Spatial and temporal patterns of habitat use in anadromous Arctic charr *Salvelinus alpinus* in nearshore marine and overwintering lake environments

by

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Author's Declaration

I hereby declare that I am the sole author of this thesis. This is a true copy of the thesis, including any required final revisions, as accepted by my examiners.

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

Statement of Contributions

Chapter 2: Winter movement activity patterns of anadromous Arctic charr in two Labrador lakes. I.M. Mulder, C.J. Morris, J.B. Dempson, I.A. Fleming, M. Power.

While the research was my own, all authors provided valuable contributions to the research. IMM conducted part of the fieldwork, analysed the data and wrote the paper. CJM conducted the other part of the fieldwork. The idea for the study was a collaborate effort involving JBD, IAF and MP, whereas study design was a contribute effort between all authors. IAF and MP contributed financial support. All authors provided editorial comments to the final document. The chapter was published as:

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Chapter 3: Overwinter thermal habitat use in lakes by anadromous Arctic charr. I.M. Mulder, C.J. Morris, J.B. Dempson, I.A. Fleming, M. Power.

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Chapter 4: Diel activity patterns in overwintering Labrador anadromous Arctic charr.

I.M. Mulder, J.B. Dempson, I.A. Fleming, M. Power.

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Abstract

Even though anadromy is integral to the life history of the Arctic charr (*Salvelinus alpinus*) in many northern regions, little is known about what shapes the patterns of anadromy. Moreover, little is known about the habitat use (e.g. temperature use and/or depth distribution) in relation to movement activity, especially during the overwintering freshwater residency period. An improved understanding of their behaviour in both freshwater and the marine environment will improve our understanding of how a cold-water specialist, such as Arctic charr, may respond to a changing climate, given the predicted and observed climate changes and existing hypotheses about its likely consequences for northern fishes. Accordingly, anadromous adult Arctic charr from two populations located near the southern end of the species distributional range have been studied in 2012, 2014 and 2015, to investigate the spatial and temporal patterns of habitat use in the nearshore marine and overwintering lake environments using passive acoustic and archival telemetry methods and a mixed effects modelling framework.

Research has focussed on movement activity of anadromous Arctic charr while overwintering in freshwater lakes. Results showed that movement activity declined markedly during the ice-covered period, with low movement activity suggesting only opportunistic maintenance feeding as an energy conservation strategy. Movement activity was negatively correlated with body length, with smaller individuals being more active than larger conspecifics. Although general movement activity patterns were evident, there were significant differences among individuals, particularly in the spring immediately prior to lake departure. Lake size and individual differences in metabolic rate may account for some of this variation. Photoperiod

strongly influenced the decline in movement activity in late autumn and, in combination with ice breakup, the increase in movement activity in spring.

Arctic charr utilized a narrow temperature window (0.5-2°C) during the ice-covered period and used cooler temperatures available within the middle to upper water column. Use of the selected lower temperatures is indicative of a strategy to reduce metabolic costs and minimize energy expenditure, preserving stored lipids for overwinter survival and the energetic costs of preparation for seaward migration. As Arctic charr are visual feeders, use of the upper water column is thought to aid foraging efficiency by increasing the likelihood of prey capture.

In addition to seasonal movement patterns, this thesis also focussed on diel activity patterns. Arctic charr were observed to display diurnal activity patterns throughout the overwinter residency period, likely driven by prey and light availability in the upper water column where daylight facilitates foraging efficiency by increasing the likelihood of prey capture. Movement activity increased as a function of temperature, except during winter, where cold-water temperatures associated with increased activity were likely a by-product of (opportunistic) feeding behaviour immediately below the ice. The utilization of warmer water temperatures when activity was reduced was thought to occur for the purpose of improving assimilation efficiencies in winter and preparing for outmigration during the ice breakup period.

During the marine migration, Arctic charr utilized warmer ambient water temperatures available in the upper water column, possibly to aid in physiological processes such as digestion, whereas deeper depths were suggested to be used for feeding purposes. Size-dependent thermal preferences were evident, with larger individuals utilizing cooler water temperatures compared to smaller individuals, a pattern of temperature use suggestive of

ontogenetic changes in thermal habitat use for the purpose of growth maximization. Diurnal patterns of diving activity were interpreted to reflect the vertical migration of prey items and/or to be related to the visual capabilities of Arctic charr as daytime feeding likely remains more profitable in terms of rapid food acquisition and minimization of foraging costs. Dive duration was dependent on body size with smaller individuals performing shorter dives to maintain their core temperature and abilities to both effectively capture prey and avoid predation.

This thesis is the first to provide observations of movement activity and thermal habitat use in adult anadromous Arctic charr while overwintering in freshwater lakes, and to directly test and observe size-dependent thermal preferences in Arctic charr at sea. Together, the findings of this thesis have made an important contribution to the winter ecology and marine migration of anadromous adult Arctic charr and lays the foundation for assessing future climate change effects on Arctic charr populations in Canada and elsewhere.

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Dedication

This thesis is dedicated to my grandma, Lisa Ruth Steensgaard Mortensen, for her continued support and encouragement to start this adventure, but who did not have the chance to see me finish.

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Chapter 1. General Introduction

Arctic charr, *Salvelinus alpinus*, is a cold-water specialist and the most northerly distributed freshwater fish inhabiting Arctic, sub-arctic and temperature regions. Within its range large seasonal variations in biotic and abiotic environments prevail (Johnson, 1980; Doucett et al., 1999; Klemetsen, Amundsen, et al., 2003), requiring an essential degree of natural ecological resilience and phenotypic flexibility to successfully occupy these extreme and unstable habitats (Johnson, 1980). As annual lake productively in these areas can be low (Murray, 1998), Arctic charr have developed an anadromous life-history strategy in which they make annual migrations in summer to feed in the highly productive marine environment, while overwintering in freshwater is characterized by anorexia and energy conservation (Johnson, 1980; Boivin & Power, 1990; Klemetsen, Amundsen, et al., 2003). Even though anadromy is integral to the life history of the Arctic charr in many northern regions, little is known about what shapes the patterns of anadromy. Moreover, little is known about the habitat use (e.g., temperature and/or depth distribution) in relation to movement activity, especially during the overwintering freshwater residency period, although variations in either distribution can have potentially large implications for prey resource use, growth and reproductive development (Parmesan, 2006). The limited information available likely reflects the logistical constraints associated with working in remote (sub-) Arctic regions inhabited by the species. However, given the predicted and observed climate changes and existing hypotheses about its likely consequences on northern fishes (Reist et al., 2006), such information is of increasing importance and needed to quantify the potential responses of Arctic charr populations to a changing climate.

1.1 Life history anadromous Arctic charr

Arctic charr is mostly a lacustrine species that typically spawns on the gravel bottom of lakes (Johnson, 1980). Juveniles spend the first 2-9 years (depending on latitude) in freshwater before undergoing smoltification during which several physiological, biochemical and behavioural changes prepare the species for seaward migration (Berg & Berg, 1989; Aas-Hansen et al., 2005; Murdoch et al., 2015). The timing of the descent in spring often coincides with ice break-up and consists of both first-time and repeat migrants (Dempson & Green, 1985; Berg & Berg, 1989; Spares, Dadswell, et al., 2015). The repeat migrants consist of juveniles and adults (non-maturing and maturing) of which the former typically migrate downstream first (Grainger, 1953; Johnson, 1989). Arctic charr forage in the marine environment for 30-60 days, depending on the latitude (Johnson, 1980; Dempson & Green, 1985; Svenning & Gullestad, 2002), and remain within a 30-70 km radius from the river (J. W. Moore, 1975; Gyselman, 1984, 1994; Dempson & Kristofferson, 1987), with younger fish (≤7 years) remaining in the immediate vicinity of the river mouth (J. W. Moore, 1975). Arctic charr display fast compensatory growth in the first 2-3 weeks and can double their weight in a matter of weeks (Gyselman, 1984; Rikardsen et al., 2000). As Arctic charr lack specialized anti-freeze proteins (Fletcher, Kao, & Dempson, 1988; Svenning & Gullestad, 2002; Elliott & Elliott, 2010), all migrants, including juvenile fish, return to freshwater each year to avoid seawater temperatures that reach the lower critical limit for the species (-0.99°C) (Johnson, 1980; Fletcher, Kao, & Dempson, 1988;

Svenning & Gullestad, 2002). The upstream run occurs between July and September with maturing fish (particularly females) entering the river first, followed by non-maturing adult-sized fish and smaller smolt-sized individuals returning last (Dempson & Green, 1985; Johnson, 1989; Gulseth & Nilssen, 2000). The timing of the spawning event varies among latitudes but generally occurs between September and November (Johnson, 1980; Dempson & Green, 1985). In northern populations, however, post-spawners may require more than one summer to regain their depleted energy reserves, preventing individuals from spawning two consecutive years (Dutil, 1986). The overwintering period is characterized by reduced activity and the depletion of energy reserves (J. W. Moore & Moore, 1974; Dutil, 1986; Boivin & Power, 1990). In late winter, preparations for the seawater migration start with the re-development of hypo-osmoregulatory capacity as Arctic charr are known to lose their seawater tolerance while overwintering in freshwater (Jørgensen & Arnesen, 2002; Aas-Hansen et al., 2005).

1.2 Study sites

Arctic charr populations in southern Labrador, Canada, are located toward the southern end of the distributional range of anadromous Arctic charr populations in North America (Johnson, 1980; Jørgensen & Johnsen, 2014). Gilbert and the adjacent Alexis Bays (52.58°N, 56.02°W) are located along the southern Labrador coast and cover an area of approximately 330 km^2. These narrow coastal inlets are generally less than 30 m in depth with maximum depths of ~ 100 m near the outer headlands (Copeland et al., 2012). Anadromous Arctic charr use the area for summer feeding and are known to migrate upstream in late summer to overwinter and/or spawn in Shinneys Pond (~9 km^2, 52.61°N, 56.11°W) (Morris & Green, 2012).

A second site, Sandwich Bay (53.64°N, 57.21°W) is located a degree north of Gilbert and Alexis Bays and covers an area of ~350 km^2. The bay is generally 30-40 m deep but contains a deeper basin (~80 m) near the middle of the bay. Fiver major rivers (North River, Eagle River, White Bear River, Paradise River and Muddy Bay Brook) empty into the bay, with each contributing a significant inflow of freshwater during the spring thaw. Anadromous Arctic charr are known to overwinter only in the Muddy Bay Brook system (53.62°N, 56.87°W) and enter Sandwich Bay in spring for summer feeding. A Fisheries and Oceans Canada operated counting fence facility, located 5 km upstream of the Muddy Bay Brook river mouth, monitors the annual return of salmonids, including Arctic charr, Atlantic salmon (*Salmo salar*) and sea trout (*Salvelinus fontinalis*) (Reddin et al., 2005). Climate in these areas is classified as sub-Arctic with daily air temperatures <0°C from November to April (Environmental Canada climate data) with the result that Shinneys and Muddy Bay Ponds are ice-covered from November to May.

1.3 Winter ecology

1.3.1 Seasonal movement activity

The ecology of anadromous Arctic charr while overwintering in freshwater remains poorly understood. Although the species is generally believed to reduce or cease feeding (Sprules, 1952; J. W. Moore & Moore, 1974; Dutil, 1986; Boivin & Power, 1990; Rikardsen, Amundsen, & Bodin, 2003), movement activity remains an important knowledge gap, likely because of previous logistical constrains associated with tracking species in remote regions in winter. Few authors, however, have found lake-resident Arctic charr to feed throughout the entire winter (Klemetsen, Knudsen, et al., 2003; Svenning, Klemetsen, & Olsen, 2007; M. Power et al., 2009;

Eloranta et al., 2013), and smaller post-smolt anadromous Arctic charr in northern Norway continued to feed and grow after freshwater entry in late summer, but cease feeding as water temperatures drop (Rikardsen, Amundsen, & Bodin, 2003). If Arctic charr do not feed while in fresh water body reserves can decline by 30% during the winter for nonreproductive individuals and an additional 35-46% for postspawning individuals (Dutil, 1986; Jørgensen, Johansen, & Jobling, 1997). Although Boivin & Power (1990) suggested that Arctic charr had a negative energy budget as a result of a lack of winter feeding, Boivin (1987) reported that Arctic charr actively pursued hooks and bait in the late winter. Lack of suitable prey (Boivin & Power, 1990) or the higher energy expenditure for finding and processing food may constrain winter feeding (Rikardsen, Amundsen, & Bodin, 2003) and, if fish are not feeding, related movement activity is likely to be low given presumed linkages between movement and foraging behaviour (e.g., Harrison et al., 2017). Accordingly, the conventional understanding of overwintering Arctic charr is that during winter, food intake is low and stored lipids are mobilised to meet energetic demands, which may be controlled by circannual consumption rhythms (Sæther, Johnsen, & Jobling, 1996). Reduced caloric intake is in turn associated with declining physical activity in animals (Novak et al., 2005) and in overwintering Arctic charr is suggestive of restricted movement for reasons of energy conservation.

1.3.2 Daily movement patterns

Research aimed at understanding diel patterns has focused on the experimental study of feeding and locomotory activity in hatchery reared juveniles (e.g., Linnér et al., 1990; Alanärä & Brännäs, 1997; Brännäs, 2008, 2014), on summer movement and foraging behaviour in stream-dwelling populations (Larranaga & Steingrímsson, 2015; Fingerle, Larranaga, & Steingrímsson, 2016), or on the displacement patterns of lacustrine Arctic charr (Hawley et al., 2018). Therefore, diel variation in activity patterns in overwintering wild anadromous Arctic charr remains poorly characterized. In laboratory experiments, activity patterns of Arctic charr during winter have demonstrated high variability, changing from bimodal diurnal activity to nocturnal patterns (Linnér et al., 1990). Most juvenile salmonids, but not all (e.g., Bachman, Reynolds, & Casterlin, 1979; Linnér et al., 1990), switch from being predominantly diurnal in summer to being increasingly nocturnal in winter (Bradford & Higgins, 2001; Hiscock et al., 2002; Reebs, 2002). Diel activity patterns often occur as a result of a trade-off between growth and survival that accounts for things like light intensity, temperature, predation risk, food availability, habitat condition and competition (Metcalfe, Fraser, & Burns, 1999; Reebs, 2002; Railsback et al., 2005; Brännäs, 2008, 2014; Larranaga & Steingrímsson, 2015; Fingerle, Larranaga, & Steingrímsson, 2016). Studies on the thermal dependence of locomotory activity have noted a distinct reduction in locomotory performance capacity at low body temperatures (Bennett, 1990) and a trend toward increased nocturnalism in juvenile fish as water temperatures decrease (Reebs, 2002). Other studies have concluded that photoperiod mainly influences activity patterns (Hawley et al., 2018) and that temperature simply affects the amplitude of the activity, with increased activity at warmer temperatures (Müller, 1978; Olla & Studholme, 1978).

Most salmonid diel activity research, however, has been based on observations of juvenile fish (Reebs, 2002), where the main challenge is to maximize growth (survival is often size dependent, e.g., Post & Parkinson, 2001) and avoid being eaten (Metcalfe, Fraser, & Burns, 1999). Environmental factors might affect diel activity patterns differently in adult fish, as predator avoidance behaviour by large (generally >40 cm) adult overwintering anadromous Arctic charr seems unlikely given that such fish will be among the largest in the lake and more likely to be predators than prey (Hobson & Welch, 1995; Guiguer et al., 2002).

1.3.3 Temperature use

While the physiological responses to low temperatures (e.g., growth, metabolism) are understood (e.g., Baroudy & Elliott, 1994; Garvey, Ostrand, & Wahl, 2004; Siikavuopio, Knudsen, & Amundsen, 2010; Helland et al., 2011), specifics of the use of thermal habitat for overwintering Arctic charr also remains poorly characterized as most research has focussed on the summer period or juvenile phase of the life-history (e.g., Power, O'Connell, & Dempson, 2012; Spares et al., 2012; Sinnatamby et al., 2013; Siikavuopio et al., 2014). In both laboratory experiments and in the field, juvenile and adult Arctic charr have been reported to survive temperatures at or below 1°C for extended periods of time (Fletcher, Kao, & Dempson, 1988; Klemetsen, Knudsen, et al., 2003; Amundsen & Knudsen, 2009; Siikavuopio, Knudsen, & Amundsen, 2010; Jensen & Rikardsen, 2012). Compared to other salmonids, Arctic charr have the lowest temperature tolerance, and are considered best adapted to cold water environments (Elliott & Elliott, 2010). Studies in Norway and Sweden have reported seasonal movements by lake-resident Arctic charr from summer occupied pelagic or profundal zones to the richer littoral zone in winter (Langeland et al., 1991; Hammar, 1998). Movements were thought to result from seasonal changes in the competitive interactions with co-resident brown trout (*Salmo trutta*), allowing Arctic charr to expand its dietary niche and better compete for food resources in winter because they are less affected by low light and water temperatures (Hammar, 1998; Helland et al., 2011). However, as anadromous Arctic charr are known to reduce or cease feeding while overwintering (Sprules, 1952; J. W. Moore & Moore, 1974; Dutil, 1986; Boivin & Power, 1990; Rikardsen, Amundsen, & Bodin, 2003), the selection of winter habitat is likely to be driven by factors other than the suitability of the habitat for foraging.

Among the factors which may explain or be associated with habitat use is temperature, especially as energy use may differ as a function of ambient temperature and any experienced fluctuations in temperature (Jobling, 1997). Thermal optima, the temperatures at which physiological processes are maximal, vary between consumption (feeding/digestion), respiration and reproduction (Angilletta, Niewiarowski, & Navas, 2002; Hasnain, Shuter, & Minns, 2013). Fish can use behaviour or physiology to regulate body temperature within a narrower range than the full range of available environmental temperatures to optimize physiological responses (Angilletta, Niewiarowski, & Navas, 2002). For example, studies with juvenile Arctic charr have noted that individuals behaviourally thermoregulate by selecting thermal microhabitats in summer to avoid thermal stress and/or maintain optimal temperatures for growth (e.g., Murdoch & Power, 2013; Sinnatamby et al., 2013). Temperature selection may also occur because fluctuating temperature regimes are more energetically demanding than constant temperature regimes (E. S. Hansen & Rahel, 2015; Oligny-Hébert et al., 2015). Facultative behaviour that minimizes metabolic demands in winter in fish often involves selection of thermally stable microhabitats (e.g., groundwater inflows, deeper areas in the water column) and is consistent with a strategy of choosing habitats to minimize energy costs (Cunjak & Power, 1986a).

1.4 Marine migration

The marine migration period is important in terms of restoring and accumulating annual energy reserves (Gyselman, 1984), incrementing size (i.e., growth) and determining fecundity and eventual population growth rates (Jørgensen, Johansen, & Jobling, 1997; Dempson, Shears, & Bloom, 2002). While dispersal at sea, and linkages to food intake and growth, are generally understood (Dempson & Kristofferson, 1987; Sæther, Johnsen, & Jobling, 1996; Spares et al., 2012), diel variation in temperature and depth use and their effects on marine activity patterns remains poorly characterized (Rikardsen, Diserud, et al., 2007; Morris & Green, 2012; Spares et al., 2012).

In the marine environment Arctic charr is a shallow water feeder that spends the majority of its time in the upper three meters of the water column (Rikardsen, Diserud, et al., 2007; Morris & Green, 2012; Spares et al., 2012; Jensen et al., 2016), but will descend to depths below 30 meters with short (<7 min) consecutive repetitive dives (Rikardsen, Diserud, et al., 2007; Spares et al., 2012; Jensen et al., 2016). Similar diving behaviour has been observed in other salmonids, such as Dolly Varden (*Salvelinus malma*) and Atlantic salmon (*Salmo salar*), and occurs largely during the daytime (Hedger et al., 2009; Courtney et al., 2016) with fish following the diel vertical migrations of invertebrate prey (Hays, 2003; Courtney et al., 2016) or taking advantage of daylight hours to optimize foraging efficiency (Reddin et al., 2011; Courtney et al., 2016).

Rikardsen et al. (2007) noted that deep dives were frequently followed by a marked drop in temperature for externally tagged fish, but not for internally tagged fish, suggesting that dives were too short in duration to change the internal body temperature (Rikardsen, Diserud, et al., 2007). The thermal optimum is dependent on fish behaviour and physiology and can vary among biological processes such as feeding, growth and reproduction (Angilletta, Niewiarowski, & Navas, 2002; Hasnain, Shuter, & Minns, 2013) with the result that fish may shift thermal habitats to optimize different physiological processes. For example, Spares et al. (2012) observed diving behaviour with repetitive deep dives into colder water for foraging purposes (Rikardsen, Diserud, et al., 2007; Spares et al., 2012) followed by time spent near the surface in a heat recovery phase (Spares et al., 2012) where physiological processes such as digestion, osmoregulation and respiration may be enhanced (Fry, 1971). Thus, while Arctic charr encounter and use sub-zero temperatures, they typically appear to avoid decreasing body temperatures below 0°C (Johnson, 1980; Elliott & Elliott, 2010; Spares et al., 2012).

Ontogenetic changes in thermal habitat may lead to fish partitioning thermal resources between size or age classes (Magnuson, Crowder, & Medvick, 1979; Elliott & Elliott, 2010; Morita et al., 2010). In Pacific salmonids, the optimal temperature for growth is known to decrease with increasing body size, with larger and older individuals utilizing cooler temperatures and smaller and younger individuals preferring warmer temperatures (Morita et al., 2010; Jonsson & Jonsson, 2011). For larger individuals growth is likely enhanced in cold conditions as a result of the bioenergetics advantage gained by size (Morita et al., 2010). As a result, the most frequently observed temperatures used by adult Arctic charr in the wild are typically lower than commonly cited laboratory-derived optima for juveniles, varying from 9 to 11 °C in surface waters (Rikardsen, Diserud, et al., 2007; Spares et al., 2012), and averaging 3.7 °C for individuals undertaking deep subtidal dives (Spares et al., 2012). Moreover, when ambient water temperatures change, thermal equilibrium must be re-established (Elliott, 1981). Although the gills are an effective heat exchanger, most heat (70-90%) transfers through the body wall (Elliott, 1981) and there is a time lag in reaching the thermal equilibrium which depends on fish mass. Small fish, therefore, are more susceptible to fluctuations in water temperature than larger fish (Elliott, 1981; Rikardsen, Diserud, et al., 2007) and may be expected to differentially utilize available thermal habitats as a result of the physiological constraints placed on them by body size.

1.5 Methodology

Early studies of fish migration, using acoustic transmitters, actively tracked individual fish between different habitats as long as ocean conditions and vessel or researcher stamina allowed (Nielsen et al., 2009). New technologies allow researchers to track individual fish remotely using radio and acoustic platforms, which are periodically transmitted to receivers or downloaded upon recovery (Cooke et al., 2004). Acoustic and archival tags can now be equipped with sensors (e.g., temperature, pressure, acceleration) that increase the range of behaviours that can be studied (Cooke et al., 2004) and have led to considerable advances in our understanding of fish ecology (Cooke et al., 2004; Donaldson et al., 2014). Biotelemetry provides data that are time-stamped, and allow for the near-continuous tracking of animal behaviour over long periods of time, through seasons, and in remote locations where fieldwork can be challenging (Cooke et al., 2004; Donaldson et al., 2014). Biotelemetry also allows for the simultaneous collection of data from multiple individuals. Furthermore, as tags are individually coded, sex or body size dependent behaviours can be modelled (Donaldson et al., 2014; M. K. Taylor & Cooke, 2014).

