Appendix 1.3. Table of mean CPUEs and standard error by season and habitat for both systems. CPUE is represented as number of fish caught per hour.

	2011	2012	2012	2013	Fall	Winter
PG027	<i>Fall</i>	<i>Winter</i>	<i>Fall</i>	<i>Winter</i>	Combined	Combined
Littoral	9.4 ± 0.3	3.9 ± 1.1	25.9 ± 15.6	4.0 ± 2.4	16.5 ± 7.6	4.0 ± 0.9
Benthic	40*	2.84 ± 0.03	9.9 ± 3.2	3.3 ± 0.6	17.6 ± 7.6	3.1 ± 0.3
Pelagic	15.07*	2.2 ± 0.2	5.1 ± 5.1	2.5 ± 1.6	8.4 ± 4.4	2.4 ± 0.7
Mean CPUE		3.3 ± 0.6	14.8 ± 6.2	3.3 ± 0.8	15.1 ± 3.4	3.3 ± 0.5
Qinniqtuq						
Littoral	-	0.1 ± 0.1	0.3 ± 0.1	0.04 ± 0.03	0.3 ± 0.1	0.09 ± 0.04
Benthic	-	0.3 ± 0.1	0.04 ± 0.04	0.01 ± 0.03	0.05 ± 0.05	0.17 ± 0.08
Pelagic	-	0.2 ± 0.1	0	0	0	0.12 ± 0.06
Mean CPUE	-	0.20 ± 0.07	1.83 ± 0.07	0.06 ± 0.02	0.18 ± 0.07	0.13 ± 0.04

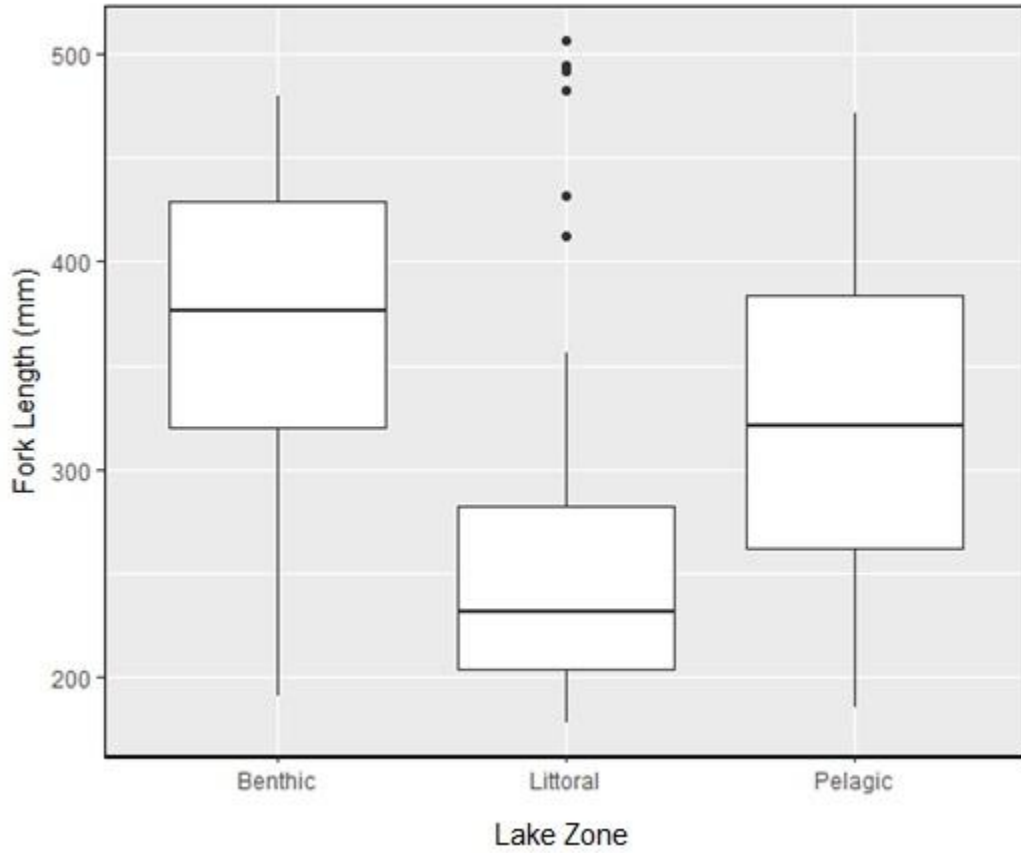
Appendix 1.4. Logistic regression model fit for A) Age at maturity and B) Length at maturity predictions for Anadromous (black dots, solid line) and landlocked (grey dots, dashed line) charr.



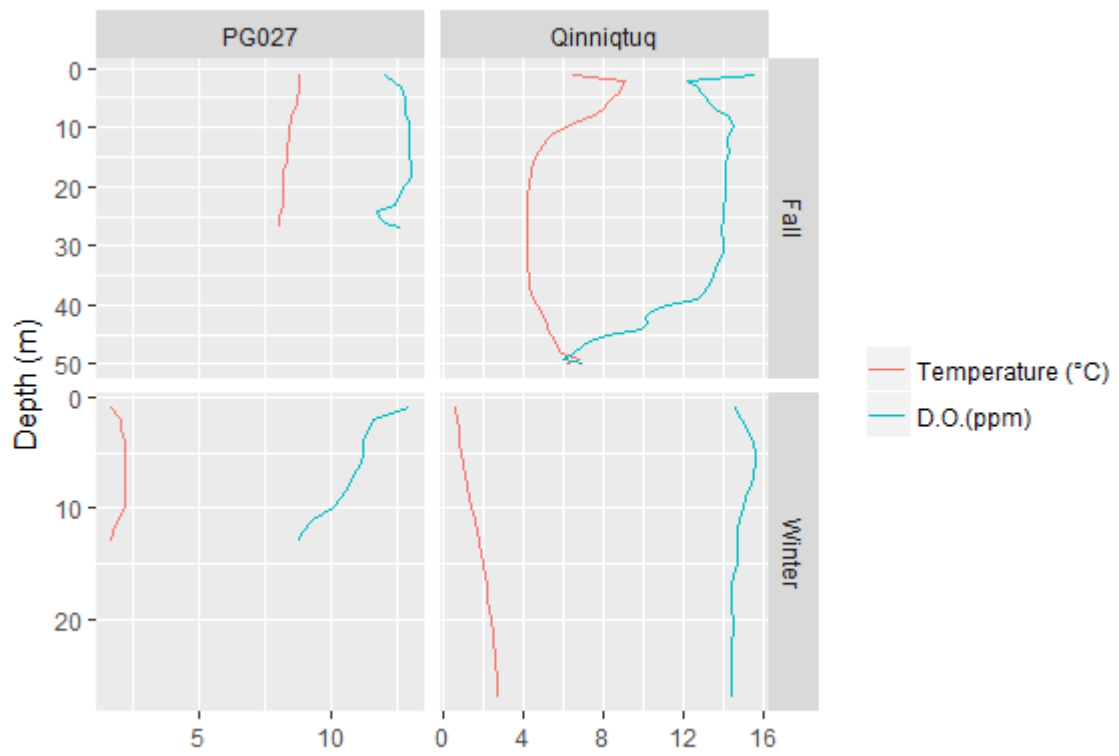
Appendix 1.5. Logistic regression fits for for A) Sex and D.O. and B) Sex and Water Temperature for anadromous charr in the fall; linear regression fit for C) Fork Length and D.O. for anadromous charr in the winter; and the logistic regression fit for D) Sex and Water Temperature for anadromous charr in the winter.



Boxplot displaying distribution of fork length by habitat type (lake zone) for landlocked charr in combined seasons. Boxes denote first quartile, median and third quartile while whiskers denote minimum and maximum values. Dots represent outliers greater than 1.5x the interquartile range.



Appendix 1.6. Example water column profiles of water temperature and D.O. from PG027 and Qinniqtuq in the fall and winter.