While biotelemetry provides a unique opportunity to further our understanding of animal ecology, telemetry data comes with statistical challenges. The independence of successive measures of observation in telemetry data is of most concern, as it violates the assumption of independence required in most statistical analyses (Rogers & White, 2007). Mixed effects models, however, account for correlations within repeatedly measured individuals by incorporating separate intercepts and/or slopes for individuals (Zuur, Ieno, & Smith, 2007). In these models, individual fish are treated as a random effect and the behaviour and habitat variables as fixed effects. Mixed effect statistical software (for example, R package lme4, https://cran.r-project.org) also provides the opportunity to incorporate the spatial and temporal correlation between detections from the same individual, which can bias results when not properly accounted for (Rooney, Wolfe, & Hayden, 1998; Zuur et al., 2009).

1.6 Research objectives

Given the above background, this thesis aims to investigate anadromous Arctic charr spatial and temporal patterns of habitat use in the nearshore marine and overwintering lake environments using passive acoustic and archival telemetry methods and a mixed effects modelling framework. The hypotheses of each chapter in this thesis are outlined below.

Chapter 2: Winter movement activity patterns of anadromous Arctic charr in two Labrador lakes.

This study used acoustic telemetry methods to study the movement activity patterns, including individual variation, of 57 overwintering adult anadromous Arctic charr from two lakes in southern Labrador, Canada. Specifically, the study sought to test the hypotheses that: [i] movement activity is reduced in winter after lake entry and spawning; [ii] in the fall and spring (prior to spring break-up), movement activity is positively correlated with the number of daylight hours; and [iii] ice break-up has a significant effect on the timing of the outmigration.

Chapter 3: Overwinter thermal habitat use in lakes by anadromous Arctic charr.

In this study, the thermal habitat use of 37 overwintering anadromous Arctic charr was studied during the ice-covered period in two locations in southern Labrador, Canada, using acoustic and archival telemetry methods. Telemetry data collected were used to test the hypotheses that: [i] anadromous Arctic charr show low temporal (e.g., diel, within and among years) variability in temperature use, given the metabolic advantage of stable and constant ambient temperatures; and, [ii] from among the temperatures available to anadromous Arctic charr they would use cooler water temperatures, implying residency in the upper water column.

Chapter 4: Diel activity patterns in overwintering Labrador anadromous Arctic charr.

In this study, 21 anadromous Arctic charr were double tagged with temperature sensing and accelerometer acoustic tags to determine the overwinter diel activity patterns in Muddy Bay Brook, Labrador. Specifically, this study investigated the following hypotheses: [i] Arctic charr display diel activity patterns throughout the overwinter freshwater residency period, with higher movement activity during the day; [ii] movement activity is positively correlated with temperature; and, [iii] movement activity is negatively correlated with body size.

Chapter 5: Body size and diel period shape marine temperature and depth use in anadromous Arctic charr.

In this chapter, acoustic and archival telemetry methods were used to explore relationships between body size and temperature and their effects on activity patterns in 115 anadromous Arctic charr when feeding at two locations in the marine environment. Specifically, this study sought to test the following hypotheses: [i] temperature use depends on body size with larger individuals utilizing cooler water temperatures; [ii] temperature use is related to diel period with fish [a] utilizing cooler temperatures at greater depth during the day, and [b] displaying increased vertical activity during daylight hours; [iii] diving activity depends on temperature and body size, with [a] increased vertical activity occurring at warmer body temperatures, and [b] dive duration being positively correlated with both ambient water temperature and body size.

Chapter 2: Winter movement activity patterns of anadromous Arctic charr in two Labrador lakes.

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2.1 Introduction

Arctic charr, *Salvelinus alpinus,* is the most northerly distributed freshwater fish and exhibits co-occurring anadromous and non-anadromous life history types (Johnson, 1980; Klemetsen, Amundsen, et al., 2003). Anadromous Arctic charr feed in the marine environment for several months during the summer, migrate back to freshwater in late summer to spawn and/or overwinter (Klemetsen, Amundsen, et al., 2003) and thus avoid sub-zero sea temperatures that reach the critical lower temperature limit for the species (Johnson, 1980; Svenning & Gullestad, 2002; Elliott & Elliott, 2010; Spares, Dadswell, et al., 2015). Both sexually mature and immature fish perform migrations between freshwater and the marine environment. Most Arctic charr ascend the river between July and September (Johnson, 1980; Dempson & Green, 1985; Berg & Berg, 1989; Rikardsen, Svenning, & Klemetsen, 1997; Gulseth & Nilssen, 2000). The run is often size-structured, with maturing fish (particularly females) entering the river first, followed by non-maturing adult-sized fish and smaller smolt-sized individuals returning last (Dempson & Green, 1985; Johnson, 1989; Gulseth & Nilssen, 2000).

Less is known about the descent of anadromous Arctic charr in spring, compared to the ascent during fall, although timing of transitions between salt and fresh water may be influenced locally by river of origin (J. S. Moore et al., 2016) or geographic location (Johnson, 1980). In the

Vardnes River, north Norway, first time and repeat migrants begin descent at ice break-up (Berg & Berg, 1989). Similar coincidence of ice break-up and seaward movement has been observed in Canadian rivers (Dempson & Green, 1985; Dutil, 1986; Johnson, 1989; Spares, Stokesbury, et al., 2015). Seaward migration generally occurs from early May to mid-June and is characterized by a structured size-precedence where the arrival at sea of larger fish precedes that of smaller ones (Grainger, 1953; Johnson, 1989).

While overwintering, anadromous Arctic charr are generally believed to reduce or cease feeding (Sprules, 1952; J. W. Moore & Moore, 1974; Dutil, 1986; Boivin & Power, 1990; Rikardsen, Amundsen, & Bodin, 2003). They are also poorly described in the literature in terms of their winter movement activity. Radio telemetry has been used to locate spawning and overwintering sites used by riverine anadromous Arctic charr in the Hornaday River (L. A. Harwood & Babaluk, 2014), while acoustic and archival tags have tracked movements of Norwegian riverine Arctic charr between freshwater and the marine environment and demonstrated utilization of both habitats in winter (Jensen & Rikardsen, 2008, 2012). However, movement activity in winter lake-dwelling anadromous Arctic charr populations remains poorly understood.

While lake resident Arctic charr have been found to feed throughout the entire winter (Klemetsen, Knudsen, et al., 2003; Svenning, Klemetsen, & Olsen, 2007; M. Power et al., 2009; Eloranta et al., 2013), studies of anadromous Arctic charr have indicated that upon freshwater entry feeding is reduced or absent (Sprules, 1952; Dutil, 1986; Rikardsen, Amundsen, & Bodin, 2003), with little to no feeding having been observed in studied Baffin Island (J. W. Moore & Moore, 1974) and Ungava Bay (Boivin & Power, 1990) populations. Rikardsen, Amundsen, & Bodin (2003) noted that smaller post-smolt anadromous Arctic charr continued to feed and grow after freshwater entry in late summer, but ceased feeding as water temperatures drop. If Arctic charr do not feed while in freshwater, body reserves can decline by 30% during the winter for non-reproductive individuals and an additional 35-46% for post-spawning individuals (Dutil, 1986; Jørgensen, Johansen, & Jobling, 1997). Although Boivin & Power (1990) suggested that Arctic charr had a negative energy budget as a result of a lack of winter feeding, Boivin (1987) reported that Arctic charr actively pursued hooks and bait in the late winter. Lack of suitable prey (Boivin & Power, 1990) or the higher energy expenditure for finding and processing food may constrain winter feeding (Rikardsen, Amundsen, & Bodin, 2003) and, if fish are not feeding, related movement activity is likely to be low given presumed linkages in movement and foraging behaviour (e.g., Harrison et al., 2017). Accordingly, the conventional understanding of overwintering Arctic charr is that during winter, food intake is low and stored lipids are mobilized to meet energetic demands which may be controlled by circannual consumption rhythms (Sæther, Johnsen, & Jobling, 1996). Reduced caloric intake is in turn associated with declining physical activity in animals (Novak et al., 2005) and in overwintering Arctic charr is suggestive of restricted movement for reasons of energy conservation.

Given the limited information on overwintering anadromous Arctic charr, this study used telemetry data collected from two sites to describe movement activity patterns including inter-individual variation, and to test the hypotheses that: [i] - movement activity is reduced in winter post lake entry and spawning; [ii] - in the fall and spring (prior to spring breakup) movement activity is positively correlated with increasing daylight hours; and, [iii] - ice breakup has a significant effect on the timing of the outmigration.

2.2 Methods

2.2.1 Study areas

Shinneys Pond (SP; 52.617^o N, 56.111^o W), is located in southern Labrador (Figure 2.1 - SP) and discharges via Shinneys River (~1 km long) into Gilbert Bay, part of a marine protected area established in 2005 to protect and conserve the local population of Atlantic cod, *Gadus morhua* (Canada Gezette, 2005). Throughout the summer months anadromous Arctic charr feed in Gilbert Bay and the adjacent Alexis Bay before starting the return upstream migration into the Shinneys River watershed to spawn and/or overwinter in Shinneys Pond (~9 km^2) (Morris & Green, 2012). Shinneys River is characterised by a short and steep channel, containing several low-relief falls that impede upstream fish migration when water levels are low (Morris & Green, 2012).

Muddy Bay Pond (MBP; 53.621° N, 56.879° W) empties via Muddy Bay Brook into Sandwich Bay and is located about 130 km north of Gilbert Bay (Figure 2.1 – MBP). Anadromous Arctic charr feed in Sandwich Bay throughout the summer before starting their upstream migration into Muddy Bay Brook towards their overwintering areas. Most Arctic charr are believed to overwinter in Muddy Bay Pond, the largest available lake (~13 km^2) closest to the river mouth (~15 km upstream). Muddy Bay Brook is a long and relatively wide river compared to Shinneys

River, and contains several deep pools. Both Muddy Bay and Shinneys Ponds are ice-covered from November to May.

2.2.2 Tagging and tracking

Arctic charr were captured using monofilament gill nets (63-89 mm mesh size, 25 m long) set within a 13 km radius from the river mouth in either Gilbert and Alexis Bays or Sandwich Bay, and during their upstream migration at a Fisheries and Oceans Canada operated fish counting fence at Muddy Bay Brook (Reddin et al., 2005) located 5 km upstream from the river mouth. The number of fish captured, fork length (cm), tag type and tagging dates are given in Table 2.1. Captured Arctic charr were implanted with Vemco V9 (21x9 mm, 2.2 g in water, random delay: 40-80 s), V9T (36x9 mm, 2.2 g in water, random delay: 55-85 s), V9T (36x9 mm, 2.2 g in water, random delay: 150-250 s for 60 days, 550-650 s for the following 459 days), V13T (48x13 mm, 6.5 g in water, random delay summer: 55-85 s, for 90 and 60 days the following summer, random delay winter: 570-630 s for 210 days), or V13T (48x13 mm, 6.5 g in water, random delay summer: 55-85 s, for 90 and 120 days the following summer, random delay winter: 510-630 for 240 days) coded tags. In the Muddy Bay Pond study area, an external Floy tag was attached in addition to the insertion of an acoustic tag for ease of identification at the Fisheries and Oceans Canada counting fence facility.

Individuals to be tagged were anaesthetized in a clove oil bath and measured to the nearest millimetre following loss of equilibrium. A mid-ventral incision (~2 cm) was made anterior to the pelvic girdle, after which the tag was inserted into the body cavity and pushed posteriorly, as described by Wagner et al. (2011). The incision was closed with two to three non-absorbable silk sutures (Sofsilk™ Tyco Healthcare). The surgical procedure took < 2 minutes and fish were released at or near the site of capture once they regained equilibrium. Tagging procedures followed standards and guidance provided by the Canadian Council on Animal Care (protocol # 14-12-IF), and were approved by the Northwest Atlantic Fisheries Centre animal care committee protocol (NAFC 2013-05).

An array of five acoustic receivers (model VR2W, 69 kHz, Vemco Ltd., NS, Canada) was deployed in Shinneys Pond in 2012 (6 June and 30 July 2012) and 2014 (5 June 2014) (Figure 2.1 - SP), and were ultimately downloaded and retrieved in October 2013 and July 2015 when the lifetime of all acoustic tags had expired. Similarly, an array of 10 acoustic receivers (model VR2W, 69 kHz, Vemco Ltd., NS, Canada) was deployed in Muddy Bay Pond in July and August 2015 (Figure 2.1 - MBP) and positioned to track fish throughout the lake. One receiver in Muddy Bay Pond was retrieved at the end of the field season (August) to prevent loss due to winter ice movements as it was deployed in shallow water (≤3 m). The remainder of the receivers were retrieved at the end of July 2016. All receivers were attached to buoyed lines and suspended approximately 2-8 m above the lake bottom using a chain and sub-surface buoy mechanism.

2.2.3 Data analyses

To reduce the likelihood of false detections, detections were only used in statistical analyses if a tag was detected ≥2 times per 24 hour period (Heupel, Semmens, & Hobday, 2006). Arctic charr were considered to have entered the lake from the marine environment when fish were detected by one of the lake deployed receivers. In spring, immediately before and after ice-out, fish were assumed to have left the lake after their last detection by the receivers placed nearest to the river outlet and if they were no longer detected by any other lake receivers. Arctic charr movement activity during the overwinter lake residency period was calculated using the center-of-activity method as described by Simpfendorfer, Heupel, & Hueter (2002). In our study, the mean-position estimate was calculated for Δt using a 24 hour time period, a period sufficient to capture signal receptions that represent a significant level of movement (Simpfendorfer, Heupel, & Hueter, 2002).

Daily movement activity was further analysed using linear mixed models (Gelman & Hill, 2007; Zuur et al., 2009) which were fitted using the lme4 package (Bates et al., 2015) in the statistical software R (R Core Team, 2015). The response variable of movement activity per day (m) was cube root transformed to achieve normality in the residuals, and homogenise variance across the fixed effects (Zuur et al., 2009). As year was not found to be a significant predictor of daily movement activity in Shinneys Pond ($F_{1,23.67}$=0.436, p>0.050), data from both years (2012, 2014) were combined for further analyses. The following categorical fixed effects: season and location; and continuous fixed effect: fork length, were included in the model. The continuous variable was mean centered, and all two-way interactions between fixed effects were considered. Season was categorised according to the solstices and equinoxes occurring each year: summer (22 June – 23 September), fall (24 September – 21 December), winter (22 December – 21 March), and spring (22 March – 21 June). Location included Shinneys Pond (July 2012 – May 2013, July 2014 – June 2015), and Muddy Bay Pond (July 2015 – June 2016).

Hierarchical random intercepts were fitted following Gelman & Hill (2007). Random intercepts included: Ind, representing individual Arctic charr, and the nested level $series$, a combination of individual and month. The method accounts for temporal auto-correlation at a monthly level (Gelman & Hill, 2007; Araya-Ajoy, Mathot, & Dingemanse, 2015). The final model took the form:

(Equation 2.1)

$$y_{ijk} = \left(\beta_0 + Ind_{0j} + series_{0jk}\right) + Season_{ijk} + Location_{ijk} + Fork\ length_j$$
$$+ Season \times Location_{ijk} + Season \times Fork\ length_{ijk} + e_{0ijk}$$

Where y_{ijk} is equivalent to the movement activity per day (m) at instance i, for individual fish j, during tracking series k. Backwards selection was performed for all fixed and random effect components using the lmerTest package (Kuznetsova, Brockhoff, & Christensen, 2015) in R. The p-values for the fixed effects were calculated from the F-test based on Sattethwaite's approximation, whereas the p-values for the random effects were based on likelihood ratio tests (Kuznetsova, Brockhoff, & Christensen, 2015).

To test whether the decrease in movement activity in fall, and the increase of movements in spring were driven by decreasing and increasing daylight hours, nonlinear regressions (Ratkowsky, 1990) were fitted to the data. The response variable (mean daily averaged movement activity) was averaged for all detected fish for each day in the fall and spring. Averaged movement activity data were cube root (spring) or square root (fall) transformed to satisfy model assumptions. The continuous variable day length (hours) was mean centered and included as the fixed effect. Day length was calculated using sunset and sunrise times at 52.617°N, 56.111°W for Shinneys Pond, and at 53.621°N, 56.879°W for Muddy Bay Pond (www.nrc-cnrc.gc.ca/eng/services/sunrise/advanced.html), as day length varies considerably over a year at this northern latitude. Times were computed using standard scientific formulae as adopted by the national almanac offices of the United States, United Kingdom and the NRC Herzberg Institute of Astrophysics in Canada and are considered accurate to ±2 minutes for the period 1900-2100 (www.nrc-cnrc.gc.ca/eng/services/sunrise/accuracy.html). The nonlinear regressions for fall and spring were compared between locations using analysis of residual sum of squares as follows (Haddon, 2001):

(Equation 2.2)

$$F = \frac{RSS_p - \sum_{i=1}^{m} RSS_i \;/\; DF_p - \sum_{i=1}^{m} DF_i}{\sum_{i=1} RSS_i \;/\; DF_i}$$

Where RSS_p defines the residuals sum of squares derived from the nonlinear regression estimated using the pooled movement data in fall (or spring) from Shinneys Pond and Muddy Bay Pond, DF_p is the degrees of freedom associated with the pooled model, RSS_i is the residual sum of squares for i th compared location, DF_i is the associated degrees of freedom for the i th location specific movement model and m is the number of models compared (Haddon, 2001).

To test the timing of ice breakup as a predictor for departure time (absence or presence in lake during the period of outmigration), a generalized linear model with a binomial distribution and logit fit was used. Timing of ice breakup was based on the onset of spring turnover, when the lakes mixed and water temperatures became equal throughout the water column (Wetzel, 2001). Water temperature data were collected by data loggers (one hour sampling interval, accuracy 0.53 °C, resolution 0.15 °C; Onset Hobo Data Loggers UA-001-64/UA-002-64) deployed year around at different depths in both lakes. As a result, ice breakup was estimated to start 18 May 2015 in Shinneys Pond (coinciding with one day prior to peak river discharge), and on 19 May 2016 in Muddy Bay Pond. No water temperature data were available in Shinneys Pond 2013, therefore ice breakup was based on discharge data (data from Department of Environment and Climate Change) from the neighbouring Alexis River which is similar in catchment area and river characteristics (personal communication C.J. Morris). Ice breakup was estimated to start on 16 May 2013, a day prior to peak discharge. All analyses were performed using the statistical software R, with significance judged at the $\alpha=0.050$ level of significance.

2.3 Results

In Gilbert Bay, 39% and 46% of the Arctic charr implanted with an acoustic tag were detected entering Shinneys Pond in 2012 and 2014, respectively (Figure 2.2), whereas 65% of the Arctic charr implanted with an acoustic tag entered Muddy Bay Pond (Figure 2.2). There was a small (x=2.5 cm) but significant difference in the mean fork length of detected Arctic charr between years in Shinneys Pond (two-sample t-test $p=0.041$), but no significant difference between locations (two-sample t-test $p=0.536$).

Not all Arctic charr were detected throughout their entire lake residency period as some tags had insufficient battery power to sustain continual overwinter transmission. In Shinneys Pond, 15 of 22 charr that entered in 2012 (mean fork length ± SD: 39.5 ± 3.2 cm), and 14 of 16 that entered in 2014 (mean fork length: 40.9 ± 3.5 cm) were detected throughout their entire lake residency period (July-May/June). Similarly, 28 of 53 charr that entered Muddy Bay Pond in

2015 (mean fork length: 41.6 ± 3.2 cm) were detected during their entire residency in freshwater.

2.3.1 Migration timing

Tagged fish entered Shinneys Pond between 14 July - 15 August 2012, with 90% of all fish entering between 14 July - 24 July 2012. The upstream migration in 2014 was more protracted with Arctic charr entering between 13 July - 23 September (90% between 13 July - 25 August 2014). Tagged Arctic charr entered Muddy Bay Pond between 15 July - 17 September, with 90% of all fish entering between 15 July - 11 August 2015. A size-precedence was visible in the Muddy Bay Pond data, with larger fish entering first, but this was not observed in Shinneys Pond. Arctic charr migrated upstream (distance between the river mouth and the lake) with an average speed of 534 ± 368 m/day and 2781 ± 1174 m/day in Shinneys and Muddy Bay Ponds, respectively. At both locations, Arctic charr migrated directly into the lakes and made no attempts to re-enter the estuary.

In Shinneys Pond the outmigration occurred from 12-29 May in 2013 (90% between 12-24 May 2013) and from 23 May – 3 June in 2015 (90% of all fish departing between 23 May – 31 May 2015). At Muddy Bay Pond outmigration began 7 May and continued until 6 June 2016 (90% between 7 May – 30 May 2015). No structured size-precedence was observed during the descent at either of the two study locations.

2.3.2 Movements

In the model relating individual movement activity (m/day) to season, location, fork length and its interactions, season and location were found to be significant predictors of movement activity, although season was moderated by fork length and location ($p<0.050$, Table 2.2). Movement activity differed significantly between locations and was generally higher in Muddy Bay Pond during all seasons, except spring (Figure 2.3). Winter activity declined considerably in comparison to the summer and fall in both lakes (Figure 2.3). Fork length had no direct effect on movement activity ($p=0.090$, Table 2.2), however, the interaction between fork length and season was a significant predictor of daily movement activity ($p<0.001$, Table 2.2, Figure 2.4). In summer, movement activity was positively correlated with fork length, where larger Arctic charr had higher movement rates. During the fall, winter and spring, movements were negatively correlated with fork length (Figure 2.4). The interaction between fork length and location was not a significant predictor of movement activity ($F_{1,74.51}=0.002$, $p>0.050$) and was removed through backwards selection.

There was an increase in spring movement activity prior to ice-out in all years and lakes, although individual patterns varied between locations. Plots of average movement activity per day over the 7-21 day period preceding lake departure (Figure 2.5) indicated that Arctic charr in both locations moved similar distances (215 m/day ± 30 m/day). Differences between the two lakes became more apparent closer to the departure date. In the last week prior to outmigration (day 14-21, Figure 2.5) Arctic charr increased their movement activity to 531 m/day ± 233 m/day and 917 m/day ± 261 m/day in Shinneys and Muddy Bay Ponds, respectively. Fork length was not a significant predictor of movement activity ($F_{1,47.47}$=3.116, p>0.050) during the period immediately prior to ice-out.

Individual movement activity observed during the pre-ice-out period was categorized into three types (Figure 2.6). Type 1 patterns showed increased movement immediately prior to lake departure and varied from 1-10 days and 1-6 days in Muddy Bay Brook and Shinneys Pond, respectively. Type 2 movement patterns depict pulsed activity with Arctic charr moving towards the river outlet followed by a period of non-activity prior to departure. This pattern was mostly observed in Shinneys Pond (N=7), especially in 2013 (N=6), and only once in Muddy Bay Pond (Figure 2.6). Type 3 patterns showed active movement throughout the three weeks prior to lake departure, with alternating periods of movement and rest. Based on individual trackings, the movement was not directed towards positioning the fish at the river outlet until a few days before departure. The relative frequency of the patterns in both Shinneys and Muddy Bay Ponds are presented in Figure 2.6, with Type 1 behaviour dominating in Shinneys Pond, particularly in 2015, and Type 1 and 3 behaviours equally prevalent in Muddy Bay Pond.

As movement activity (m/day) was not significantly different between years in Shinneys Pond (Figure 2.3), both years (2012, 2014) were combined for further analyses. Movement activity was positively correlated with day length, as activity levels declined with decreasing daylight hours in fall (SP, $F_{2,172}$=22.77, $p<0.001$, R^2=0.204; MBP, $F_{2,86}$=73.29, $p<0.001$, R^2=0.622) (Figure 2.7, A-B), and increased with increasing daylight hours in the period prior to spring breakup (SP, $F_{3,131}$=42.15, $p<0.001$, R^2=0.479; MBP, $F_{3,68}$=134.80, $p<0.001$, R^2=0.849) (Figure 2.7, C-D).

Location was a significant predictor of movement activity in spring ($p<0.050$), as Arctic charr in Muddy Bay Pond showed a greater increase in activity with increasing daylight hours compared to Arctic charr in Shinneys Pond (Figure 2.7, C-D). Location had no significant effect ($p>0.050$) on fall movement activity.

The timing of ice breakup had a significant effect ($p<0.001$) on departure time. The probability of leaving the lake immediately after ice breakup was significantly greater (0.927, CI: 0.818-0.972) than departing before ice breakup (0.073, CI: 0.018-0.254). Respectively, 92.3%, 50.0%, and 87.5% of the tagged Arctic charr departed Shinneys Pond (2013, 2015) and Muddy Bay Pond (2016) within 10 days following ice breakup.

2.4 Discussion

Data collected on anadromous Arctic charr from the two lakes were consistent with the presumed reductions in movement activity during the ice-covered period. As hypothesized, movement activity was positively correlated with ambient light levels rising in spring and falling in autumn. Although general movement patterns were evident, there were significant differences among individuals, particularly in spring immediately prior to outmigration.

Reduced winter activity observed in this study is not uncommon among fish (Huusko et al., 2007; Shuter et al., 2012), especially as fish are ectotherms whose activity levels are primarily controlled by water temperature through its effect on critical biological rates and metabolic processes (Fry, 1971; Shuter et al., 2012). Low water temperatures reduce movement activity and feeding, with lower activity suggestive of opportunistic maintenance feeding as an energy conservation strategy in winter (Huusko et al., 2007). Similar observations have been reported in stream salmonids where the composition of diet in winter reflects reduced opportunistic feeding from both the drift and benthos (Cunjak & Power, 1987; Huusko et al., 2007). The late fall, early winter period (October – December) is the most energetically demanding for stream fish as it is characterized by acclimatization to declining temperatures (Cunjak & Power, 1987; Cunjak, 1988). Temperature acclimation and reproduction can deplete energy reserves (Cunjak, 1988), with depletion of lipid levels and increased body water content noted in winter sampled Arctic charr, brook charr (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) (Cunjak & Power, 1986b, 1987; Dutil, 1986; Cunjak, 1988), particularly in post-spawning fish (Jørgensen, Johansen, & Jobling, 1997; Hutchings et al., 1999). As cold-water temperatures reduce appetite and lower assimilation efficiencies (Cunjak & Power, 1987; Huusko et al., 2007), the energetic value of consumed foods may be insufficient to provide maintenance metabolism (Cunjak & Power, 1987). In this context, reduced winter activity in Arctic charr, as noted here, may be an energy minimizing strategy that both improves winter survival and conserves energy for subsequent outmigration.

Correlations between movement activity and daylight hours in the fall and spring accord well with what is known about general relationships between salmonid activity and physiology. In salmonids, photoperiod is known to be an important environmental cue for initiating physiological changes, such as smoltification or timing of outmigration (Bradshaw & Holzapfel, 2007). Additionally, changes in photoperiod can alter evacuation rates in Atlantic salmon

(*Salmo salar*), independent of water temperature (J.E. Thorpe, in Cunjak & Power (1987)). Increases in (late winter) photoperiod are also known to initiate increased growth rates in juvenile salmonids (Higgins & Talbot, 1985; T. Hansen, Stefansson, & Taranger, 1992; J. F. Taylor et al., 2005), and improve swimming performance in other species (Kolok, 1991). Declining photoperiod has been reported to depress growth (Skilbrei, Hansen, & Stefansson, 1997; Duncan & Bromage, 1998) and reduce activity (Fritz, Meredith, & Lotrich, 1975). In this context, photoperiod is suggested to depress or initiate movement activity in Arctic charr in preparation for the winter or spring (outmigration). However, the timing of these events itself is likely influenced by immediate environmental conditions, such as water temperature, flow or ice breakup, that account for the annual variation in the thermal environment (Bradshaw & Holzapfel, 2007).

In addition to photoperiod, other factors are likely to contribute to the change in movement activity in the fall and spring. Lab experiments have shown that seasonal cycles in food consumption in Arctic charr persist under constant photoperiod and temperature (Sæther, Johnsen, & Jobling, 1996; Tveiten, Johnsen, & Jobling, 1996). Moreover, Arctic charr growth is not especially prone to acute photostimulation (Bottengård & Jørgensen, 2008) or chronic melatonin implantation (Aarseth, Frøiland, & Jørgensen, 2010). These results are suggestive of the importance of stronger endogenous rhythms or threshold conditions for determining activity levels. Sæther, Johnsen, & Jobling (1996) concluded that the seasonal rhythms of appetite and growth in Arctic charr follow an endogenous rhythm of close to 12 months. It is expected then, that fish anticipate food availability and activate their physiological processes in advance to avoid risk or exploit food resources more efficiently (Houlihan, Boujard, & Jobling, 2001), even at the low ambient light levels associated with ice-cover and short day lengths in winter.

Tveiten, Johnsen, & Jobling (1996) also suggested that low condition and depleted energy reserves may stimulate fish to increase food intake and associated foraging activity. Size appears to moderate the effect, as noted in our data by the negative correlation between fork length and movement activity in both spring and fall. Higher metabolic rates in smaller fish result in a greater proportion of stored energy reserves being used over the winter (Love, 1980; Byström et al., 2006), likely requiring smaller fish to forage and move more than larger fish. This is supported by a previous study which concluded that small Arctic charr are more likely to starve during winter if unable to feed (Byström et al., 2006).

Inter-individual variation in movement was evident particularly in the three weeks prior to lake departure, with more and less active patterns evident in all lakes in all years. Consistent inter-individual variation of spatial behavioural differences are increasingly recognized as revealed by animal telemetry (M. K. Taylor & Cooke, 2014; Harrison et al., 2015; Spares, Stokesbury, et al., 2015; Villegas-Ríos et al., 2017). Personality-dependent home range, movement and dispersal have been reported for burbot (*Lota lota*) in which behaviour types ranged from ‘resident’ individuals with small home ranges, to ‘mobile’ individuals with large home ranges (Harrison et al., 2015). Similar relationships have also been reported for Atlantic salmon (Cutts, Metcalfe, & Taylor, 1998) and Arctic charr (Cutts, Adams, & Campbell, 2001). Individual differences within populations may result from individual variation in resting metabolic rate (Careau et al., 2008). Animals with higher metabolic rates require higher foraging efforts to satisfy metabolic demands that are probably correlated with increased activity, particularly in spring when energy reserves are actually low or non-existent.

Onset of seaward migration before ice breakup has been anecdotally reported in other systems in Baffin Island (Grainger, 1953; J. W. Moore, 1975). The majority of fish, however, appear to depart coincidently with, or immediately after, ice breakup (this study, Dempson & Green, 1985; Berg & Berg, 1989; Johnson, 1989). While outmigration has been reported to follow a size-structured sequence, with the largest Arctic charr descending first (Grainger, 1953; Johnson, 1989), no size-precedence was detected in tagged fish from either Shinneys Pond or Muddy Bay Pond. The small sample size and relatively narrow size range, however, may have confounded detection of any patterns in this study.

Differences in the intensity of movement between sites are suggestive of the importance of lake size for determining movement activity patterns. Home range has been reported to be a continuous function of water body size, in which fish increase their home range with increasing lake size (Woolnough, Downing, & Newton, 2009). When unhampered, fish swim longer distances more frequently, possibly in search of increased resource availability (Boisclair & Tang, 1993; Breau & Grant, 2002). This accords with the increased movement activity observed in Muddy Bay Pond, which is a larger elongated shaped lake compared to the smaller, more confined Shinneys Pond.

2.5 Conclusions

This study provides some of the first observations of movement activity in anadromous Arctic charr while overwintering in freshwater lakes. Results show that movement activity declines markedly during the ice-cover period, with low movement activity suggesting only opportunistic maintenance feeding. Although general movement activity patterns were evident, there were significant differences among individuals, particularly in the spring immediately prior to lake departure. Lake size and individual differences in metabolic rate may account for some of this variation. Photoperiod strongly influenced the decline in movement activity in late autumn and, in combination with ice breakup, the increase in movement activity in spring. As the populations in this study originate from the southern end of the distributional range of anadromous Arctic charr, further investigations are required to determine the generality of the results for more northerly populations.

Table 2.1. Tagging data for Arctic charr tagged in Gilbert Bay (2012, 2014) and Muddy Bay Brook (2015)

Location	Year	Tagging dates	Tag type	No. fish tagged	Mean fork length ± SD (cm)
Gilbert Bay	2012	9-13 June, 31 July	V9T	10	34.9 ± 4.5
			V13T	46	38.7 ± 3.2
	2014	3, 4 June	V13T	35	40.8 ± 3.1
Muddy Bay Brook	2015	4 June – 6 July[†]	V9	10	28.5 ± 6.7
			V9T	21	34.3 ± 5.2
			V13T	20	40.5 ± 3.4
		13, 14 July[‡]	V9T	30	42.7 ± 3.1

[†] Fish tagged in the marine environment.

[‡] Fish tagged at the Fisheries and Oceans Canada operated counting fence.

Table 2.2. The final model (equation 2.1) including the random and fixed effects for the linear mixed effect model of movement activity (m/day) in Arctic charr. Marginal and conditional R^2 values were calculated using the methods described in Nakagawa & Schielzeth (2013). Parameter significance is shown, displaying degrees of freedom (df), F values, and P values calculated from F-tests based on Sattethwaite's approximation (Kuznetsova, Brockhoff, & Christensen, 2015).

Final model	$R^2_{marginal}$	$R^2_{conditional}$
Season + Location + Fork length + Season:Location + Season:Fork length + Ind + Series	0.103	0.305
Parameters	**Chi.sq/F value**	**P value**
Random effects:		
Ind (Arctic charr)	20.42, df=1	0.000
Series (Arctic charr*month)	1457.66, df=1	<0.001
Fixed effects:		
Fork length	2.93, ndf=1, ddf=96.47	0.090
Season	36.13, ndf=3, ddf=2531.90	<0.001
Location	75.91, ndf=1, ddf=58.69	<0.001
Fork length:Season	6.69, ndf=3, ddf=2996.44	0.001
Season:Location	34.28, ndf=3, ddf=2562.60	<0.001

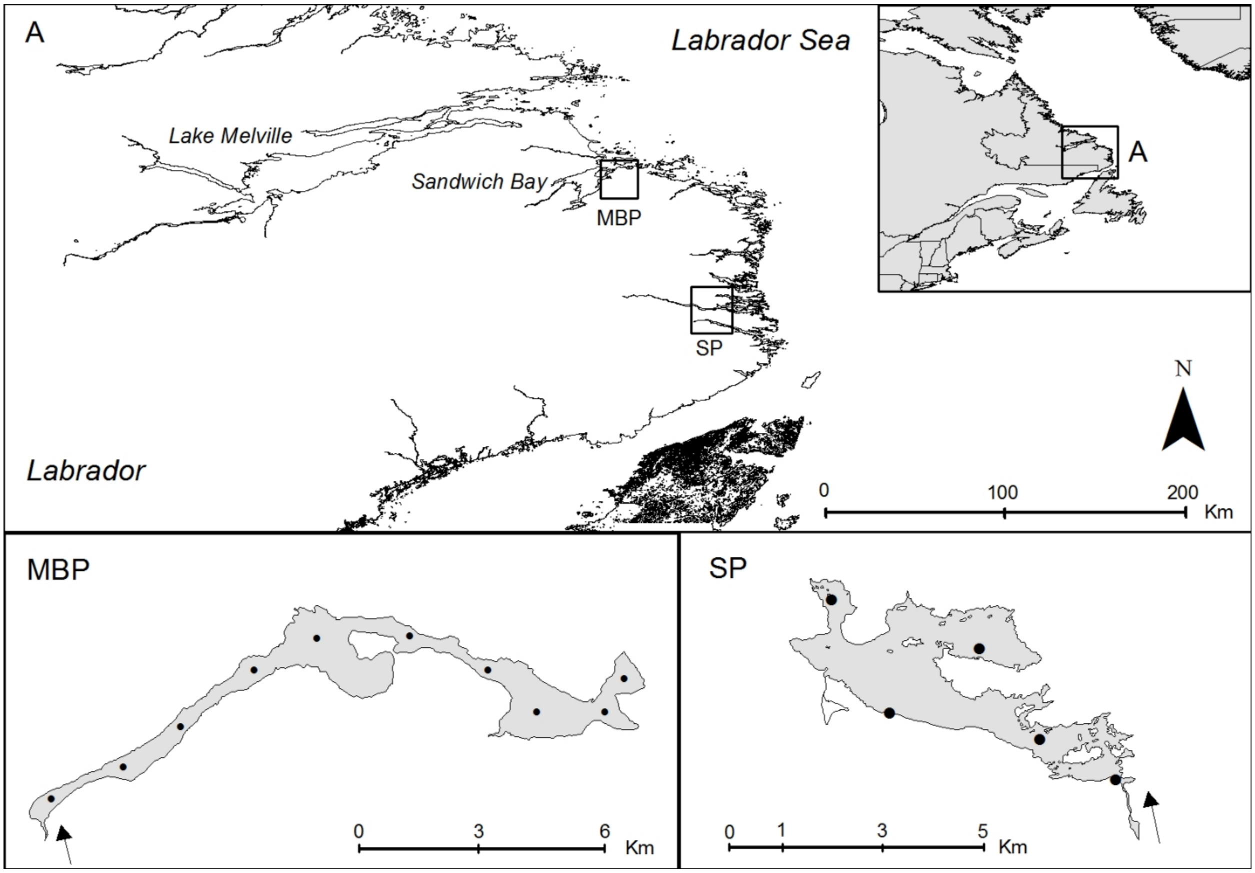

Figure 2.1. Map of the study area showing the locations of Shinneys Pond (SP) and Muddy Bay Pond (MBP) with respect to the Labrador coast. The black dots (bottom panels) indicate receiver locations, and the arrows indicate the location where Arctic charr enter each pond.

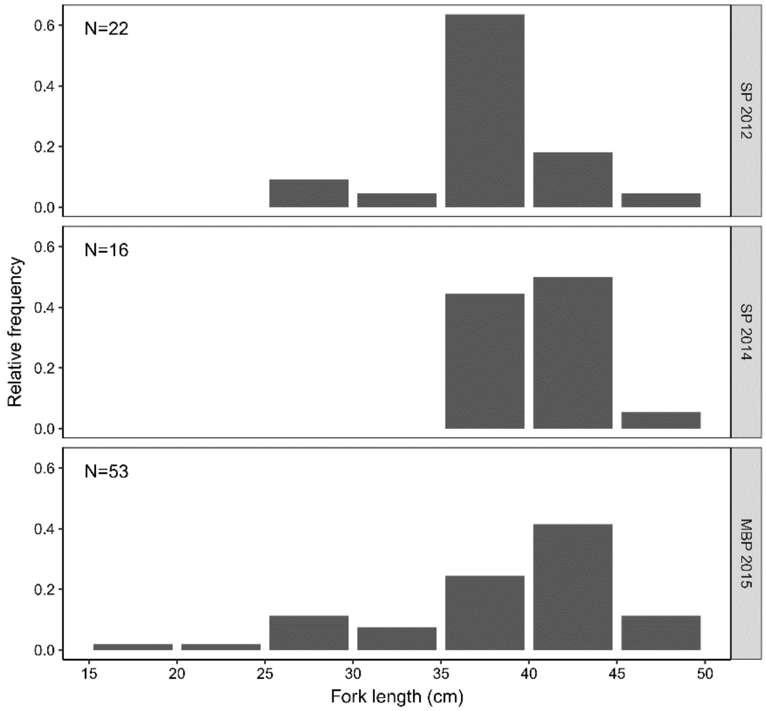

Figure 2.2. Length frequency distribution and number of acoustically tagged Arctic charr detected in Shinneys Pond (2012-2015) and Muddy Bay Pond (2015-2016).

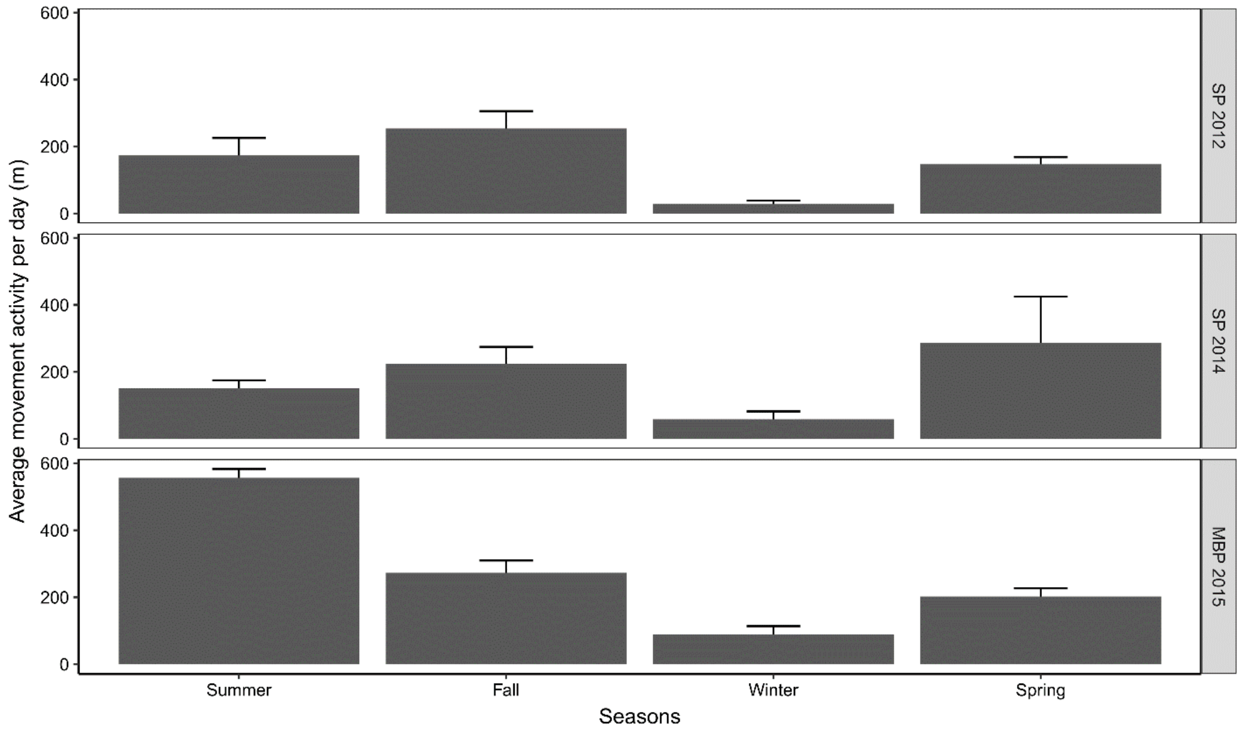

Figure 2.3. Seasonal average daily movement activity for Arctic charr in Shinneys Pond (2012, 2014) and Muddy Bay Pond (2015). The standard errors are indicated by the error bars. Summer and spring considered freshwater residency period only.

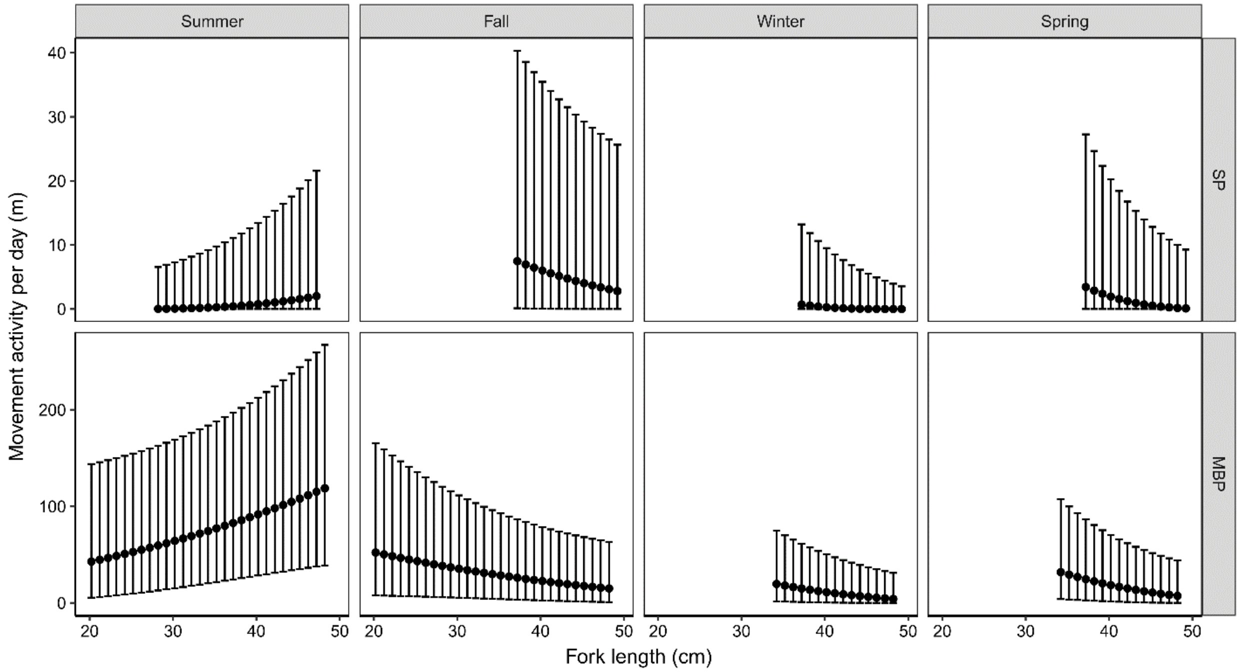

Figure 2.4. Model estimates (equation 1, Table 2.2) of Arctic charr movement activity (m/day) by season, location (SP, MBP) and fork length (cm). The 95% confidence intervals are based on the uncertainty of both the fixed and random effects. Summer and spring considered only the freshwater residency period. Note that the y-axes display different ranges in movement activity between locations.

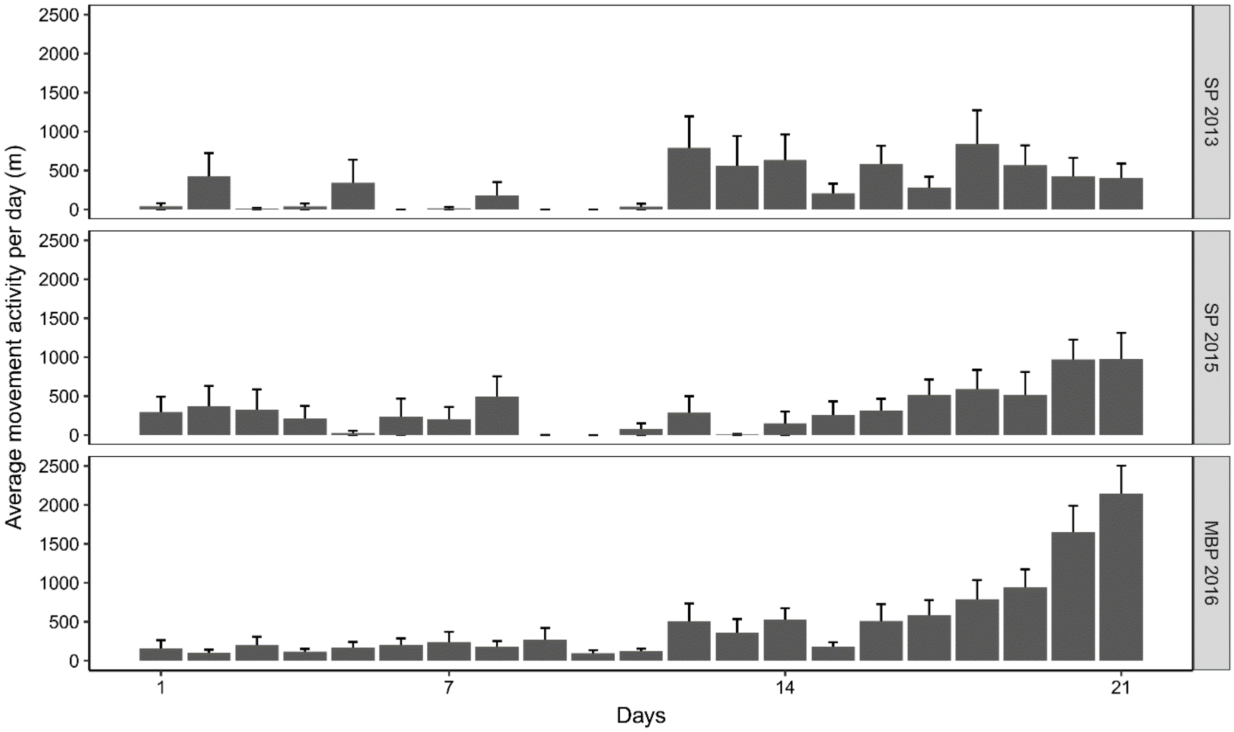

Figure 2.5. Average movement activity (m/day) of Arctic charr during the three weeks preceding outmigration from overwintering in Shinneys Pond during 2013 (SP2013) and 2015 (SP2015), and Muddy Bay Pond during 2016 (MBP2016). The standard errors are indicated by the error bars.