Appendix 1.7. Example R code for Gompertz growth model.

```
## Load Packages
library(FSA)

## Read data
anad <- read.csv("Anadromous.VBGM.csv")
lock <- read.csv("Landlocked.VBGM.csv")
comb <- rbind(anad,lock)

## Make some colors for plotting
# solid colors
clrs <- c("black", "gray")

## Exploratory plots
hist(Age~Form,data=comb,nrow=2,ncol=1,w=1,same.ylim=FALSE)
hist(FL~Form,data=comb,nrow=2,ncol=1,w=10,same.ylim=FALSE)
plot(FL~Age,data=comb,col=clrs[Form],pch=19,xlim=c(0,26),ylim=c(0,800))

#### Gompertz
## Declare Typical function
gomp <- GompertzFuns()
## Fit to anadromous fish
# try different Linf, gi, and ti values to find good starting values
plot(FL~Age,data=anad)
curve(gomp(x,Linf=715,gi=0.2,ti=6),add=TRUE)
svgAnad <- list(Linf=715,gi=0.2,ti=6)
fitgAnad <- nls(FL~gomp(Age,Linf,gi,ti),data=anad,start=svgAnad)
## Fit to landlocked fish
# try different Linf, gi, and ti values to find good starting values
plot(FL~Age,data=lock)
curve(gomp(x,Linf=500,gi=0.1,ti=6),add=TRUE)
( svgLock <- list(Linf=500,gi=0.1,ti=6) )
fitgLock <- nls(FL~gomp(Age,Linf,gi,ti),data=lock,start=svgLock)
## Examine fits
plot(FL~Age,data=comb,col=clrs[Form],pch=19,xlim=c(0,26),ylim=c(0,800))
curve(gomp(x,coef(fitgAnad)),from=0,to=27,col=clrs[1],lwd=2,add=TRUE)
curve(gomp(x,coef(fitgLock)),from=0,to=27,col=clrs[2],lwd=2,add=TRUE)

## Comparing Gompertz fits

gompLGT <- FL~Linf[Form]*exp(-exp(-gi[Form]*(Age-ti[Form])))
gompLG <- FL~Linf[Form]*exp(-exp(-gi[Form]*(Age-ti)))
gompLT <- FL~Linf[Form]*exp(-exp(-gi*(Age-ti[Form])))
```

```

gompGT <- FL~Linf*exp(-exp(-gi[Form]*(Age-ti[Form])))
gompL <- FL~Linf[Form]*exp(-exp(-gi*(Age-ti)))
gompG <- FL~Linf*exp(-exp(-gi[Form]*(Age-ti)))
gompT <- FL~Linf*exp(-exp(-gi*(Age-ti[Form])))
gomp0 <- FL~Linf*exp(-exp(-gi*(Age-ti)))

svLGT <- list(Linf=c(679,504),gi=c(0.366,0.127),ti=c(5.34,5.70))
svLG <- list(Linf=c(679,504),gi=c(0.366,0.127),ti=5.55)
svLT <- list(Linf=c(679,504),gi=0.25,ti=c(5.34,5.70))
svGT <- list(Linf=575,gi=c(0.366,0.127),ti=c(5.34,5.70))
svL <- list(Linf=c(679,504),gi=0.25,ti=5.55)
svG <- list(Linf=575,gi=c(0.366,0.127),ti=5.55)
svT <- list(Linf=575,gi=0.25,ti=c(5.34,5.70))
sv0 <- list(Linf=575,gi=0.25,ti=5.55)

fitLGT <- nls(gompLGT,data=comb,start=svLGT)
fitLG <- nls(gompLG,data=comb,start=svLG)
fitLT <- nls(gompLT,data=comb,start=svLT)
fitGT <- nls(gompGT,data=comb,start=svGT)
fitL <- nls(gompL,data=comb,start=svL)
fitG <- nls(gompG,data=comb,start=svG)
fitT <- nls(gompT,data=comb,start=svT)
fit0 <- nls(gomp0,data=comb,start=sv0)

extraSS(fitLG,fitLT,fitGT,com=fitLGT,
        sim.names=c("Linf & gi differ","Linf & ti differ","gi & ti differ"),
        com.name="All differ")
## pretty clear evidence that Linf differs ... not surprising
## leas evidence that ti differs ... thus move forward with that as complex model
extraSS(fitL,fitG,com=fitLG,
        sim.names=c("Linf differs","gi differs"),
        com.name="Linf & gi differ")
## neither simpler model is adequate. Keep model where both Linf and gi differ by form
coef(fitLG)

cbind(Anadromous=coef(fitgAnad),Landlocked=coef(fitgLock))
## Profile likelihood confidence intervals for mean lengths at ages
confint(fitgAnad)
confint(fitgLock)

plot(FL~Age,data=comb,col=clrs[Form],pch=19,xlim=c(4,26),ylim=c(0,800),ylab="Fork
Length")
curve(gomp(x,coef(fitgAnad)),from=0,to=27,col=clrs[1],lwd=2,add=TRUE)
curve(gomp(x,coef(fitgLock)),from=0,to=27,col=clrs[2],lwd=2,add=TRUE)
legend("topleft",legend=c("Anadromous","Landlocked"),pch=19,col=clrs,bty="n")

tis <- rbind(c(est=coef(fitgAnad)[["ti"]],confint(fitgAnad)[["ti",]]),