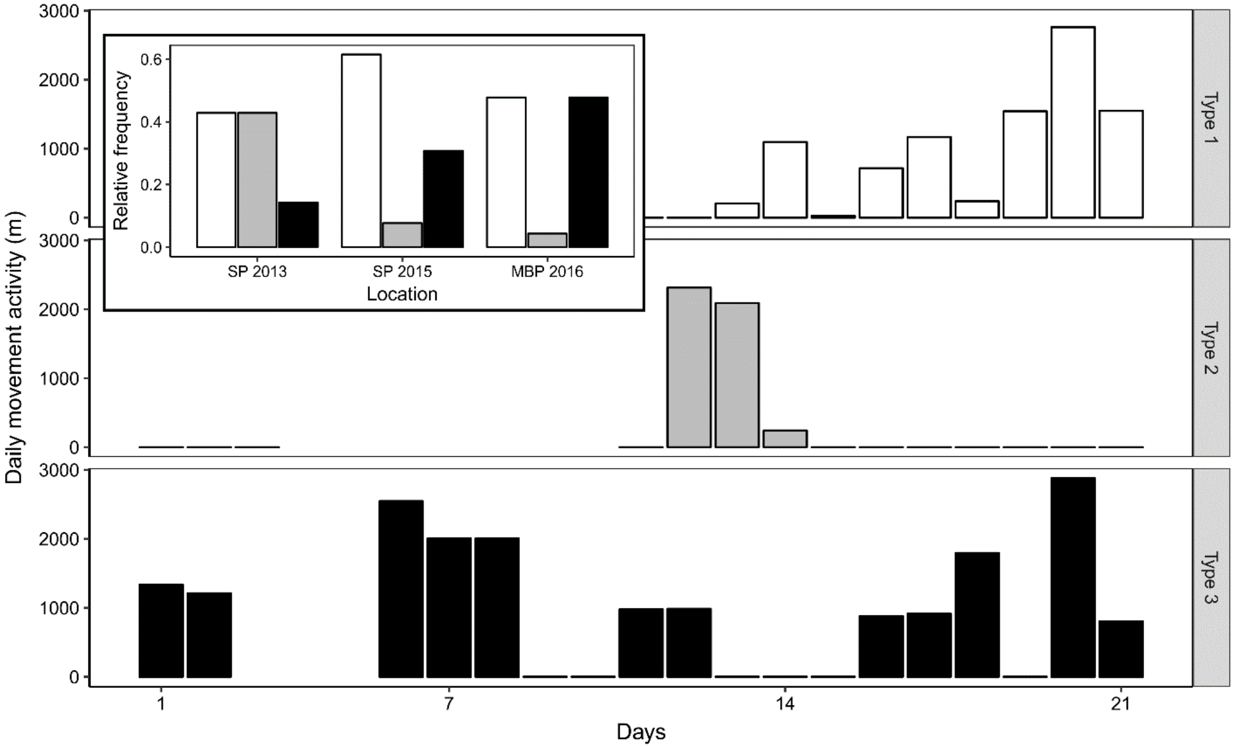

Figure 2.6. Examples of characteristic movement activity patterns by Arctic charr, displayed during the three weeks preceding outmigration. Departure times are standardized to occur on day 21. Type 1 (open bars) shows increasing activity immediately prior to departure. Type 2 (shaded bars) depicts pulsed activity, with the fish moving toward the lake outlet followed by a period of non-activity prior to departure. Type 3 (solid bars) shows intermittent movement activity prior to lake departure. The relative frequency of these patterns in Shinneys Pond (2013, 2015) and Muddy Bay Pond (2016) are presented in the upper left corner panel.

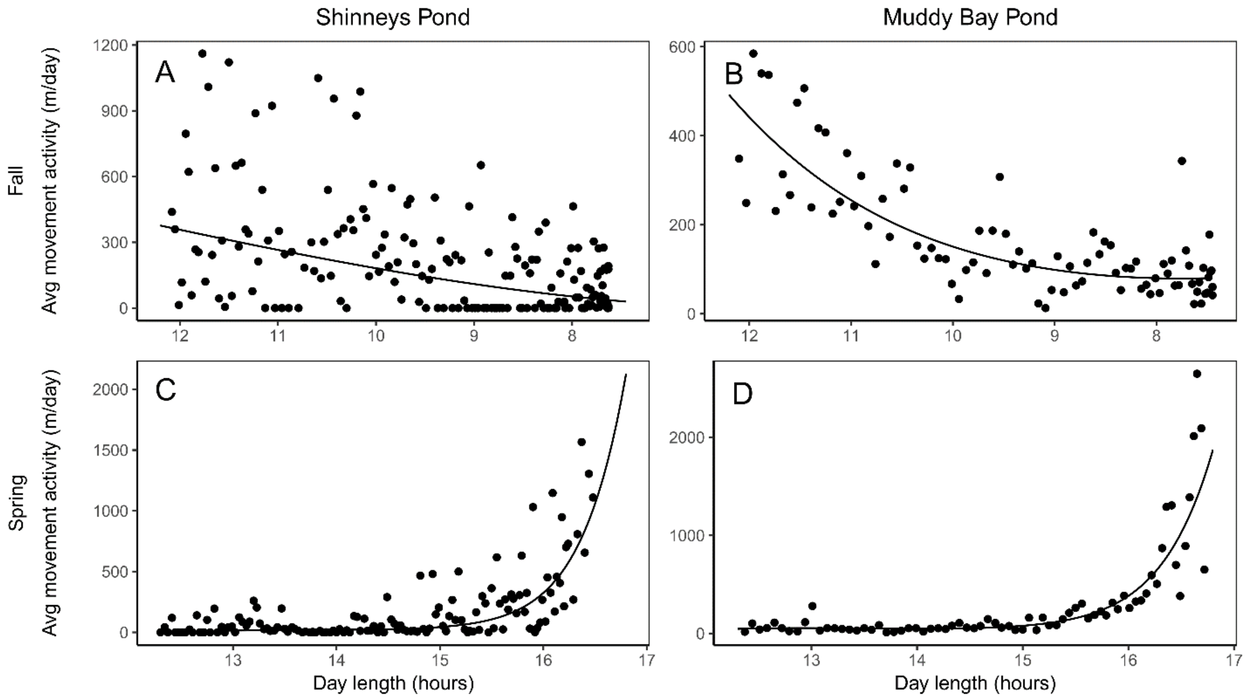

Figure 2.7. The relationship between average movement activity (m/day) and day length during fall (top panels) and spring (bottom panels) in Shinneys Pond (left panels) and Muddy Bay Pond (right panels). Smoothing functions were modelled from the nonlinear regressions using a quadratic (fall) and cubic (spring) regression spline. Note the x-axes are reversed in panels A and B, and the y-axes display different ranges in movement activity and day length between seasons and locations.

Chapter 3: Overwinter thermal habitat use in lakes by anadromous Arctic charr

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3.1 Introduction

Anadromous Arctic charr (*Salvelinus alpinus*) achieve most of their growth by feeding in the marine environment for one to two months each summer, and migrate back to freshwater in late summer to reproduce and/or overwinter (Johnson, 1980; Klemetsen, Amundsen, et al., 2003). Overwintering in freshwater is generally thought to be related to low salinity tolerance in combination with winter marine temperatures that reach the critical lower limit for the species (Johnson, 1980; Svenning & Gullestad, 2002; Elliott & Elliott, 2010). Arctic charr lack specialized anti-freeze proteins to allow them to survive water temperatures <−0.99°C at which their blood freezes and thus are believed to avoid such risk by migrating into freshwater as marine temperatures approach 0°C (Fletcher, Kao, & Dempson, 1988; Svenning & Gullestad, 2002).

Upon freshwater entry in late summer, feeding is reduced or absent in anadromous Arctic charr populations (Sprules, 1952; J. W. Moore & Moore, 1974; Dutil, 1986; Boivin & Power, 1990; Rikardsen, Amundsen, & Bodin, 2003) and movement activity is restricted (Mulder et al., 2018a), with the main purpose of minimizing energy to improve overwinter survival (Huusko et al., 2007; Shuter et al., 2012). Within ice-covered lakes temperature will vary between 0 and 4°C, with warmer temperatures predominating at depth (Matthews & Heaney, 1987; Wetzel, 2001). While the physiological responses to low temperatures (e.g., growth, metabolism) are understood (e.g., Baroudy & Elliott, 1994; Garvey, Ostrand, & Wahl, 2004; Siikavuopio, Knudsen, & Amundsen, 2010; Helland et al., 2011), specifics of the use of thermal habitat for overwintering Arctic charr remains poorly characterized as most research has focussed on the summer period or juvenile phase of the life-history (e.g., Power, O'Connell, & Dempson, 2012; Spares et al., 2012; Sinnatamby et al., 2013; Siikavuopio et al., 2014).

In laboratory experiments, juvenile Arctic charr have been reported to survive temperatures at or below 1°C for extended periods of time (Fletcher, Kao, & Dempson, 1988; Siikavuopio, Knudsen, & Amundsen, 2010). Similar observations have been made in the field, where resident juvenile and adult Arctic charr are known to feed and grow under ice cover at temperatures close to 0°C (Brännäs & Wiklund, 1992; Klemetsen, Knudsen, et al., 2003; Larsson et al., 2005; Byström et al., 2006; Amundsen & Knudsen, 2009; Siikavuopio et al., 2009; Helland et al., 2011). Moreover, limited data (N=6) from archival tagged anadromous Arctic charr from the Skibotn River, north Norway, have shown fish will reside at temperatures as low as 1.4°C for extended periods of time (Jensen & Rikardsen, 2012). Compared to other salmonids, Arctic charr have the lowest temperature tolerance, and are considered best adapted to cold water environments (Elliott & Elliott, 2010).

Studies in Norway and Sweden have reported seasonal movements by lake-resident Arctic charr from summer occupied pelagic or profundal zones to the richer littoral zone in winter (Langeland et al., 1991; Hammar, 1998). Movements are thought to result from seasonal changes in the competitive interactions with co-resident brown trout (*Salmo trutta*), allowing Arctic charr to expand its dietary niche and better compete for food resources in winter because they are less affected by low light and water temperatures (Hammar, 1998; Helland et al., 2011). Similar habitat shifts have been reported for lake trout (*Salvelinus namaycush*) that move from a summer profundal to a winter pelagic zone in Canadian shield lakes, with the winter distribution linked to ambient light levels that strongly influence lake trout foraging efficiency (Blanchfield et al., 2009). Among cutthroat trout (*Oncorhynchus clarki*), winter habitat shifts from streams to lake littoral zones have been associated with temperature (Nowak et al., 2004). In stream-dwelling salmonids, limited availability of suitable refuge habitats in winter may promote intense competition, with experimental evidence pointing to the willingness of fish to move in winter to find suitable sheltering or foraging habitats (A. J. Harwood et al., 2002). As anadromous Arctic charr are known to reduce or cease feeding while overwintering (Sprules, 1952; J. W. Moore & Moore, 1974; Dutil, 1986; Boivin & Power, 1990; Rikardsen, Amundsen, & Bodin, 2003), the selection of winter habitat is likely to be driven by factors other than the suitability of the habitat for foraging.

Among the factors which may explain or be associated with habitat use is temperature, especially as energy use may differ as a function of ambient temperature and any experienced fluctuations in temperature (Jobling, 1997). Thermal optima, the temperatures at which physiological processes are maximal, vary between consumption (feeding/digestion), respiration and reproduction (Angilletta, Niewiarowski, & Navas, 2002; Hasnain, Shuter, & Minns, 2013). Fish can use behaviour or physiology to regulate body temperature within a narrower range than the full range of available environmental temperatures to optimize physiological responses (Angilletta, Niewiarowski, & Navas, 2002). For example, studies with juvenile Arctic charr have noted that individuals behaviourally thermoregulate by selecting thermal microhabitats in summer to avoid thermal stress and/or maintain optimal temperatures for growth (e.g., Murdoch & Power, 2013; Sinnatamby et al., 2013). Temperature selection may also occur because fluctuating temperature regimes are more energetically demanding than constant temperature regimes (E. S. Hansen & Rahel, 2015; Oligny-Hébert et al., 2015). For example, the standard metabolic rate of juvenile Atlantic salmon (*Salmo salar*) increased by 33.7% when exposed to temperature fluctuations in warmer water (Oligny-Hébert et al., 2015), suggesting that selection of habitat for minimization of thermal variation may benefit fish through reductions in energy use. Facultative behaviour that minimizes metabolic demands in winter in fish often involves selection of thermally stable microhabitats (e.g., groundwater inflows, deeper areas in the water column) and is consistent with a strategy of choosing habitats to minimize energy costs (Cunjak & Power, 1986a).

Given the limited information on the overwintering ecology of anadromous lake dwelling Arctic charr, this study used acoustic and archival telemetry from two locations in southern Labrador to study thermal habitat use during the ice-covered period. Telemetry data were used to test the hypotheses that: [i] - anadromous Arctic charr show low temporal (e.g., diel, within and among years) variability in temperature use, given the metabolic advantage of stable and constant ambient temperatures; and, [ii] from among the temperatures available to anadromous Arctic charr they use cooler water temperatures, implying residency in the upper water column.

3.2 Methods

3.2.1 Study areas

Shinneys Pond (SP; 52.61° N, 56.11° W) is located in southern Labrador and discharges via Shinneys River (~1 km long) into Gilbert Bay (Figure 3.1 – SP). Anadromous Arctic charr feed in Gilbert and the adjacent Alexis Bay during the summer and migrate back to Shinneys Pond (~9 km^2) to spawn and/or overwinter (Morris & Green, 2012). The pond is generally shallow (6-11 m) but contains one deeper basin (26 m) on the south side of the lake (Figure 3.1 – SP).

Muddy Bay Pond (MBP; 53.62° N, 56.87° W) discharges via Muddy Bay Brook into Sandwich Bay and is located a degree of latitude north of Shinneys Pond (Figure 3.1 – MBP). In summer, anadromous Arctic charr feed in Sandwich Bay before returning to Muddy Bay Pond (~13 km^2) located ~15 km upstream from the river mouth. The pond is generally shallow (≤10 m), particularly at the entry point, but contains several deeper basins (15-22 m) near the middle and at the eastern side of the lake (Figure 3.1 – MBP).

Climate in this area is sub-Arctic with a daily mean annual air temperature of 0.0°C and mean daily air temperatures < 0° C from November to April (Environment Canada climate data, Cartwright, Labrador, 1981-2010), with the result that Shinneys and Muddy Bay Ponds are ice-covered from November to May. Winter conditions (data from Department of Environment and Natural Resources Canada) varied between years and sites (mean ± SD): Shinneys Pond 2012 (-5.6 ± 6.8°C), Shinneys Pond 2014 (-10.8 ± 7.2°C), Muddy Bay Pond 2015 (-9.6 ± 6.5°C).

3.2.2 Tagging and tracking

Monofilament gill nets (63-89 mm stretched mesh size, 25 m long), set within a 13 km radius from the river mouth, were used to capture Arctic charr in the marine environment of Gilbert, Alexis and Sandwich Bays. Additionally, Arctic charr were captured during their upstream migration at a Fisheries and Oceans Canada operated fish counting fence at Muddy Bay Brook (Reddin et al., 2005), located 5 km upstream from the river mouth. Captured individuals were implanted with either temperature-sensing acoustic tags (VEMCO V13T-1x, 48 mm x 13 mm, 6.5 g in water, accuracy ± 0.5°C, resolution 0.1°C, random delay (two programming options): 55-85 s for 90 d, 570-630 s the next 210 d (or 510-630 s for 240 d), and 55-85 s the following 60 d (or 120 d), VEMCO, Halifax, NS, Canada) or data storage tags (DST). The number of fish tagged, fork length (cm), tag type and tagging dates are given in Table 3.1. At Muddy Bay Brook, an external Floy tag having a unique number was also attached for ease of identification of all DST or acoustic tagged fish.

The DSTs (LAT2810ST) were light-based geolocation tags (38 mm x 11 mm, 3.5 g in water, 60 s sampling interval, LOTEK Wireless Inc., St. John's, NL, Canada). Internal and external temperatures (°C) and depth (dbar) were recorded and stored on the tag in relation to time. External temperature data were measured via an external stalk, as the tag was designed for implantation in the peritoneal cavity of the fish with the sensor stalk protruding outside. Tag temperature measurement ability ranged from -5 to 30 °C, with an accuracy of ∀ 0.2 °C and a resolution of 0.05°C. Pressure, a proxy for depth, was measured in dbars to a maximum of 50 dbars. Pressure recordings had an accuracy and resolution of 1 and 0.05% of the full scale, respectively. A dbar is equivalent to approximately 1 m in depth, but is dependent on the density of water at the specific time and/or location where the measurement is taken (Saunders & Fofonoff, 1976). The data stored on the DSTs were retrieved after fish recapture by connecting the tag to an upload box linked to a computer.

Surgical procedures for acoustic tag implants followed standards of practice as described in Mulder, Morris, et al. (2018a) and Wagner et al. (2011). DSTs were implanted in the peritoneal cavity 2 cm to the right of the fish centerline through a 2 cm incision in the abdominal wall anterior to the pelvic girdle. The tag was inserted with the sensor stalk protruding laterally along one side of the lower abdomen and was secured by a single suture to the interior wall of the peritoneal cavity. The incision was closed with two or three non-absorbable silk sutures (Sofsilk^{TM} Tyco Healthcare, Keene, NH). The surgical procedure took approximately 3 minutes, after which fish were transferred to a holding tank and released at, or near, the site of capture once they regained equilibrium. Tagging procedures followed standards and guidance provided by the Canadian Council on Animal Care (protocol # 14-12-IF), and were approved by the Northwest Atlantic Fisheries Centre animal care committee protocol (NAFC 2013-05).

A network of five omnidirectional hydro-acoustic receivers (model VR2W, 69 kHz, VEMCO, Halifax, NS, Canada) was positioned in Shinneys Pond in 2012 (6 June and 30 July 2012) and 2014 (5 June 2014) (Figure 3.1 - SP), with data offloaded in October 2013 and July 2015. Similarly, a network of ten omnidirectional hydro-acoustic receivers (model VR2W, 69 kHz, VEMCO, Halifax, NS, Canada) was deployed in Muddy Bay Pond in July and August 2015 (Figure 3.1 - MBP). To prevent receiver loss due to winter ice movements, one receiver deployed in shallow water (≤3 m) at the entrance to the pond was retrieved at the end of the field season (August 2015). The remainder of the receivers were retrieved and offloaded at the end of July 2016. Each receiver was attached to a buoyed line and suspended 2-8 m above the lake bottom with a weighted anchor and subsurface buoy mechanism (Mulder et al., 2018a).

3.2.3 Temperature logging

The fall turnover in Muddy Bay and Shinneys Ponds was completed in early and late November, respectively, based on the occurrence of inverse mixing with the coldest water temperatures being near the surface and the warmest temperatures being near the bottom (Wetzel, 2001; Pierson et al., 2011). Spring turnover occurred mid-May in both lakes when the lakes mixed and water temperatures became homogenous throughout the water column (Wetzel, 2001). Water temperature data were collected by a temperature logger chain (loggers dispersed at 2-10 m intervals, one hour sampling interval, accuracy ∀ 0.53 °C, resolution 0.15 °C; Onset Hobo Data Loggers UA-001-64/UA-002-64, Onset Computer Corp., Bourne, MA) deployed year around in the deepest part of Shinneys Pond (2014) and Muddy Bay Pond (2015) (Figure 3.1 – SP/MBP). No temperature logger chain was deployed in Shinneys Pond in 2012.

3.2.4 Data analyses

As the fall and spring turnover occurred in November and May, respectively, only detections recorded from December through April were selected for analyses to represent the overwinter under-ice period. To reduce the likelihood of false detections, data were only used in statistical analyses if a tag was detected ≥2 times per 24 hour period (Heupel, Semmens, & Hobday, 2006).

To test hypotheses related to the temporal constancy of temperature use across varying time scales (days, months and years), temperature use data were analysed with linear mixed models (Gelman & Hill, 2007; Zuur et al., 2009) fitted using the lme4 package (Bates et al., 2015) in the statistical software R (R Core Team, 2015). Owing to the limited number (N=3) of DST tags recovered, and differences in the frequency and accuracy of temperature between tag types, only acoustic data were used for model estimation. The number of detections recorded by the receivers deployed in the two lakes, and over two years in one lake, resulted in 440,786 usable detections during the ice-covered period (December – April). To model the data, temperature recordings were averaged daily by diel period, for each individual fish throughout the study period (resulted in N=9035 observations). Temperature (°C) was modelled as a function of the categorical fixed effects: diel period (day, night), month and year (SP 2012, SP 2014, MBP 2015) and the continuous fixed effect fork length (cm). The continuous variable was mean centred, and all two-way interactions with fixed effect variables were considered. The diel period was calculated following methods described by Mulder, Morris, et al. (2018a).

Hierarchical random intercepts were fitted following Gelman & Hill (2007). Random intercepts included: Ind, representing individual Arctic charr, and the nested level variable $series$, a combination of individual and month. The method accounts for the temporal auto-correlation at a monthly level (Gelman & Hill, 2007; Araya-Ajoy, Mathot, & Dingemanse, 2015). The final model was as follows:

$$y_{ijk} = (\beta_0 + Ind_{0j} + series_{0jk}) + Diel\,period_{ijk} + Year_{ijk} + Diel\,period \times Year_{ijk} + e_{0ijk}$$

where y_{ijk} is temperature use at instance i, for individual fish j, in tracking series k. Backwards selection was used for all random and fixed effect component estimates as implemented in the lmerTest package (Kuznetsova, Brockhoff, & Christensen, 2015) in R. The p-values for the fixed effects were calculated from the F-test based on Sattethwaite's approximation, whereas the p-values for the random effects were based on likelihood ratio tests (Kuznetsova, Brockhoff, & Christensen, 2015).