```

```
      c(est=coef(fitgLock)[["ti"]],confint(fitgLock)[["ti",])
rownames(tis) <- c("Anad","Lock")
tis

library(plotrix)
lines(x=rep(tis["Lock","est"],2),y=c(-30,
      predict(fitgLock,data.frame(Age=tis["Lock","est"]))),
      col=clrs[2],lty=2,lwd=2)
lines(x=rep(tis["Anad","est"],2),y=c(-30,
      predict(fitgAnad,data.frame(Age=tis["Anad","est"]))),
      col=clrs[1],lty=2,lwd=2)
```

Appendix 1.8. Example R code for linear univariate model of condition.

```
library(FSA)
library(dplyr)
library(car)
setwd("C:/Users/Quester/Desktop/Both")

Both <- read.csv("Both.Lakes.R.csv")%>%
  mutate(logFL=log(FL),logGWT=log(GWT))
str(Both)
Anad <- filterD(Both,Form=="Anadromous")
Lock <- filterD(Both,Form=="Landlocked")
Fall <- filterD(Both,Season=="Fall")
Wint <- filterD(Both,Season=="Winter")
Anad_Fall <- filterD(Anad,Season=="Fall")
Anad_Wint <- filterD(Anad,Season=="Winter")
Lock_Fall <- filterD(Lock,Season=="Fall")
Lock_Wint <- filterD(Lock,Season=="Winter")

#### Perform DVR
lm1 <- lm(logGWT~logFL*Form*Season,data=Both)
anova(lm1)

### Fit model with only significant terms
lm2 <- lm(logGWT~logFL+Form+Season+Form:Season,data=Both)
anova(lm2)

##Fit model which treats each group separately to determine statistical differences in
intercepts
Both$Group <- Both$Form:Both$Season
lm2a <- lm(logGWT~logFL+Group,data=Both)
complIntercepts(lm2a,digits=4)

#Predict weights
FLs <- seq(200,800,100)
reps <- length(FLs)
newdf <- data.frame(logFL=rep(log(FLs),4),
                    Form=rep(levels(Both$Form),each=14),
                    Season=rep(rep(levels(Both$Season),each=7),2),
                    FL=rep(FLs,4))
newdf <- cbind(newdf,data.frame(round(exp(predict(lm2,
                                             newdf,interval="conf")),0)))
arrange(newdf[,-1],FL)
```


Appendix 1.9. Example R code for factor analysis of morphological characteristics.

```
library(FSA)
library(dplyr)
library(car)
setwd("C:/Users/Quester/Desktop/Both")
Morph<-read.csv("C:/Users/Quester/Desktop/Both/Morph.Both.Lakes.csv")

#Between population analysis
FA<-
factanal(~FL+ST_L+Snout+Up_Jaw+Eye+Pec+Pelv+Caud_Ped+Bod_Dep,factors=2,
rotation="varimax", scores="regression", data=Morph)
F1<-FA$loadings[,1]
F2<-FA$loadings[,2]

#plot factor scores
plot(F1,F2,pch=19+as.numeric(Form))
```

Appendix 1.10. Example R code for univariate morphological trait analysis.

```
#Run model
lm1<-lm(Pec~ST_L*Form,data=Morph)
summary(lm1)

#Plot the model
plot(Pec~ST_L,data=Morph,pch=1+as.numeric(Form),col=c("black","grey") [as.numeric
(Form)], xlim=c(0, 525),ylim=c (1,525) )
abline(lm(Pec[Form=="Anad"]~ST_L[Form=="Anad"]),lty=2,lwd=3,data=Morph)
abline(lm(Pec[Form=="Lock"]~ST_L[Form=="Lock"]),lty=3,col=grey,lwd=3,data=Morph)

#check residuals
E1<-resid(lm1,type="pearson")
F1<-fitted(lm1,type="response")
plot(F1,E1,xlab="Fitted values",ylab="Pearson residuals")
abline(h=0,lty=2)
hist(E1)
```

Appendix 1.11. Example R code for Multiple Discriminant Analysis

```
library(MASS)
library(ggplot2)

setwd("C:/Users/Quester/Desktop/Both")
Both<-read.csv("C:/Users/Quester/Desktop/Both/Morph.Both.Lakes.csv")
Anad<-filterD(Both,Form=="Anadromous",Size %in% c("Small","Large"))
Lock<-filterD(Both,Form=="Landlocked", Size %in% c("Small","Medium",
"Large"),!is.na(Pec))
Lock$Size <- factor(Lock$Size,levels=c("Small","Medium","Large"))

#Landlocked population
str(Lock)
Discr_L<-
lda(Size~Snout+Up_Jaw+Eye+Pec+Pelv+Caud_Ped+FD+Bod_Dep,prior=c(12,19,32)/6
3,data=Lock)
summary(Discr_L)
Discr_L
predict(Discr_L)
plot(Discr_L)
Discr_L$prior
Discr_L$counts
Discr_L$means
Discr_L$scaling
Discr_L$svd
prop = Discr_L$svd^2/sum(Discr_L$svd^2)
prop
plda <- predict(object = Discr_L,newdata = Lock)
dataset = data.frame(Size = Lock[, "Size"],
                      Ida = plda$x)

#Create plot
p1 <- ggplot(dataset) + geom_point(aes(lda.LD1, lda.LD2, colour = Size, shape = Size),
size = 2.5)+labs(x = paste("LD1 (", percent(prop[1]), "%)", sep=""),y = paste("LD2 (",
percent(prop[2]), "%)", sep=""))
```

Appendix 1.12. Example R code for logistic regression of prey as a function of body size.

```
library(FSA)
library(dplyr)
library(car)

setwd("C:/Users/Quester/Desktop/Both")
Length<-read.csv("Prey.Fish.Lengths.csv")

#####
##
#Perform regression

#mutate to log
Len<-mutate(Length,logF=log(Fish.L),logP=log(Prey.L))

lm1<-lm(logP~logF, data=Len)
summary(lm1)

#Plot model
library(plyr)
library(ggplot2)

MyData <- ddply(Len,.(logF),
               summarize,
               logP = seq(min(logP),
                           max(logP),
                           length = 10))

MyData

P <- predict(lm1, newdata = MyData, se = TRUE)

#Add fitted values and confidence bands
MyData$mu <- P$fit #Fitted values
MyData$selow <- P$fit - 2 * P$se.fit #lower bound
MyData$seup <- P$fit + 2 * P$se.fit #upper bound
head(MyData)

p <- ggplot()
p <- p + geom_point(data = Len,
                   aes(y = logP, x = logF),
                   shape = 16,
                   size = 3)

p
p <- p + xlab("log(Fish Length mm)") + ylab("log(Prey Length mm)")
```

```
p
p <- p + theme(text = element_text(size=15))
p
p <- p + geom_line(data = MyData,
  aes(x = logF, y = mu),
  colour = "black")
p

p <- p + geom_ribbon(data = MyData,
  aes(x = logF,
    ymax = seup,
    ymin = selow ),
  alpha = 0.5)
p
p <- p + theme (panel.background=element_blank(),panel.border = element_rect(colour
= "black", fill=NA, size=1))
p
```