Cumulative probability of detection plots were used to characterize the relative use of colder waters (hypothesis ii) by overwintering Arctic charr in all sites and years following methods outlined in Zar (2010). Data were plotted using average daily temperature values for individual fish, and daily temperature averages computed for all fish on a given day. Arctic charr utilized temperatures outside the range of those recorded by the temperature logger chains, as was evident from the difference in maximum temperatures recorded by the loggers (max. 2.5°C) and by the tags implanted in the Arctic charr (max. 3.9°C). Using temperature and density profiles from a wide variety of ice-covered lakes, Matthews & Heaney (1987) mathematically modelled the theoretical range (0-4°C) of available temperatures, noting that the density of water is greatest at 4°C and that density-driven water movements promote mixing via convective currents thereafter to limit temperatures to within a 0-4°C range, not considering groundwater input (see also Wetzel (2001)). The theoretical 0-4°C range was used to test for significant differences in the proportionate use of colder water below the median (2°C) of the theoretical range using two-sample z-tests (Zar, 2010) with significance judged at $\alpha=0.05$ level of significance. Cumulative probability plots were also used to characterize depth use by Arctic charr in Muddy Bay Pond based on the three DSTs, with differences in the use of the upper (0-5 m) and lower (>5 m) portions of the water column compared using two-sample z-tests (Zar, 2010). To test for the significance of a relationship between temperature use and depth, data recorded by the DSTs were averaged by day for each fish and correlated using nonlinear regression methods (Ratkowsky, 1990).

3.3 Results

3.3.1 Tagging

In Gilbert Bay, 32.6% (mean fork length ± SD: 39.5 ± 3.2 cm) and 37.1% (41.1 ± 3.5 cm) of Arctic charr implanted with an acoustic tag were detected throughout the ice-covered period (December-April) in Shinneys Pond in 2012 and 2014, respectively. In Muddy Bay Pond, 45.0% (38.8 ± 3.2 cm) of the Arctic charr were detected during the same period. There was no significant difference between years in fork length (acoustically tagged fish only) of detected Arctic charr in Shinneys Pond (two-sample t-test $p=0.222$) or between study systems (two-sample t-test $p=0.250$).

Fourteen of the 64 (21.9%, 41.3 ± 3.9 cm) Arctic charr implanted with DSTs were recaptured the following summer (2016) during their upstream migration at the Fisheries and Oceans Canada fish counting facility at Muddy Bay Brook or by local fishermen. On average, fish had grown 1.8 cm (SD=1.0 cm) in the mark-recapture period (380 ± 16 days). Only three (43.7 ± 2.1 cm) of the 14 Arctic charr still contained the DST, whereas the remaining 11 fish showed healed scars where the tag had been implanted.

3.3.2 Temperature profiles within the lakes

The temperature logger chain deployed in the deepest part of each lake (Figure 3.1 - SP/MBP) showed inverse mixing of the water column in both lakes during the ice-covered period, with warmer temperatures near the bottom and colder water near the surface (Figure 3.2 & 3.3). Average recorded bottom and near surface temperatures throughout the study period were 1.05 ± 0.28°C and 0.61 ± 0.20°C in Shinneys Pond 2014, and 2.38 ± 0.20°C and 1.24 ± 0.08°C in Muddy Bay Pond 2015, respectively (Figure 3.3).

3.3.3 Temperature use Arctic charr

The mean (of individual fish means) temperature ± SD recorded by the acoustic tags was 1.59 ± 0.25 °C (range 0.14-3.72 °C, N=180,020) and 0.86 ± 0.28 °C (range 0.046-3.90 °C, N=161,724) in Shinneys Pond 2012 and 2014, respectively (Figure 3.3), throughout the ice-covered period. Mean tag recorded temperature in Muddy Bay Pond during the same overwinter period was 1.44 ± 0.43 °C (range 0.046-2.96 °C, N=99,042) (Figure 3.3). The three Arctic charr in Muddy Bay Pond tagged with DSTs recorded similar mean temperatures ± SD as the acoustic tags: 1.09 ± 0.61 °C (range 0.02 – 2.06 °C, N=205,259), 1.31 ± 0.60 °C (range 0.08 – 2.42, N=218,880), and 1.22 ± 0.27 °C (range 0.54 – 2.46 °C, N=218,875), respectively (Figure 3.4-3.6).

In the model relating temperature use (°C) to fork length, diel period, month, year and its interactions, diel period and year were found to be significant predictors of temperature use in Arctic charr, although diel period interacted with year ($p=0.030$, Table 3.2). Temperature use differed significantly between years in Shinneys Pond where Arctic charr utilized higher temperatures in Shinneys Pond 2012 (Figure 3.3). There was no difference in temperature use between Shinneys Pond in 2012 and Muddy Bay Pond in 2015, and temperature use in both years was found to be significantly higher compared to Shinneys Pond 2014 ($p<0.001$, Figure 3.3). Temperatures used during the day were significantly higher than those used at night in Shinneys Pond (day-night difference: 0.04°C in 2012 and 2014) ($p<0.001$), but not in Muddy Bay Pond ($p=0.730$). The random effects accounted for 44.3% of the variation in the thermal habitat use over the range of fish tagged (34.0 to 49.5 cm). The proportion accounted for by between-individual variation was 0.35 for the duration of the study, or 0.67 over a monthly period. Within-individual variation accounted for less than 0.33 of the total random effect variance. Thus, there was a significant difference in temperature use between individuals, but individual fish utilized relatively consistent temperatures in winter. Month ($F_{4,138.85}=2.439$, $p=0.050$) and fork length ($F_{1,32.78}=0.223$, $p>0.050$) were not found to be a significant predictors of temperature use in winter and were removed through backwards selection.

Cumulative probability of detection plots (Figure 3.7) showed that in all years and locations, the probability of detection in waters below the 2°C median of the theoretical winter range of lake waters was significantly higher (probability range: 0.78-1.00, $z=30.06$-54.12, $p<0.001$) compared to detection in water above 2°C. The results were consistent when calculated using mean daily temperature use values for individual fish (Figure 3.7) or daily temperature averages computed for all fish on a given day (probability range: 0.94-1.00, z=15.31-17.43, p<0.001) (Figure 3.7).

3.3.4 Depth use

The three Arctic charr implanted with DSTs resided at an average depth ± SD of 4.1 ± 3.3 m (range 0.1 – 14.2 m, N=205,259), 3.1 ± 1.3 m (range 0.1 – 15.4 m, N=218,880) and 2.8 ± 0.55 m (range 0.04 – 13.9 m, N=218,875), respectively, throughout the ice-covered period (Figure 3.4-3.6) assuming each dbar measure is equivalent to approximately 1 m in depth (see methods). Data describe only the vertical distribution, and not the horizontal distribution (e.g., littoral vs. pelagic) of the fish. Arctic charr in this study showed a relatively uniform depth use as they spent 81.8%, 98.2% and 99.8%, respectively, of their time within the top 5 m of the water column. The analyses from the cumulative probability of detection plots confirmed this as the probability of each Arctic charr (N=3) utilizing the upper water column (<5 m) was significantly higher (probability range: 0.82-0.99, z=406.73-659.26, p<0.001) compared to utilizing deeper depths. When in deeper water (5-15.4 m), time spent at depth was typically brief (Figure 3.4-3.6), except for T1827 which spent prolonged periods of time at depth in early winter (Figure 3.4, Figure 3.8). The brief periods at depth ranged from 2-12 hours at depths between 5-7 m, but only 0.02-0.05 hours each time at depths > 9 m. Models of the depth-temperature relationship showed significant positive relationships (R^2=0.84, p<0.001; R^2=0.83, p<0.001; R^2=0.39, p<0.001; respectively) between daily average depth and temperature use (Figure 3.8).

3.4 Discussion

Our study demonstrated that anadromous Arctic charr displayed minimal temporal variation in temperature use as hypothesized. Although statistical evidence indicated diel temperature shifts, the difference was less than the measurement precision of the tag type and therefore considered to be biologically insignificant. Our data also indicated that Arctic charr used cooler waters (<2°C) and generally favoured use of waters (<5 m) in the upper water column during the ice-covered period.

Studies of lake-resident Arctic charr have inferred overwinter temperature use (0.2-1.3°C) based on catches in the littoral zone (e.g., Klemetsen, Knudsen, et al., 2003; Svenning, Klemetsen, & Olsen, 2007; Amundsen & Knudsen, 2009) comparable with those recorded for overwintering anadromous Arctic charr in this study (0.86-1.66°C). Similarly, anadromous Arctic charr using estuarine fjord waters in the overwinter period frequented temperatures in the 1.4°C range (Jensen & Rikardsen, 2012), which were warmer than the 0.7°C mean reported for related anadromous brook trout (*Salvelinus fontinalis*) resident in Antigonish Harbour, Nova Scotia, Canada (Spares et al., 2014). While the geographic location of cited studies varies considerably, differences in reported temperature use are small, suggesting that overwintering Arctic charr have thermal preferences related to survival and energy conservation strategies presumably selected for during previous evolutionary periods in periglacial environments (G. Power, 2002).

While there is limited information on overwintering temperature use for north temperate and northern fish species, available data for winter specialists such as burbot (*Lota lota*), have shown them to actively select temperatures <2°C to optimize thermal conditions for pre-spawning maturation and winter spawning (Harrison et al., 2016). Similarly, adult Chinook salmon (*Oncorhynchus tshawytscha*) use behavioural strategies to maintain internal temperatures 2.5°C below ambient river temperatures and gain metabolic advantages during the months prior to spawning. Maintaining consistently lower temperatures resulted in a 12-20% decrease in basal metabolic demand, optimizing both energy conservation and increasing available energy for the behavioural and physiological processes associated with successful reproduction (Berman & Quinn, 1991). Acclimation to declining temperatures in the late fall/early winter period, and increasing temperatures in spring can be energetically demanding for salmonids (Cunjak & Power, 1987; Cunjak, 1988), particularly in post-spawning fish (Jørgensen, Johansen, & Jobling, 1997; Hutchings et al., 1999). Thus, maintaining consistently lower temperatures throughout the winter likely allows Arctic charr to reduce energetic demand and conserve energy for metabolically costly processes like preparation for seaward migration (i.e., osmoregulatory transformation), with numerous studies having shown 20 to >50% of the total fish energy budgets can be dedicated to osmoregulation (Bœuf & Payan, 2001). Similarly, in late winter Arctic charr enhance liver metabolic processing capacity to fuel energy demanding processes such as (re-) developing hypo-osmoregulatory capacity (Aas-Hansen et al., 2005; Jørgensen & Johnsen, 2014).

In addition to utilizing lower temperatures, the minimization of temperature variability observed in this study likely both reduces and conserves energy, as exposure to temperature fluctuations can increase metabolic demand and decrease growth (Biette & Geen, 1980; Mehner et al., 2011; Oligny-Hébert et al., 2015). Behavioural strategies aimed at reducing metabolic demand and increasing bioenergetic efficiency have been demonstrated in a variety of freshwater and marine fish species (e.g., Sims et al., 2006; Mehner, 2012), with some such as dogfish (*Scyliorhinus canicula*) saving up to 4% of their metabolic expenditure by migrating between different temperature layers (Sims et al., 2006). Behavioural strategies may be employed for reasons other than temperature modulation, including predator avoidance or optimizing feeding opportunity (Mehner, 2012), which could simultaneously reduce environmental temperature as a side effect. For example, reservoir resident burbot undertake vertical migrations year around even in homothermic winter environments where no obvious differences in temperature exist (Harrison et al., 2013). Here, predator avoidance behaviour by large (generally >40cm) adult anadromous Arctic charr is unlikely given that such fish will be among the largest in the lake. Furthermore, Arctic charr are known to reduce or cease feeding while overwintering (Sprules, 1952; J. W. Moore & Moore, 1974; Dutil, 1986; Boivin & Power, 1990), which suggests that minimization of temperature variation is not a significant by-product of feeding opportunity maximization as feeding is opportunistic (Eloranta et al., 2013). Thus, in our view the lack of movement between different temperature layers suggests the utilization of constant temperatures in a low variability environment aimed at improving bioenergetic efficiency and contributing to reduction and conservation of energy for important future metabolic processes, i.e. development of hypo-osmoregulatory capacity for return marine migration.

Temperature and associated depth data showed that fish in Muddy Bay Pond utilized the upper water column immediately below the ice cover, whereas fish in Shinneys Pond (2014) were positioned lower in the water column as suggested by their temperature use, potentially avoiding prolonged periods of exposure to <0.5°C. Direct contact with ice crystals has been known to be fatal in super-cooled environments (Scholander et al., 1957; Fletcher, Kao, & Dempson, 1988) and Arctic charr are known to actively avoid marine temperatures < 0°C (Fletcher, Kao, & Dempson, 1988; Svenning & Gullestad, 2002). As Arctic charr are considered visual feeders, increased light intensity associated with upper water column use will aid foraging efficiency. For example, predation rates by related lake char (*Salvelinus namaycush*) increase rapidly at low light levels (Mazur & Beauchamp, 2003) and Arctic charr are known to be especially effective foraging at low temperature and light levels (Siikavuopio, Knudsen, & Amundsen, 2010; Elliott, 2011). Winter residency in the upper water column may, therefore, further bioenergetically advantage Arctic charr by maximizing the potential for incidental feeding and the acquisition of essential fatty acids.

The use of the upper water column and littoral zone has previously been observed for lake-resident Arctic charr (Klemetsen, Knudsen, et al., 2003; Amundsen & Knudsen, 2009; Eloranta et al., 2013) and was predominately driven by increased food availability, and reduced competition and predation risk (Klemetsen, Knudsen, et al., 2003). However, winter feeding is often reduced or absent in anadromous lake-dwelling Arctic charr populations (Sprules, 1952; J. W. Moore & Moore, 1974; Dutil, 1986; Boivin & Power, 1990). Yet, anadromous post smolts in Norway feed on planktonic prey and appear to maintain their pelagic feeding behaviour in freshwater after returning from the sea (Rikardsen, Amundsen, & Bodin, 2002, 2003). Zooplankton is a qualitatively superior food compared to zoobenthos, as zooplankton contains high percentages of essential fatty acids (Eloranta et al., 2013; Mariash, Cusson, & Rautio, 2017), especially during their overwintering period (Mariash, Cusson, & Rautio, 2017). Furthermore, mid-winter water circulation might increase prey availability in the upper water column as a result of within lake circulation characterized by constant lateral shoreward and downslope movement of water masses that entrain and circulate nutrients (Welch & Bergmann, 1985).

The pattern of differences and similarities in temperature use among years and between sites suggests that the success of Arctic charr in selective use of temperature is constrained by the physical conditions encountered in any one year. Use of colder waters in Shinneys Pond in 2014 was likely as much dependent on the prevailing colder environmental conditions (see methods) as on active selection of temperature by Arctic charr, with reduced in-lake thermal heterogeneity precluding active temperature selection use. Thus, even with ice cover the environment can influence the thermal habitat use in Arctic charr as temperature use differences between populations and years found in this study have indicated, with Arctic charr seeking temperatures within a narrow band of those available immediately below the ice cover. Prolonged temperature use below 0.5°C seems to be avoided, although Arctic charr did show periods of residency at temperatures close to 0°C likely associated with under-ice feeding (e.g., Brännäs & Wiklund, 1992).

Increasing water temperatures associated with climate change, may impact the condition and duration of lake ice-cover (Reist et al., 2006; Prowse & Brown, 2010). Ice-cover leads to inverse mixing of the water column (Wetzel, 2001), providing a colder and stable temperature environment, increasing protection from predation (e.g., by avian or mammalian predators, Jensen & Rikardsen, 2008), and affecting competitive interactions between species through interspecific variations in their physiological performance under ice (Hammar, 1998; Finstad et al., 2004; Helland et al., 2011). As Arctic charr are adapted to these conditions, the species can feed and grow in cold temperatures and under reduced light levels (Klemetsen, Knudsen, et al., 2003; Amundsen & Knudsen, 2009; Siikavuopio, Knudsen, & Amundsen, 2010; Helland et al., 2011). Loss of ice cover, therefore, may significantly impact Arctic charr through a reduction in the period of competitive superiority (e.g., Elliott, 2011; Helland et al., 2011) and through temporal reductions in the availability of lower and stable water temperatures that facilitate strategies aimed at reducing metabolic demand and preserving energy stores for out-migration the following spring.

To our knowledge, this study provides the first detailed data set on the thermal overwintering of anadromous *Salvelinus alpinus*. Results showed that individuals utilized a narrow temperature window (0.5-2°C) during the ice-covered period and used cooler temperatures available within the middle to upper water column. Use of the selected lower temperatures is indicative of a strategy to reduce metabolic costs and minimize energy expenditure, preserving stored lipids for overwinter survival and the energetic costs of preparation for seaward migration. Evidence of constraints imposed on thermal strategies by environment or lake morphology suggests further studies of overwintering Arctic charr from across the latitudinal range of their distribution should be undertaken to develop a more complete picture of overwinter thermal habitat use, the implications of interactions between Arctic charr and other resident sympatric species, and the anticipated effects of increases in water temperatures and reduced ice cover that may result from climate change.

Table 3.1. Tagging specifications for Arctic charr tagged in Gilbert Bay (2012, 2014) and Muddy Bay Brook (2015).

Location	Year	Tagging dates	Tag type	No. fish	Mean fork length ± SD (cm)
Gilbert Bay	2012	9-13 June	V13T	46	38.7 ± 3.2
	2014	3, 4 June	V13T	35	40.8 ± 3.1
Muddy Bay Brook	2015	4 June – 5 July[†]	V13T	20	40.5 ± 3.4
		4 June – 14 August[‡]	DST	64	44.1 ± 4.4

[†] Fish tagged in the marine environment.

[‡] N=10 fish tagged in the marine environment and N=54 fish tagged at the Fisheries and Oceans Canada operated fish counting fence.

Table 3.2. The final model (see equation) including the random and fixed effects for the linear mixed effects model of thermal habitat use (°C) by Arctic charr. Marginal and conditional R^2 values were calculated using the methods described in Nakagawa & Schielzeth (2013). Parameter significance is shown, displaying degrees of freedom (df), Chi.sq/F values, and P values calculated from F-tests based on Sattethwaite’s approximation (Kuznetsova, Brockhoff, & Christensen, 2015).

Final model	$R^2_{marginal}$	$R^2_{conditional}$
Diel period + Year + *Diel period:Year + Ind + Series*	0.343	0.786
Parameters	**Chi.sq/F**	**P value**
Random effects:		
Ind (Arctic charr)	61.08, df=1	<0.001
Series (Arctic charr*month)	4598.38, df=1	<0.001
Fixed effects:		
Diel period	19.69, ndf=1, ddf=8852.88	0.000
Year	22.99, ndf=2, ddf=33.80	0.000
Diel period:Year	3.50, ndf=2, ddf=8852.94	0.030

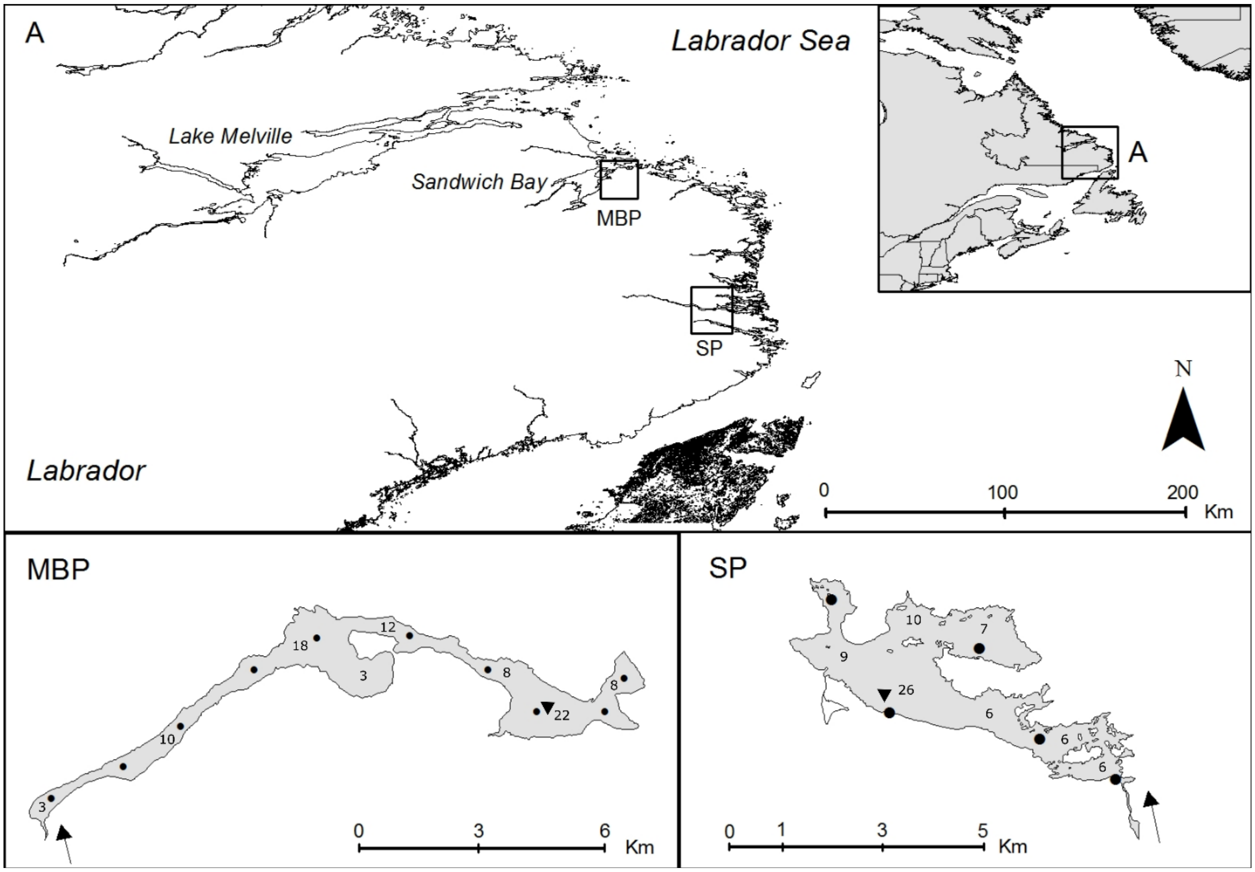

Figure 3.1. Map of the study area showing the locations of Muddy Bay Pond (MBP) and Shinneys Pond (SP) with respect to the Labrador coast. Receiver locations in each pond are indicated by small black dots and thermal-logger chains by black triangles in the lower panels. Depths (m) are also indicated and the locations where Arctic charr enter each pond are identified by the arrow.

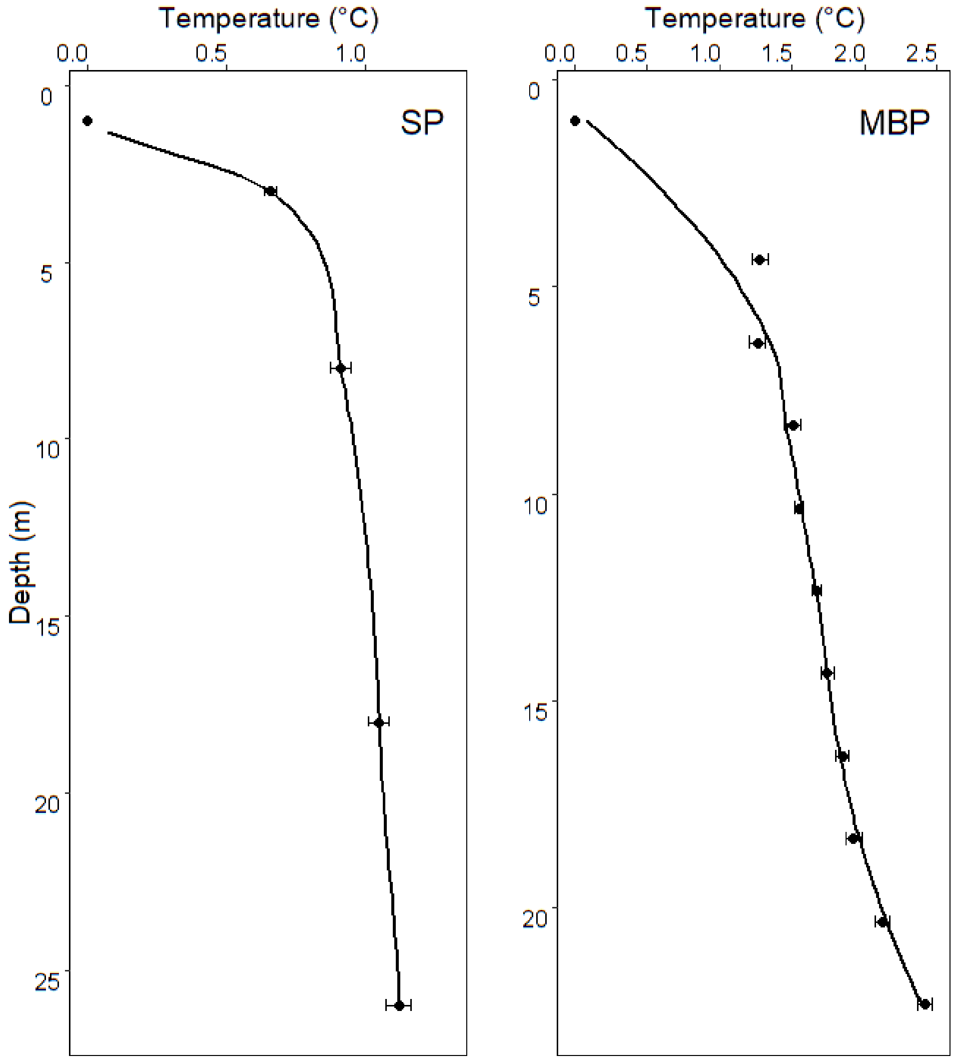

Figure 3.2. Mid-winter (February) temperature-depth profile (monthly mean ± SD) in Shinneys Pond 2015 (left, N=4 loggers) and Muddy Bay Pond 2016 (right, N=10 loggers), with the added assumption that the temperature is 0°C at the water-ice transition zone (~1 m depth, see methods).

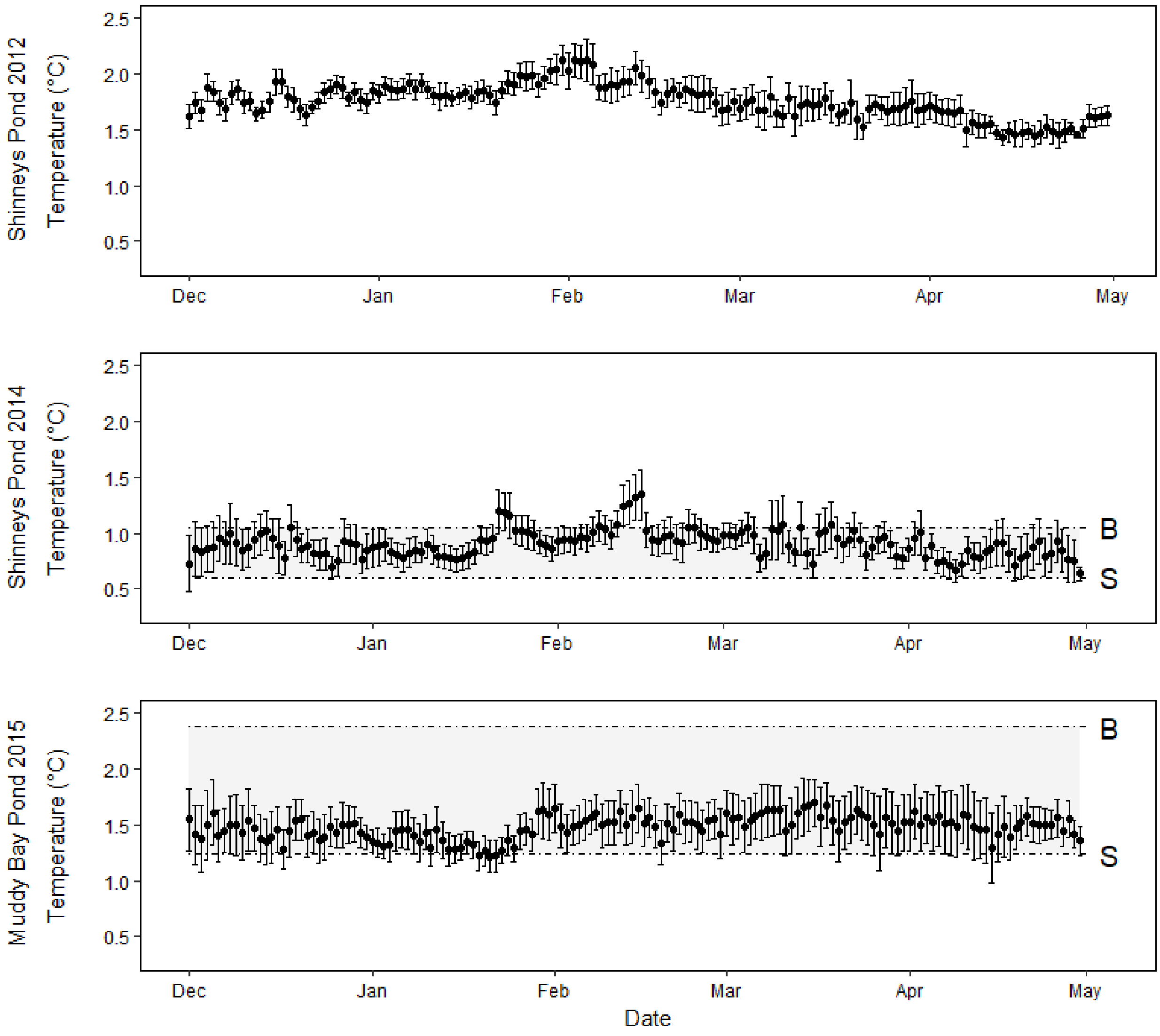

Figure 3.3. Daily temperature averages of individual fish means (°C; closed circles (±SE)) recorded for Arctic charr during the ice-covered period in winter (December – April). The top and middle panels plot data for Shinneys Pond in 2012-2013 and 2014-2015, respectively, whereas the bottom panel plots data for Muddy Bay Pond 2015-2016. The two lines indicate the recorded average bottom (B; 26 m deep SP, 23 m deep MBP) and near-surface (S; 3m deep SP, 4m deep MBP) temperatures (°C) throughout the study period.

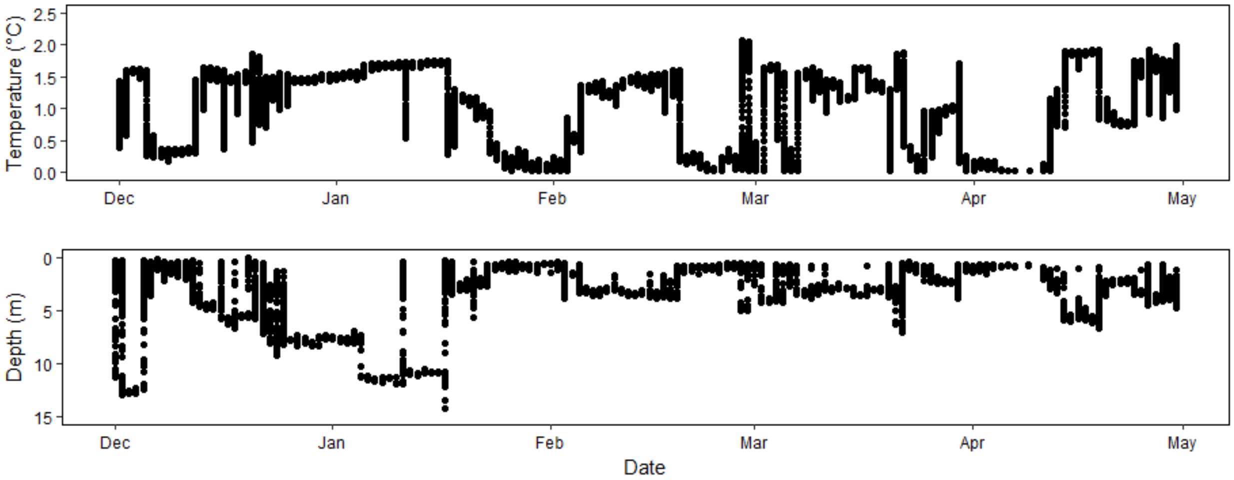

Figure 3.4. Body temperature (°C) (top) and depth (m) (bottom) data recorded by a DST tag implanted in Arctic charr (T1827) during the ice-covered winter period (December-April) in Muddy Bay Pond 2015-2016. Values are given every minute.

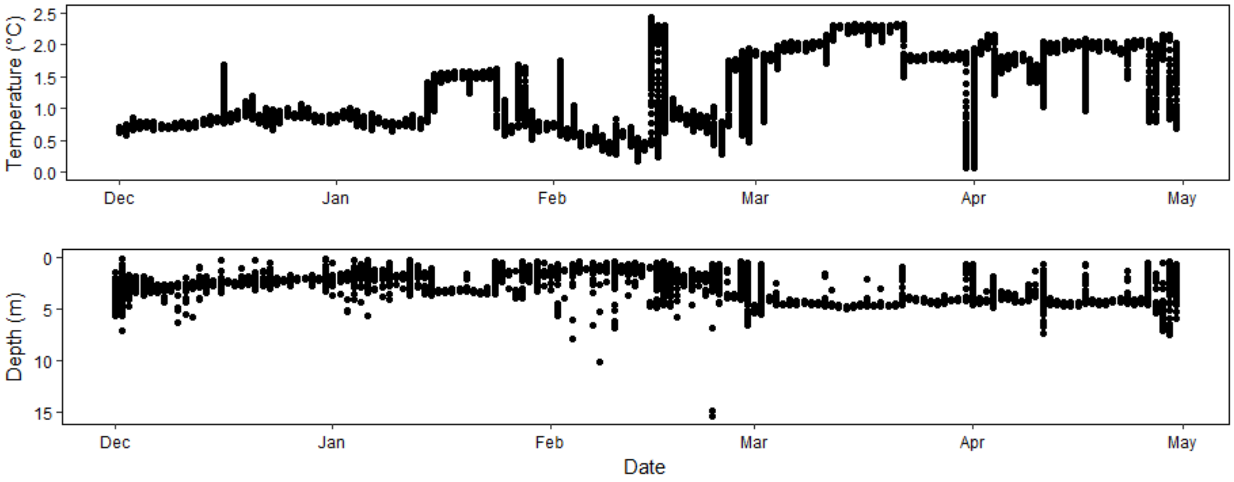

Figure 3.5. Body temperature (°C) (top) and depth (m) (bottom) data recorded by a DST tag implanted in Arctic charr (T1833) during the ice-covered period (December-April) in Muddy Bay Pond 2015-2016. Values are given every minute.

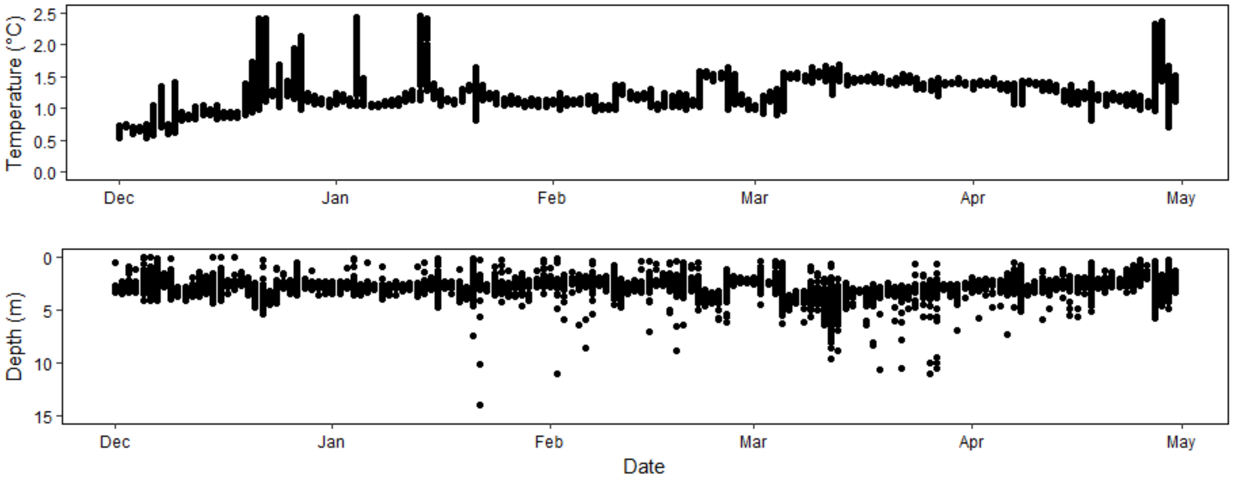

Figure 3.6. Body temperature (°C) (top) and depth (m) (bottom) data recorded by a DST tag implanted in Arctic charr (T2001) during the ice-covered period (December-April) in Muddy Bay Pond 2015-2016. Values are given every minute.

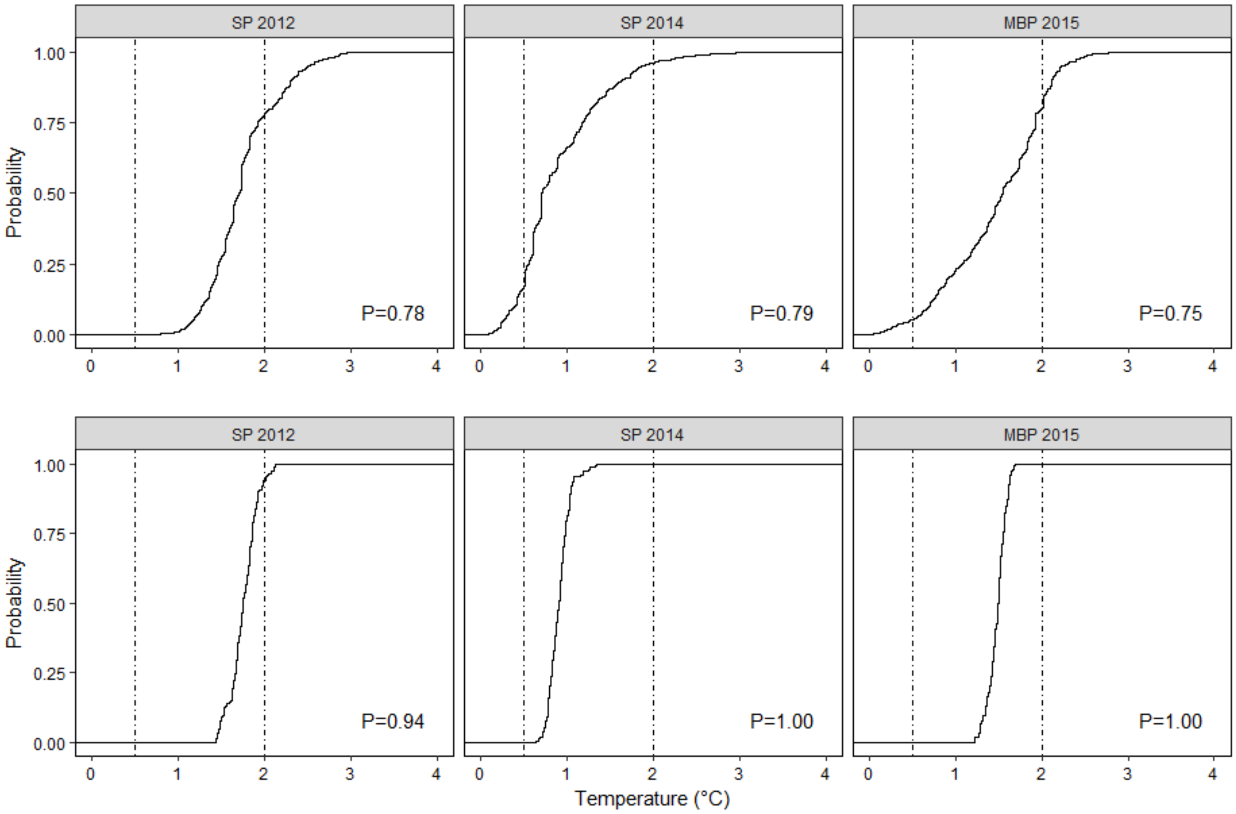

Figure 3.7. Cumulative distribution functions giving the probability that Arctic charr use water temperatures below a temperature as defined on the horizontal axis. The distributions were fitted using the mean daily averages for each individual fish (top) or daily temperature averages computed for all fish on a given day (bottom). P defines the probability of a fish using temperatures between 0.5 and 2°C.

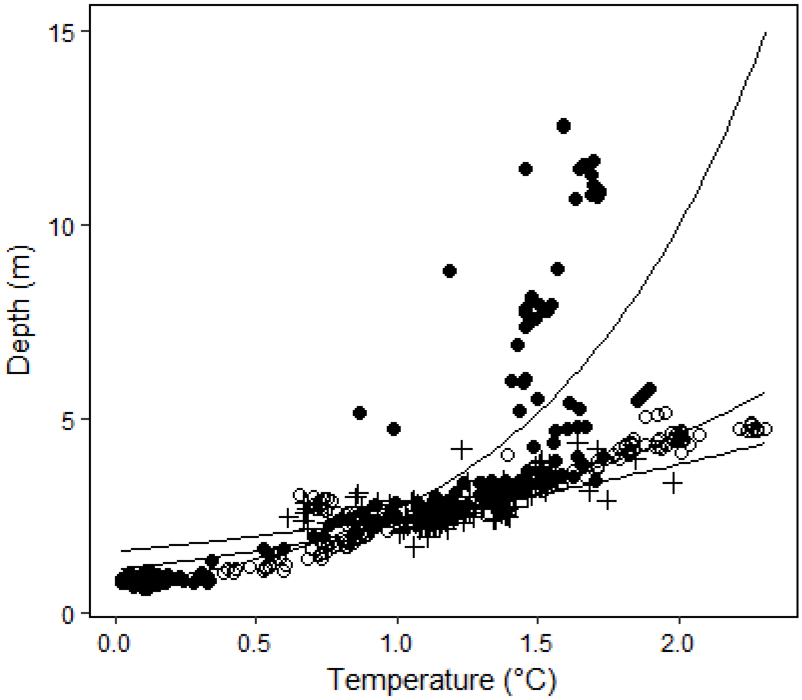

Figure 3.8. Correlations between the daily averaged temperature (°C) and depth (m) data recorded by the three DSTs (T1827 (•), T1833 (◦), T2001 (+)) recovered from recaptured Arctic charr in Muddy Bay Brook. Smoothing functions were modelled from the nonlinear regressions using an exponential regression.

Chapter 4: Diel activity patterns in overwintering Labrador anadromous Arctic charr

4.1 Introduction

Arctic charr, *Salvelinus alpinus*, is a cold-water specialist and the world's northernmost distributed freshwater fish inhabiting Arctic, sub-arctic and temperate regions with large seasonal variations in biotic and abiotic environments (Johnson, 1980; Klemetsen, Amundsen, et al., 2003). The species displays an anadromous life history strategy throughout most of its range in North America where it feeds in the productive marine environment for varying periods of time in summer, and migrates back to freshwater in late summer to spawn and/or overwinter (Doucett et al., 1999; Van der Velden et al., 2012). As Arctic charr lack specialized anti-freeze proteins (Fletcher, Kao, & Dempson, 1988; Svenning & Gullestad, 2002; Elliott & Elliott, 2010), all migrants, including juvenile fish, must return to freshwater each year to avoid seawater temperatures that reach the lower critical limit for the species (-0.99°C) (Johnson, 1980; Fletcher, Kao, & Dempson, 1988; Svenning & Gullestad, 2002).

While overwintering in freshwater, feeding is believed to be reduced or absent in anadromous Arctic charr populations (J. W. Moore & Moore, 1974; Boivin & Power, 1990; Rikardsen, Amundsen, & Bodin, 2003), movement activity reduced (Mulder et al., 2018a), and utilization of colder (0.5-2°C range) water temperatures within the upper water column is typical (Mulder et al., 2018b). Seasonal movement patterns have also shown a marked decline of activity during the late autumn, limited winter movement and increasing activity as ice break-up approaches

(Mulder et al., 2018a), with lower winter activity suggestive of opportunistic maintenance feeding as an energy conservation strategy (Huusko et al., 2007; Shuter et al., 2012). While seasonal variation in movement activity, and the linkages to food intake and growth are generally understood (Linnér et al., 1990; Sæther, Johnsen, & Jobling, 1996; Tveiten, Johnsen, & Jobling, 1996; Jørgensen & Johnsen, 2014; Mulder et al., 2018a), diel variation in activity patterns in overwintering wild anadromous Arctic charr remains poorly characterized. Rather, research that has aimed to understand diel patterns has focussed on the experimental study of feeding and locomotory activity in hatchery reared juveniles (e.g., Linnér et al., 1990; Alanärä & Brännäs, 1997; Brännäs, 2008, 2014), on summer movement and foraging behaviour in stream-dwelling populations (Larranaga & Steingrímsson, 2015; Fingerle, Larranaga, & Steingrímsson, 2016), or on the displacement patterns of lacustrine Arctic charr (Hawley et al., 2018).

In laboratory experiments, activity patterns of Arctic charr during winter have demonstrated high variability, changing from bimodal diurnal activity to nocturnal patterns (Linnér et al., 1990). Most juvenile salmonids, but not all (e.g., Bachman, Reynolds, & Casterlin, 1979), switch from being predominantly diurnal in summer to being increasingly nocturnal in winter (Bradford & Higgins, 2001; Hiscock et al., 2002; Reebs, 2002). Diel activity patterns often occur as a result of a trade-off between growth and survival that accounts for things like light intensity, temperature, predation risk, food availability, habitat condition and competition (Metcalfe, Fraser, & Burns, 1999; Reebs, 2002; Railsback et al., 2005; Brännäs, 2008, 2014; Larranaga & Steingrímsson, 2015; Fingerle, Larranaga, & Steingrímsson, 2016). For example, low condition or food availability, or high density increase the risk of starvation enough that adjustment to greater daytime feeding and activity offers higher fitness despite the increased risk of predation (Railsback et al., 2005; Fingerle, Larranaga, & Steingrímsson, 2016).

As Arctic charr are ectotherms, activity levels are primary controlled by water temperature through its effect on critical physiological rates and metabolic processes (Fry, 1971; Shuter et al., 2012). Low temperatures reduce movement activity and feeding (Huusko et al., 2007; Shuter et al., 2012). Therefore, changes in water temperature can disrupt or change diel activity rhythms (Olla & Studholme, 1978; Fraser, Metcalfe, & Thorpe, 1993; Fraser et al., 1995). For example, juvenile Atlantic salmon (*Salmo salar*) switch from diurnal to nocturnal feeding when temperatures drop below 10°C, independent of photoperiod (Fraser, Metcalfe, & Thorpe, 1993; Fraser et al., 1995). Indeed, studies of the thermal dependence of locomotory activity have noted a distinct reduction in locomotory performance capacity at low body temperatures (Bennett, 1990) and a trend toward increased nocturnalism in juvenile fish as water temperatures decrease (Reebs, 2002). Other studies have concluded that photoperiod mainly influences activity patterns (Hawley et al., 2018) and that temperature simply affects the amplitude of the activity, with increased activity at warmer temperatures (Müller, 1978; Olla & Studholme, 1978). Body size is another variable that can influence some of the variation in diel activity patterns (Metcalfe, Fraser, & Burns, 1998; Hiscock et al., 2002; Railsback et al., 2005). Hiscock et al. (2002) observed a general increase in activity levels with decreasing body size in juvenile Atlantic salmon. In winter, size may also drive smaller fish to increase foraging activity to reduce starvation-related mortality risks (Hiscock et al., 2002; Byström et al., 2006).