Appendix 1.13. Example R code for logistic regression of length at piscivory.

```
library(FSA)
library(dplyr)
library(car)

setwd("C:/Users/Quester/Desktop/Both")
Both<-read.csv("Both.Lakes.R.csv")
Lock<-filterD(Both,Form=="Landlocked",Stom %in% c("Fish","Inverts"))
levels(Lock$Stom)

# change order of levels so that 1=fish, so that predictions are of piscivory
Lock$Stom <- factor(Lock$Stom,levels=c("Inverts","Fish"))
levels(Lock$Stom)

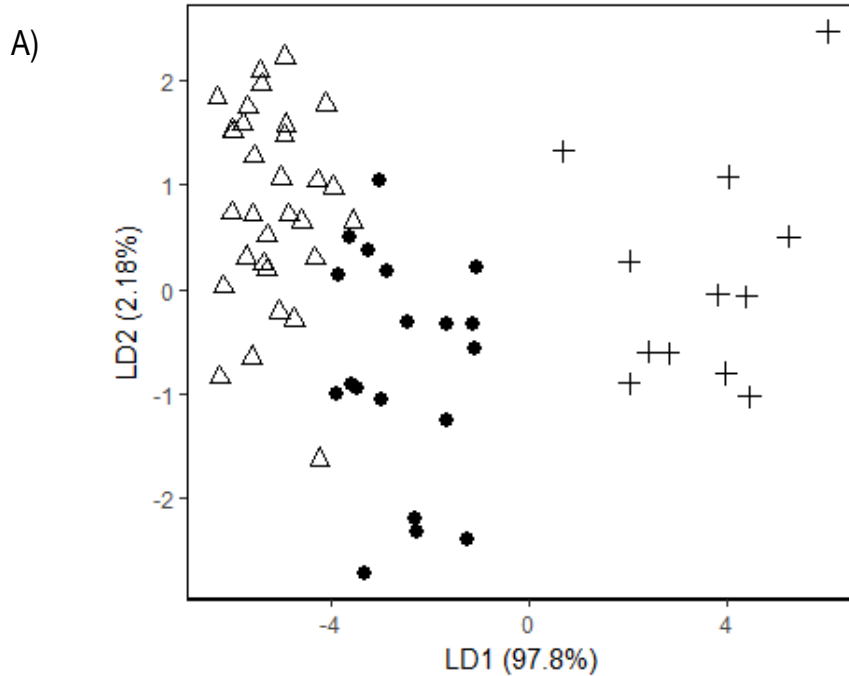
# Exploratory plots
par(mar=c(3,3,1,3),mgp=c(2,0.5,0))
plotBinResp(Stom~FL,data=Lock,breaks=15,transp=3)
hist(FL~Stom,data=Lock,w=25,nrow=2,ncol=1)
which(Lock$Stom=="Inverts" & Lock$FL>400)
Lock[27,]

#fit logistic regression
glm1 <- glm(Stom~FL,data=Lock,family=binomial)
summary(glm1)
# "automatic" see fit
fitPlot(glm1,ylab="Probability of Piscivory",xlab="Fork Length (mm)")
# "manual" see fit
plot(l(as.numeric(Stom)-1)~FL,data=Lock,xlab="Fork Length (mm)",
      yaxt="n",ylab="Probability of Piscivory",
      pch=19,col=col2rgb("black",1/3))
axis(2,c(0,1))
newdf <- data.frame(FL=seq(min(Lock$FL),max(Lock$FL),length=500))
probP <- predict(glm1,newdf,type="response")
lines(newdf$FL,probP,lwd=2,col="gray70")

#fit logistic regression without fish #27 (outlier)
glm2 <- glm(Stom~FL,data=Lock[-27,],family=binomial)
probP2 <- predict(glm2,newdf,type="response")
lines(newdf$FL,probP2,lwd=2,col="black")
legend("right",c("With Outlier","Without Oulier"),lwd=2,col=c("gray70","black"),bty="n")

# Compute length where 100P% of fish are piscivorous ... using model w/o #27
lrPerc <- function(cf,p) (log(p/(1-p))-cf[[1]])/cf[[2]]
lrPerc(coef(glm2),0.5) # 50% piscivorous
lrPerc(coef(glm2),0.9) # 90% piscivorous
```

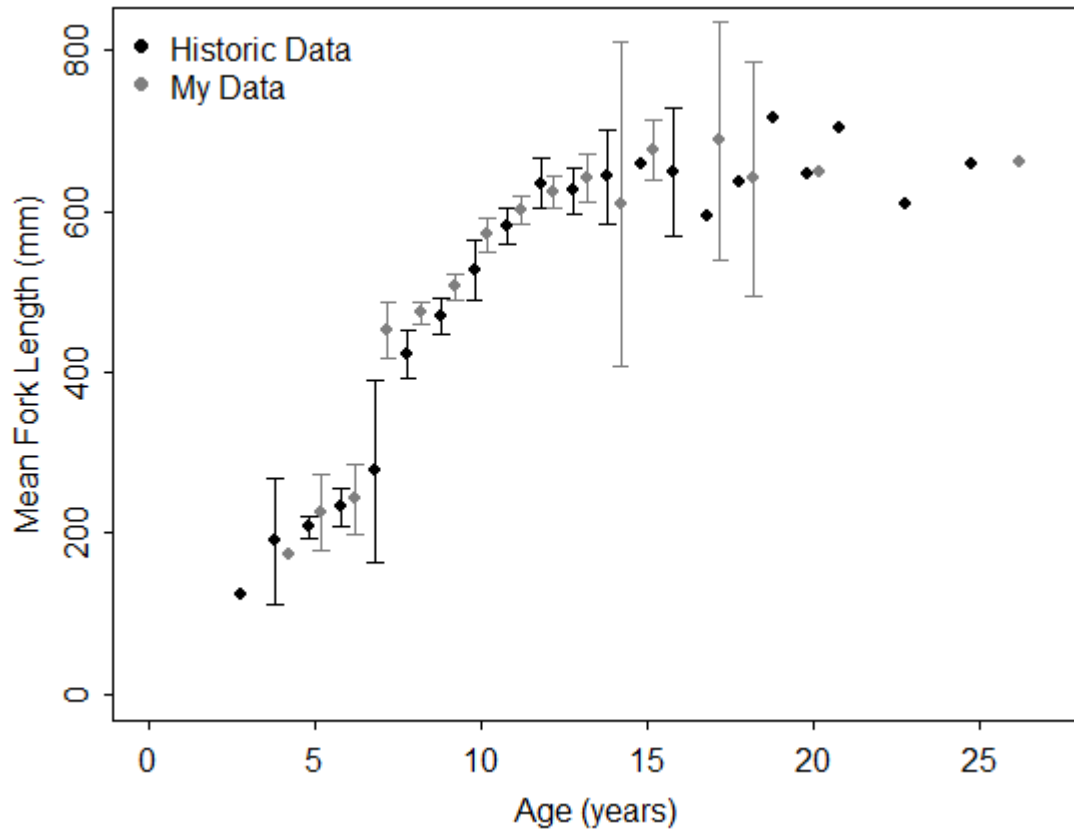
Appendix 1.14. A) Plot of MDA scores (triangles denote *Small* charr, circles denote *Medium* charr, and plus signs denote *Large* charr) and B) Table of coefficients of linear discriminants of morphological traits of landlocked charr.



B)

Morphological Characteristic	LD 1	LD 2
Body Depth	0.041	-0.035
Caudle Peduncle Width	-0.254	0.383
Eye Diameter	0.071	-1.082
Fork Depth	0.106	-0.034
Pectoral Fin Length	-0.070	-0.068
Pelvic Fin Length	-0.019	0.119
Snout Length	0.066	-0.585
Upper Jaw Length	-0.198	0.340

Appendix 1.15. Comparison graph of mean fork length at age (pooled sexes) for historic stock assessment data (2010-2014, black dots) for PG027 and the data collected by the author for this research (2011-2013, grey dots).



Appendix 1.16. Length frequency distribution of male and female landlocked charr from Qinniqtuq.