Most salmonid diel activity research, however, has been based on observations of juvenile fish (Reebs, 2002), where the main challenge is to maximize growth (survival is often size dependent, e.g., Post & Parkinson, 2001) and avoid being eaten (Metcalfe, Fraser, & Burns, 1999). Environmental factors might affect diel activity patterns differently in adult fish, as predator avoidance behaviour by large (generally >40 cm) adult overwintering anadromous Arctic charr seems unlikely given that such fish will be among the largest in the lake and more likely to be predators than prey (Hobson & Welch, 1995; Guiguer et al., 2002). In addition, maintenance daytime feeding, even in winter, will facilitate prey capture as Arctic charr are considered visual feeders (Ali, Klyne, & Einarsson, 1981).

Given the limited information on overwintering diel activity in anadromous Arctic charr, this study used acoustic telemetry data to describe their activity patterns and to test the hypotheses that: [i] - Arctic charr display diel activity patterns throughout the overwinter freshwater residency period, with higher movement activity during the day; [ii] – movement activity is positively correlated with temperature; and, [iii] movement activity is negatively correlated with body size.

4.2 Methods

4.2.1 Study area

Muddy Bay Pond (MBP; 53.62° N, 56.87° W) empties via Muddy Bay Brook into Sandwich Bay, located in southern Labrador, Canada (Figure 4.1). In summer, anadromous Arctic charr feed in Sandwich Bay and migrate upstream to spawn and/or overwinter in Muddy Bay Pond, the largest available lake (~13 km^2) located ~15 km upstream of the river mouth. The lake is generally shallow (<10 m) but contains several deeper basins (15-22 m) near the middle and at the eastern end of the lake (Figure 4.1 - MBP). The regional climate is subarctic, with mean daily air temperatures below 0°C from November through April (Environment Canada climate data, Cartwright, Labrador, 1981-2010). As a result, the lake is ice-covered (~1 m max) from November to May, with 1-2 m of snow pack in February and March (data from Environment and Natural Resources Canada).

4.2.2 Tagging and tracking

On 13-14 July 2015, thirty Arctic charr (mean fork length ± SD: 42.7 ± 3.1 cm, range: 36.0 - 48.5 cm) were captured during their upstream migration at a Fisheries and Oceans Canada operated fish counting fence facility located 5 km upstream of the mouth of Muddy Bay Brook (Reddin et al., 2005). Captured individuals were double tagged with temperature sensing (model V9T-6L, 36 x 9 mm, 2.2 g in water, random delay: 150-250 s for 60 days, 550-650 s for the following 459 days, Vemco Ltd., Shad Bay, Canada) and accelerometer acoustic tags (model V9A-2L, 43 x 9 mm, 3.3 g in water, random delay: 150-250 s, Vemco Ltd., Shad Bay, Canada). An external Floy tag was also attached for ease of identification at the Fisheries and Oceans Canada counting fence or by local fishers. Surgical procedures followed standard practices as described in Mulder, Morris, et al. (2018a) and Wagner et al. (2011), and adhered to all standards and guidance provided by the Canadian Council on Animal Care (protocol # 14-12-IF).

To sustain continual overwinter transmissions, the accelerometer tags were programmed to remain inactive during the first 90 days after implantation. These tags measured fish movement along three-dimensional axes (X, Y and Z) at a rate of 5 measurements per second with a 30 second sampling period. The tags calculated a velocity value (m/s^2) that represents the root mean square value of movement activity along all three axes (Bouten et al., 1994; Murchie et al., 2011) as: $m/s^2 = \sqrt{x^2 + y^2 + z^2}$ and transmitted only that aggregated value.

Ten omnidirectional hydro-acoustic receivers (model VR2W, 69 kHz, Vemco Ltd., Shad Bay, Canada) were deployed in Muddy Bay Pond in July and August 2015 (Figure 4.1) to record detected fish temperature and movement activity values throughout the study area. One receiver was retrieved at the end of the field season (August 2015) to prevent receiver loss due to winter ice movement, as it was deployed in shallow water (≤3 m). The remainder of the receivers were retrieved in July 2016. Each receiver was suspended approximately 2-8 m above the lake bottom using a chain and sub-surface buoy mechanism. See Mulder, Morris, et al. (2018a) for details.

4.2.3 Acceleration tag calibration

To determine the range of movement activity values that could be generated by tag implanted Arctic charr and link recorded values to their associated movement behaviour, a calibration was conducted at the field site following methods described by Murchie et al. (2011). Calibration entailed the capture of seven additional Arctic charr (mean fork length ± SD: 41.1 ± 4.9 cm, range: 35.0 - 47.5 cm) at the counting fence during their upstream migration that were implanted with accelerometer tags (as described above) on 23-25 July 2015. The test tag specifications were similar to those described above, except for the transmission period which was set to 33 second intervals (30 s sampling period). After surgery, fish were left to recover for 30 minutes in a small (108x55x46 cm) covered holding tank. A VR100 portable receiver (Vemco Ltd., Shad Bay, Canada) was used to determine the movement values for stationary behaviour, and routine and burst swimming in all seven Arctic charr. After the recovery period, movement data were collected from the holding tank while fish were allowed to swim at will for a minimum of 20 minutes. In the same holding tank, Arctic charr were then chased until a transmission occurred (approximately 30 seconds) by touching the tail to simulate burst swimming. At least two burst values were recorded for each of the seven Arctic charr. Each Arctic charr was then individually placed into the trap (~200x200x200 cm) of the counting fence, where it could rest and stationary values were recorded. While fish swam around leisurely in the holding tank or trap, their behaviour was continuously observed, either visually or by camera. Baseline stationary values for dead Arctic charr were assumed to be equal to the laboratory obtained calibration values (0.06 ± 0.01 m/s^2) reported by Murchie et al. (2011).

4.2.4 Data analyses

Arctic charr were considered to have entered the lake when fish were detected by one of the lake deployed receivers. In spring, immediately before and after ice-out, fish were assumed to have left the lake after their last detection by the receivers placed nearest to the river outlet, provided they were not subsequently detected by any of the other lake receivers. To reduce the likelihood of false detections, detections were used in statistical analyses only if a tag was detected ≥2 times within a 24 hour period (Heupel, Semmens, & Hobday, 2006). Data were used for model estimation only from the period in which both acoustic tags (temperature and accelerometer) were actively transmitting (mid-October to June).

For the purposes of analysis two diel periods were defined (day and night) for the geographical coordinates of Muddy Bay Pond using the sunrise and sunset times as computed by the National Research Council of Canada sunrise/sunset calculator (www.nrc-cnrc.gc.ca/eng/services/sunrise/accuracy.html). The calculator uses standard scientific formulae as adopted by the national almanac offices of the United States, United Kingdom and the Herzberg Institute of Astrophysics in Canada that are considered accurate to ±2 minutes for the period 1900-2100 (www.nrc-cnrc.gc.ca/eng/services/sunrise/accuracy.html). As day length varies considerably over the year at northern latitudes, times relevant for each day were computed. Finally within the overwinter freshwater residency period, the data were sub-divided into relevant biological seasonal periods based on previously described life-history and activity events to include: the spawning period (mid-October – 30 October) (Johnson, 1980;

Dempson & Green, 1985), winter (1 November – 30 April) and ice breakup/outmigration period (1 May – 1 June; as identified by Mulder, Morris, et al. (2018a).

Movement activity (m/s^2) was characterized according to values recorded for stationary, routine and burst activity. The 'stationary' range was defined by values recorded below the alive stationary mean plus its associated standard deviation. The low end of the 'low activity' range was defined by the alive stationary mean plus its associated standard deviation, whereas the upper end of the 'low activity' range was defined by the routine swimming mean plus its associated standard deviation. Values recorded between the 'low activity' range and burst activity range minus its associated standard deviation, were categorized as 'high activity'. The proportion of movement values recorded for stationary, low and high activity were calculated seasonally. The Pearson's chi-square and Tukey style multiple comparisons of proportions tests were used to determine the variation of the proportions among seasons (Zar, 2010).

Additionally, movement activity (m/s^2) was analysed using linear mixed models (Gelman & Hill, 2007; Zuur et al., 2009) fitted using the lme4 package (Bates et al., 2015) in the statistical software R (R Core Team, 2015). To model the data, consisting of 408,095 post-filtered detections, movement activity and temperature recordings were averaged daily by diel period for each individual fish throughout the study period (resulting in N=4517 observations). The response variable, movement activity (m/s^2), was log transformed to achieve normality and to ensure variance homogeneity across the fixed effects (Zuur et al., 2009). The categorical fixed effects: diel period, seasonal period; and continuous fixed effects: body temperature (T_b in °C) and fork length (L_F in cm), were included in the model. The continuous variables were mean centred, and all two-way interactions between fixed effects were considered. Hierarchical random model intercepts were fitted following Gelman & Hill (2007). Random intercepts included: Ind, representing individual Arctic charr, and the nested level $series$, a combination of individual and month, accounting for the temporal auto-correlation in the data (Gelman & Hill, 2007; Araya-Ajoy, Mathot, & Dingemanse, 2015). Model selection was performed through backwards elimination of both random and fixed effect components as implemented in the lmerTest package (Kuznetsova, Brockhoff, & Christensen, 2015) in R. The p-values for the random effects were based on likelihood ratio tests (Kuznetsova, Brockhoff, & Christensen, 2015), whereas the p-values for the fixed effects were calculated from the F-test based on Sattethwaite's approximation. The final model took the following form:

$$\begin{aligned} y_{ijk} = \left(\beta_0 + Ind_{0j} + series_{0jk}\right) + \; T_{b_{ijk}} + Diel\,period_{ijk} + Seasonal\;Period_{ijk} \\ + T_b \times Seasonal\;period_{ijk} + Diel\,period\; \times Seasonal\;period_{ijk} + \; e_{0ijk} \end{aligned}$$

Where y_{ijk} is equivalent to the movement activity at instance i, for individual fish j, during the tracking series k.

4.3 Results

Field calibration of accelerometer tags provided baseline values to which the wild movement activity data could be compared and interpreted. Stationary (resting) Arctic charr had an average movement value of 0.29 ± 0.11 m/s^2, whereas the recorded mean movement activities for routine and burst swimming Arctic charr were 1.28 ± 0.25 m/s^2 and 3.46 ± <0.01 m/s^2, respectively. The 'stationary' range was calculated to include all values below 0.40 m/s^2, whereas the 'low activity' range was calculated to include values in the 0.41 and 1.53 m/s^2 interval (Figure 4.2). 'High activity' behaviour range was between 1.54 and 3.45 m/s^2 (Figure 4.2). Burst activity (0.06% of all detections, of which 25% occurred in the spawning period and 75% in winter) exceeded the measurement capacity of the tag, providing a clear activity endpoint (Figure 4.2).

Of the fish tagged for the study, twenty-one (mean fork length ± SD: 43.1 ± 3.2 cm, range: 36.0 - 48.5 cm) were detected throughout the study period (Oct 2015 – June 2016). Fish entered Muddy Bay Pond between 17 July - 13 August 2015, with 90% entering between 17 July - 4 August 2015. Outmigration occurred from 7 May - 1 June 2016 (90% between 7 - 29 May 2016). One Arctic charr entered Muddy Bay Pond but did not move throughout the study period and was presumed to have died although the exact cause remained unknown (e.g., tag malfunction, post-surgery mortality, predation). The remaining eight tagged fish were not detected in Muddy Bay Pond and may have overwintered in neighbouring ponds as Labrador Arctic charr are known to move in and out of neighbouring river systems during the return migration period (Beddow, Deary, & McKinley, 1998).

The proportion of movement activity values recorded for the ‘stationary’ (Chi-square, day: X^2=626.93, df=2, p<0.001; night: X^2=844.63, df=2, p<0.001) and ‘low activity’ ranges (Chi-square, day: X^2=594.95, df=2, p<0.001; night: X^2=750.80, df=2, p<0.001) varied most by seasonal period, with less but significant variation occurring within the ‘high activity’ range (Chi-square, day: X^2=55.37, df=2, p<0.001; night: X^2=92.17, df=2, p<0.001) (Figure 4.3). As burst activity made up such a small part of the movement behaviour, values were not compared between seasonal periods. At night, proportionate use of ‘stationary’ behaviour was found to be significantly lower during the spawning period (prop=0.918) compared to the winter (Tukey, prop=0.974, q=32.94, p<0.050) and the ice breakup (Tukey, prop=0.957, q=5.92, p<0.050) periods. During the day, proportionate use of ‘stationary’ behaviour was highest in winter (prop=0.907) compared to the spawning (Tukey, prop=0.877, q=26.53, p<0.050) and ice breakup (Tukey, prop=0.617, q=16.87, p<0.050) periods, with the spawning and ice breakup periods differing significantly (Tukey, q=7.64, p<0.050) (Figure 4.3). In contrast, daytime proportionate use of the ‘low activity’ range was significantly higher during the ice breakup period (prop=0.375) compared to the spawning (Tukey, prop=0.121, q=8.88, p<0.050) and winter (Tukey, prop=0.086, q=17.54, p<0.050) periods, with the spawning and winter periods differing significantly (Tukey, q=24.67, p<0.050) (Figure 4.3).

Arctic charr displayed diurnal activity patterns throughout the study period, where the amplitude of the activity varied with season (Figure 4.4). In the spawning, winter and ice breakup periods, the mean (of individual fish means) movement activities during the day and at night, respectively, were: spawning - 0.27 ± 0.07 m/s^2, 0.20 ± 0.05 m/s^2; winter - 0.21 ± 0.06 m/s^2, 0.15 ± 0.03 m/s^2; ice breakup - 0.37 ± 0.13 m/s^2, 0.18 ± 0.03 m/s^2 (Figure 4.4). Daytime activity peaked in the early daylight hours immediately after sunrise (spawning: 6:00-10:00, winter: 8:00-9:00, ice breakup: 5:00-11:00) and slowly decreased throughout the day (Figure 4.4). However, during the spawning and ice breakup periods, daytime activity levels peaked a second time, although to a lesser extent, for about 1-2 hours around sunset. No such increase in activity prior to sunset was observed in winter (Figure 4.4). The duration of the increased daytime activity followed the number of daylight hours, as periods of increased activity were shorter in the spawning and winter periods (8-10 hours), and longer during the ice breakup period (~16 hours) (Figure 4.4).

In the model relating movement activity (m/s^2) to diel and seasonal period, body temperature, fork length and its interactions, only body temperature, diel and seasonal period were significant predictors, although body temperature and diel period were moderated by seasonal period as a result of interactions ($p<0.050$, Table 4.1). Fork length was not a significant predictor of movement activity ($F_{1,14.21}=0.026$, $p>0.050$) and was removed through backwards selection. Movement activity in Arctic charr increased significantly during the day in all seasons (LS Means, $p<0.050$), although the extent of the increased activity varied between seasonal periods, with the least activity in the winter (mean 0.13 m/s^2) and the highest activity during the ice breakup period (mean 0.31 m/s^2) (Figure 4.4). Back-transformed model predictions revealed that movement activity was positively correlated with temperature use in the spawning and ice breakup period (Figure 4.5). In contrast, during winter Arctic charr showed increased movement activity at cooler water temperatures (Figure 4.5).

4.4 Discussion

Data collected on anadromous Arctic charr were consistent with the hypothesized display of diurnal activity patterns throughout the overwinter residency period. Movement activity was positively correlated with water temperature in the spawning and ice breakup seasonal periods, but negatively correlated in winter. Body size within the size range studied (36.0 – 48.5 cm) was not a significant predictor of movement activity in tagged Muddy Bay Brook Arctic charr.

The diurnal activity patterns observed in the wild, adult anadromous Arctic charr in this study replicated those observed in lacustrine resident Arctic charr in Lake Ellasjøen (Bear Island, 74°30'N, 19°00'E), where fish exhibited diurnal patterns throughout the overwintering period except during the winter solstice which is characterized by continuous darkness at this latitude (Hawley et al., 2018). Similarly, laboratory reared juvenile Arctic charr exhibit diurnal activity patterns in December and January, and bimodal diurnal patterns from February through June (Linnér et al., 1990). In early winter (October-November), juveniles favour nocturnal activity patterns (Jørgensen & Jobling, 1989; Linnér et al., 1990), with smaller, lower social status individuals adopting the nocturnal strategy to avoid aggression from larger and more dominant conspecifics (Alanärä & Brännäs, 1997; Brännäs, 2008).

Many size-dependent ecological factors, e.g., intraspecific competition and predation risk, have been associated with the observed plasticity in fish diel activity patterns (Reebs, 2002; Fingerle, Larranaga, & Steingrímsson, 2016), with growth maximization and predation avoidance figuring prominently as causative mechanisms in juvenile studies (Metcalfe, Fraser, & Burns, 1999). For example in the wild, Atlantic salmon juveniles are predominantly nocturnal in winter, as low temperatures make them slow and more vulnerable to predation during the daylight hours (Bradford & Higgins, 2001; Hiscock et al., 2002; Reebs, 2002). The display of clear diurnal activity patterns by adult Arctic charr in both Lake Ellasjøen (Hawley et al., 2018) and in this study, however, suggests that environmental factors figure more prominently in the determination of diel patterns of adult fish. Temperature (Mulder et al., 2018b), light intensity and food availability (Steinhart & Wurtsbaugh, 1999; Blanchfield et al., 2009) have all been identified as important factors in shaping winter dispersal and activity patterns in adult salmonids, with activity patterns in overwintering adult lacustrine Arctic charr linked to above-surface photoperiod (Hawley et al., 2018).

Predation risks for adult Arctic charr (generally >40 cm) are undoubtedly low (Guiguer et al., 2002) and, therefore, likely to have little influence on the determination of diel activity patterns. Food availability (e.g., Metcalfe, Fraser, & Burns, 1999) may, however, drive activity as a result of seasonal variations in resource use, with high latitude lacustrine fish known to shift their trophic ecology to exploit natural variations in prey abundance (Eloranta et al., 2013). Although feeding is believed to be reduced or absent in overwintering anadromous Arctic charr populations (J. W. Moore & Moore, 1974; Boivin & Power, 1990; Rikardsen, Amundsen, &

Bodin, 2003), anadromous post smolts in Norway have been shown to feed on planktonic prey after returning from the sea and to maintain their pelagic feeding behaviour in freshwater (Rikardsen, Amundsen, & Bodin, 2002, 2003). Seasonal response to resource availability can have significant implications for consumer growth and reproduction as studies with European whitefish (*Coregonus laveratus*) have shown (Hayden, Harrod, & Kahilainen, 2014), particularly as zooplankton have high percentages of essential fatty acids (Eloranta et al., 2013; Mariash, Cusson, & Rautio, 2017), are a nutritious food and have been reported to supplement the predominant benthivorous diet of top consumers such as lacustrine Arctic charr (Eloranta et al., 2013).

Although Arctic charr are more effective at feeding under low temperature and light levels compared to other salmonids (Siikavuopio, Knudsen, & Amundsen, 2010; Elliott, 2011; Helland et al., 2011), daytime feeding likely remains more profitable. Feeding efficiency in salmonids has been reported to decline by 65% under ideal night conditions (full moon and clear skies), and an additional 25% under poor night conditions (no full moon and overcast) (Fraser & Metcalfe, 1997). Prey capture probability at low temperatures (2-3°C) in drift-feeding salmonids declines significantly from capturing nearly all prey in daylight to only capturing 1% of the prey under moonlight conditions (Watz et al., 2014). Light availability influences diel activity patterns in sockeye salmon (*Oncorhynchus nerka*) undertaking diel vertical migrations into the upper water column where a combination of high prey densities and increased light levels maximized foraging success (Steinhart & Wurtsbaugh, 1999). Similarly, low ambient light levels can influence the spatial and pelagic distribution of lake trout (*Salvelinus namaycush*), with consistent winter presence in the upper water column thought to facilitate foraging efficiency as reduced light levels significantly increase foraging costs in the species (Mazur & Beauchamp, 2003; Blanchfield et al., 2009). Therefore, diurnal activity patterns observed in Arctic charr in this study, are suggested to reflect daytime feeding which remains more profitable in terms of rapid food acquisition and minimizing energy expenditure, particularly under ice and snow cover conditions, which further attenuate light levels (this study, Adams et al., 1988; Linnér et al., 1990; Alanärä & Brännäs, 1997; Larranaga & Steingrímsson, 2015; Hawley et al., 2018). Both juvenile and adult Arctic charr have shown preference for daytime activity and foraging behaviour (this study, Adams et al., 1988; Linnér et al., 1990; Alanärä & Brännäs, 1997; Larranaga & Steingrímsson, 2015; Hawley et al., 2018) when no other factors such as predation risk, competition, density or shelter availability are prioritized over feeding efficiency (e.g., Alanärä & Brännäs, 1997; Larranaga & Steingrímsson, 2015; Fingerle, Larranaga, & Steingrímsson, 2016).

Daytime activity observed in this study was characterized by a large peak of activity in the early morning and a second smaller peak of activity around sunset in the spawning and ice breakup periods. It is suggested that crepuscular periods of dawn and dusk provide an optimal balance between predator avoidance and foraging efficiency (Clark & Levy, 1988). Visual feeding piscivores such as northern pike (*Esox lucius*), increase their foraging intensity during this period as twilight provides ideal conditions in which the species can exploit a competitive advantage over prey, which react later than in full light (Baktoft et al., 2012). Winter feeding piscivorous Arctic charr may enjoy similar advantages over their prey and under some circumstances feed on fish during winter (M. Power et al., 2009). In addition, polarization values increase during crepuscular times (Flamarique & Hawryshyn, 1997), enhancing prey location in polarization sensitive fish species such as rainbow trout (*Oncorhynchus mykiss*) (Flamarique & Browman, 2001). In this context, the activity peaks observed around twilight in this study, are suggestive of Arctic charr utilizing light levels under which foraging efficiency is maximized.

Low water temperatures reduce movement activity and feeding in fish (Huusko et al., 2007; Shuter et al., 2012; Mulder et al., 2018a) as was evident from our movement data during the spawning and ice breakup periods. However, movement activity in winter was negatively correlated with temperature. Rapidly declining water temperatures in early winter (November-December) are stressful for stream fish and impose considerable energetic demands causing an early-winter depletion of lipid reserves (Cunjak & Power, 1987; Cunjak, 1988). Brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) appear to suffer a second period of lipid depletion in late winter (March) (Cunjak, 1988). If Arctic charr do not feed in the freshwater environment, body reserves can decline by 30% for non-reproductive individuals and up to 80% for post-spawning individuals between September and May (Dutil, 1986; Jørgensen, Johansen, & Jobling, 1997). Low condition and depleted energy reserves are thought to stimulate fish to increase food intake and associated foraging activity (Tveiten, Johnsen, & Jobling, 1996). The cold-water temperatures associated with increased activity as observed in our study, therefore, are likely a by-product of (opportunistic) feeding behaviour immediately below the ice where temperatures are among the coldest. The warmer winter temperatures utilized by Arctic charr when less active in this study, might be for the purpose of enhancing overall physiological function, i.e., aiding metabolic processes that improve digestion efficiencies (Shuter et al., 2012), as similar behaviour has been observed in Arctic charr in the marine environment (Spares et al., 2012).

During the ice-breakup period where the same winter range of water temperatures was utilized, movement activity increased as a function of temperature. The contrasting response to changes in temperature in this period to that in winter is suggested to result from fish preparing for outmigration. Anadromous Arctic charr are known to lose their seawater tolerance while overwintering in freshwater and undergo a pre-adaptive increase in their hypo-osmoregulatory capacity from April to May before entering seawater (Jørgensen & Arnesen, 2002; Aas-Hansen et al., 2005). Simultaneously, movement activity is known to increase significantly in spring, especially in the three weeks preceding outmigration (Mulder et al., 2018a), likely in response to increasing water temperatures signaling the onset of the spring turnover and ice breakup (Mulder – unpublished data). Utilizing warmer water temperatures enable Arctic charr to reorganise and enhance metabolic processing capacities to fuel these energy demanding processes (Aas-Hansen et al., 2005; Shuter et al., 2012). Therefore, water temperatures in this study have an indirect effect on diel activity patterns likely by enhancing metabolic processes (e.g., to improve digestion and osmoregulatory capacities) and preparing Arctic charr for outmigration.

Little is known about how fish perceive photic information in winter when subsurface day-night differences are reduced as a result of thick ice and snow cover. Cage experiments with overwintering Arctic charr have demonstrated no endogenous rhythms in pineal melatonin secretion (Migaud et al., 2007; Strand et al., 2008), with melatonin known to reflect the prevailing photoperiod (Migaud et al., 2007) and reduce locomotory activity and appetite in teleosts and other vertebrates (Angers et al., 2003; López-Olmeda, Madrid, & Sánchez-Vázquez, 2006). Nevertheless, linkages between melatonin, photoperiod and activity would predict cycles in diel activity which are consistent with the study observations given that the significant increase in movement activity occurs in daylight only. The continuously observed diurnal activity patterns in winter suggest that Arctic charr in this study were able to keep track of time under ice and snow cover even at low ambient light levels, as diel activity rhythms were found to be absent in lacustrine Arctic charr living under conditions of continuous darkness (Hawley et al., 2018).

4.5 Conclusion

This study provides some of the first observations of diel activity patterns in wild adult anadromous Arctic charr while overwintering in freshwater. The diurnal activity patterns observed may be driven by prey and light availability in the upper water column where daylight facilitates foraging efficiency by increasing the likelihood of prey capture. Movement activity increased as a function of temperature, except during winter, where cold-water temperatures associated with increased activity are thought to be a by-product of (opportunistic) feeding behaviour below the ice. Body size did not have an effect on activity patterns, although the result may have been an artefact of the limited size range of tagged fish used in this study. As the population in this study originates from the southern end of the distributional range of anadromous Arctic charr, an area characterized by distinct differences in photoperiod between day and night, further investigations are required to determine the generality of the results for more northerly anadromous populations that experience periods of constant darkness.

Table 4.1. The final model including the random and fixed effects of body temperature (T_b), diel period, seasonal period and its interactions (see equation), for the linear mixed effects model of movement activity (m/s^2) in Arctic charr. Marginal and conditional R^2 values were calculated using the methods described by Nakagawa & Schielzeth (2013). Parameter significance is shown, displaying degrees of freedom (df), Π^2/F values, and P values calculated from F-tests based on Sattethwaite's approximation (Kuznetsova, Brockhoff, & Christensen, 2015).

Final model	$R^2_{marginal}$	$R^2_{conditional}$
T_b + Diel period + Seasonal period + T_b:Seasonal period + Diel period: Seasonal period + Ind + Series	0.226	0.397

Parameters	Π^2/F	P value
Random effects:		
Ind (Arctic charr)	4.65, df=1	0.019
*Series (Arctic charr*month)*	284.37, df=1	<0.001
Fixed effects:		
T_b	0.43, ndf=1, ddf=4469.31	0.513
Diel period	81.96, ndf=1, ddf=4449.45	<0.001
Seasonal period	43.92, ndf=2, ddf=266.96	<0.001
T_B:Seasonal period	212.29, ndf=2, ddf=4284.78	<0.001
Diel period:Seasonal period	3.71, ndf=2, ddf=4430.55	0.024

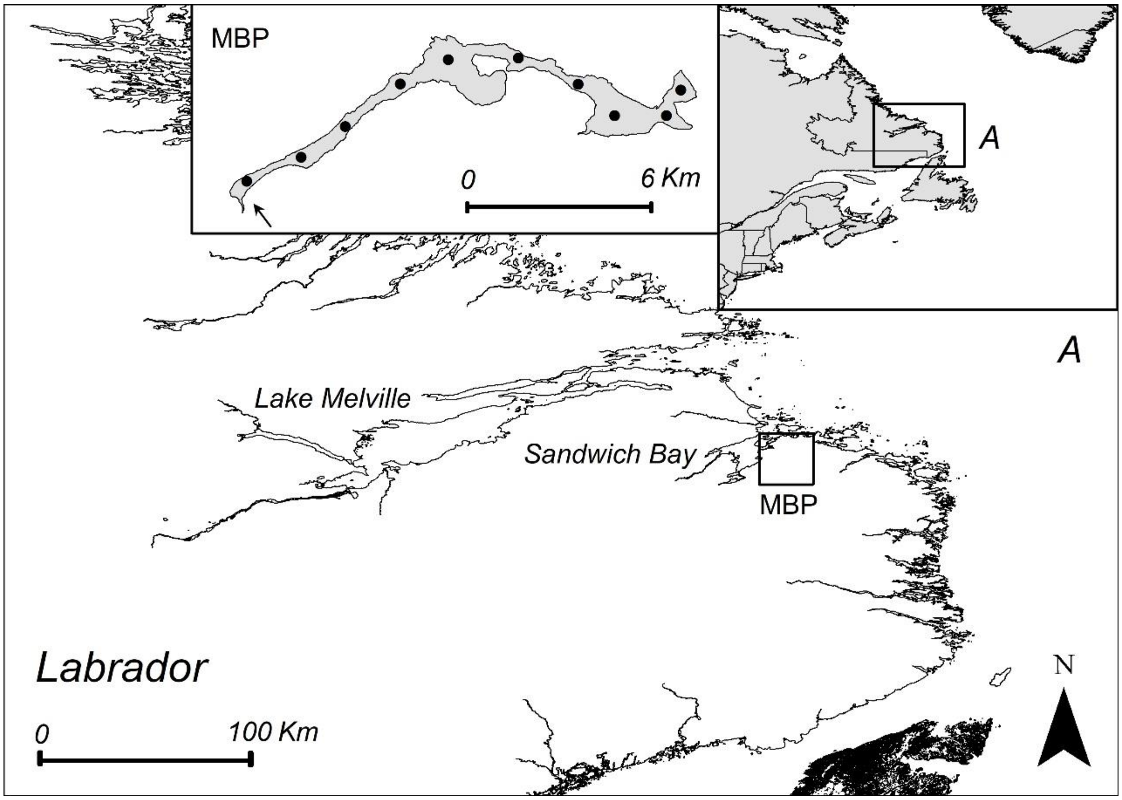

Figure 4.1. Map of Muddy Bay Pond (MBP) located with respect to the Labrador coast, Canada. Receiver locations are indicated by black dots, and the arrow indicates the location where Arctic charr enter the pond.

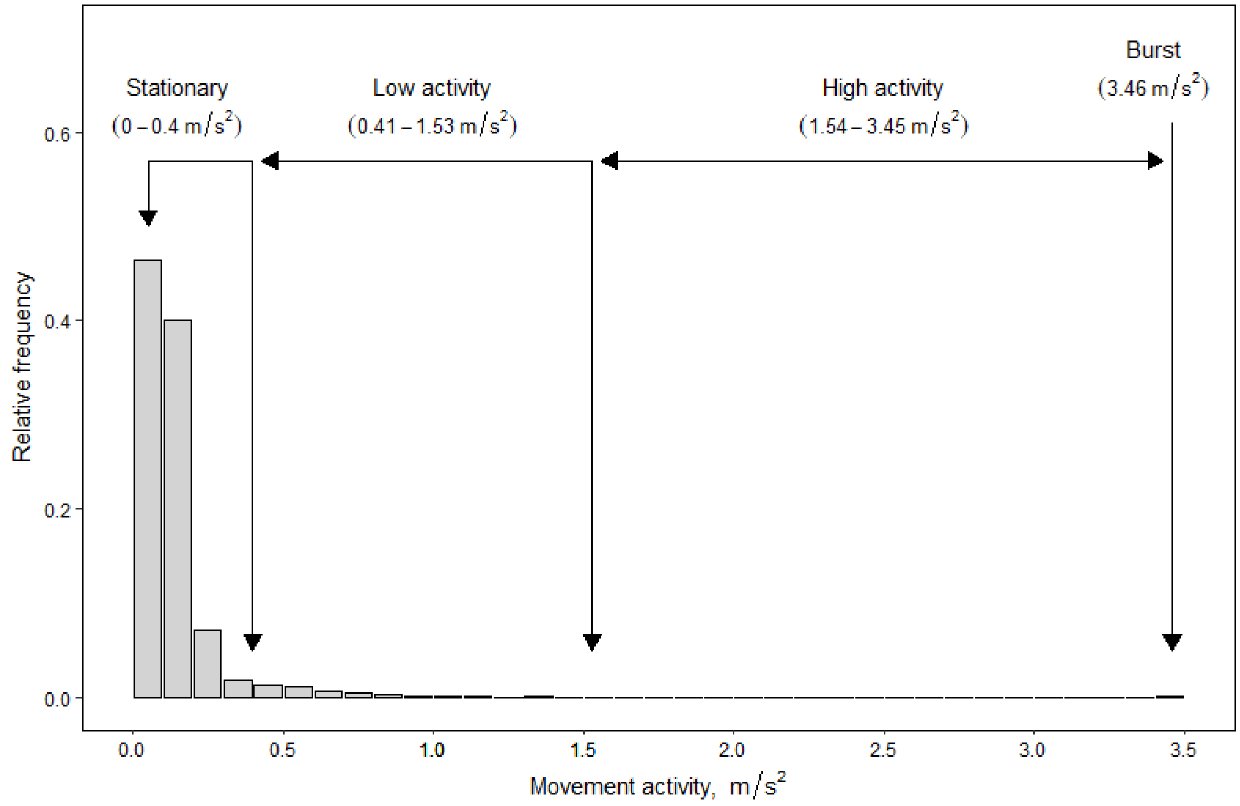

Figure 4.2. Relative frequency of Arctic charr movement activity (m/s^2) during overwinter residency in Muddy Bay Pond. Values for stationary, low activity, high activity and burst activity are overlaid on the histogram for reference.

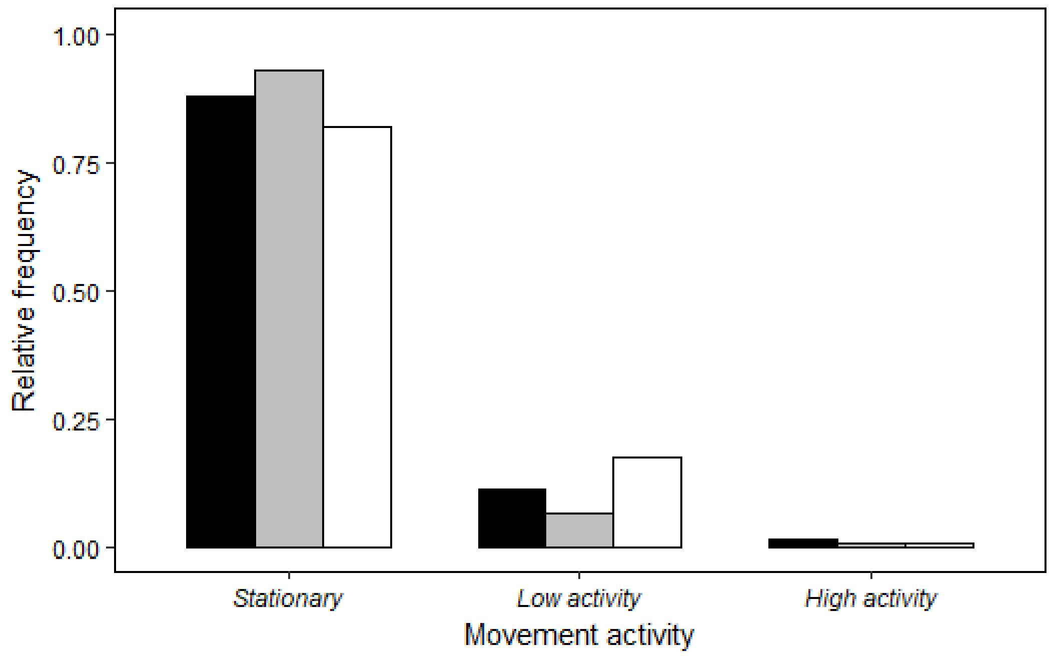

Figure 4.3. Relative frequency of individual Arctic charr daytime movement activity (m/s^2) recorded for stationary, low activity, and high activity behaviour in each season (black=spawning, grey=winter, white=ice breakup). The spawning and ice breakup period considered the freshwater residency period only.

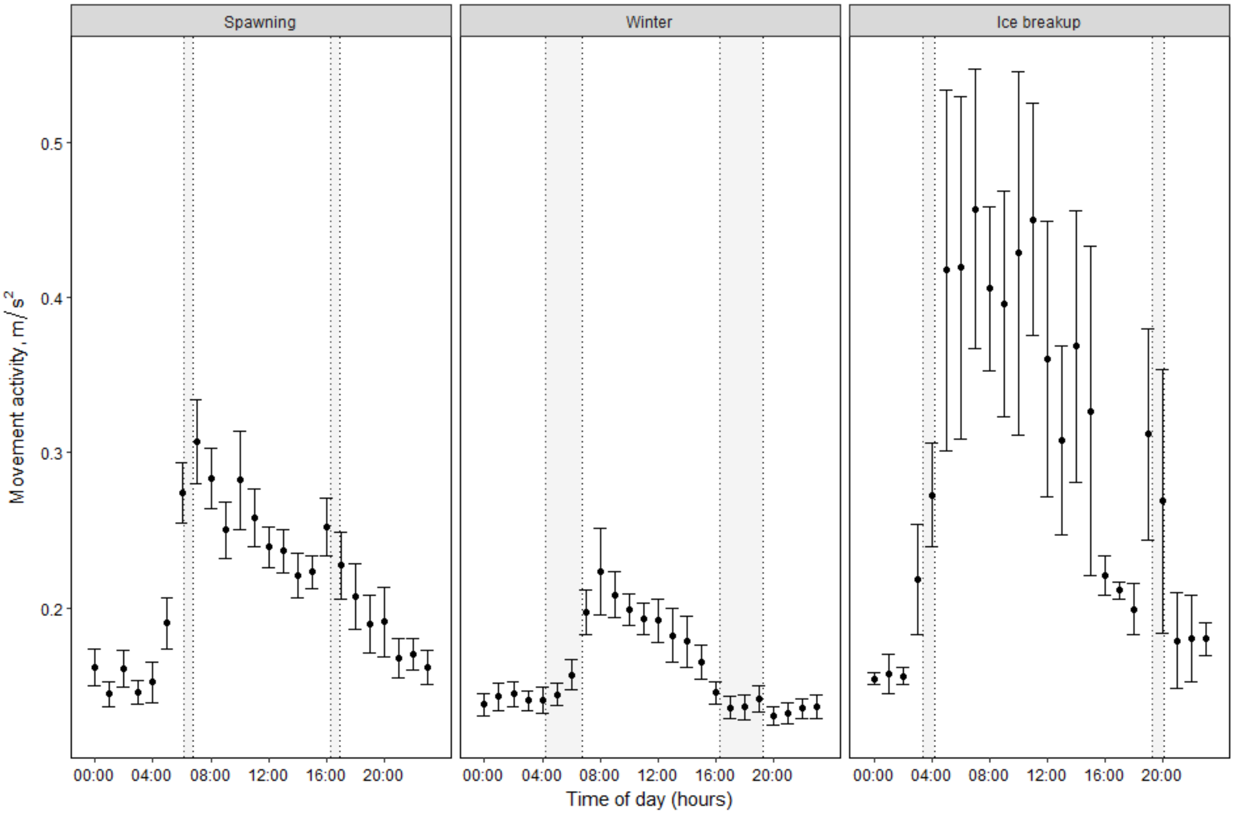

Figure 4.4. Hourly (±SE) averaged movement activity (m/s^2) of individual fish means over the spawning, winter and ice breakup diel periods in Muddy Bay Pond 2015-2016. Shaded areas indicate the variation of sunrise and sunset times within each season.

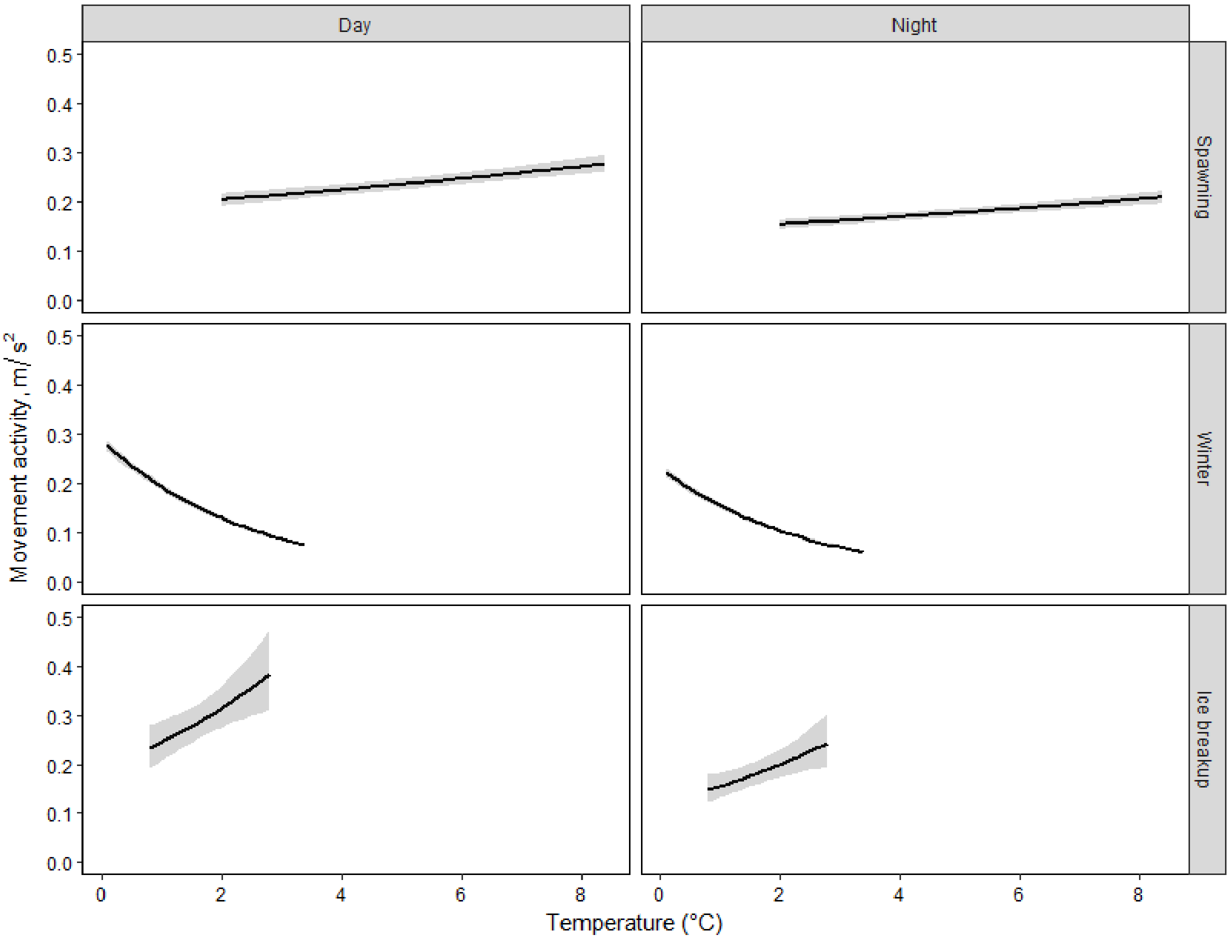

Figure 4.5. Back-transformed reduced linear mixed model (equation, Table 4.1) estimates of Arctic charr movement activity (m/s^2) among seasons in relation to temperature use. Shaded areas represent standard errors. The spawning and ice breakup periods consider freshwater residency only.

Chapter 5: Body size and diel period shape marine temperature and depth use in anadromous Arctic charr

5.1 Introduction

Arctic charr (*Salvelinus alpinus*) display an anadromous life history strategy throughout most of its North American range, where it feeds in the productive marine environment for 1-2 months in summer before returning to freshwater to spawn and/or overwinter (Doucett et al., 1999; Klemetsen, Amundsen, et al., 2003). Although limited feeding after freshwater entry may occur (Boivin & Power, 1990; Mulder et al., 2018a), reduced or no over-winter acquisition of prey implies limited opportunity for post-spawning reconditioning and the probable continued depletion of lipid reserves acquired during summer feeding (Dutil, 1986; Jørgensen, Johansen, & Jobling, 1997). The marine migration period, therefore, is important in terms of restoring and accumulating annual energy reserves (Gyselman, 1984), growth (Johnson, 1980) and future reproduction (e.g. fecundity) (Jørgensen, Johansen, & Jobling, 1997; Dempson, Shears, & Bloom, 2002). As the feeding season is short, changes in environmental conditions (e.g., as a result of climate change) can have significant effects on the ability to grow and reproduce (Dutil, 1984; Michaud, Dempson, & Power, 2010). While dispersal at sea, and linkages to food intake and growth, are generally understood (Dempson & Kristofferson, 1987; Sæther, Johnsen, & Jobling, 1996; Spares et al., 2012), diel variation in temperature and depth use and their effects on marine activity patterns remain poorly characterized (Rikardsen, Diserud, et al., 2007; Morris & Green, 2012; Spares et al., 2012).

The annual spring migration of Arctic charr to the sea coincides with ice break-up (Dempson & Green, 1985; Berg & Berg, 1989; Spares, Dadswell, et al., 2015), where the arrival at sea of larger fish generally precedes that of smaller ones (Grainger, 1953; Johnson, 1989). In the marine environment, Arctic charr is a shallow water feeder that spends the majority of its time in the upper three meters of the water column (Rikardsen, Diserud, et al., 2007; Morris & Green, 2012; Spares et al., 2012; Jensen et al., 2016), but will descend to depths below 30 meters with short (<7 min) consecutive repetitive dives (Rikardsen, Diserud, et al., 2007; Spares et al., 2012; Jensen et al., 2016). Similar diving behaviour has been observed in other salmonids, such as Dolly Varden (*Salvelinus malma*) and Atlantic salmon (*Salmo salar*), and occurs largely during the daytime (Hedger et al., 2009; Courtney et al., 2016) with fish following the diel vertical migrations of invertebrate prey (Hays, 2003; Courtney et al., 2016) or taking advantage of daylight hours to optimize foraging efficiency (Reddin et al., 2011; Courtney et al., 2016).

Rikardsen et al. (2007) noted that deep dives were frequently followed by a marked drop in temperature for externally tagged fish, but not for internally tagged fish, suggesting that dives were too short in duration to change the internal body temperature (Rikardsen, Diserud, et al., 2007). As fish are ectotherms, temperature is one of the most important environmental factors controlling activity levels through its effect on critical physiological rates and metabolic processes (Fry, 1971; Angilletta, Niewiarowski, & Navas, 2002). The thermal optimum, the temperature at which performance is maximal, is dependent on fish behaviour and physiology and can vary among biological processes such as feeding, growth and reproduction (Angilletta, Niewiarowski, & Navas, 2002; Hasnain, Shuter, & Minns, 2013) with the result that fish may shift thermal habitats to optimize different physiological processes. For example, Johnson (1980) found Arctic charr feeding in the cold salt waters (-1.35°C at 0.5-1.0 m below the ice) prior to ice breakup and returning to warmer river waters to digest their food. Similar patterns have been observed with repetitive deep dives into colder water for foraging followed by time spent near the surface in a heat recovery phase (Spares et al., 2012) where physiological processes such as digestion, osmoregulation and respiration may be enhanced (Fry, 1971). Thus, while Arctic charr encounter and use sub-zero temperatures, they typically appear to avoid allowing body temperatures to decline below 0°C (Johnson, 1980; Dempson & Kristofferson, 1987; Spares et al., 2012).

Ontogenetic changes in thermal habitat use may lead to fish partitioning thermal resources between size or age classes (Magnuson, Crowder, & Medvick, 1979; Elliott & Elliott, 2010; Morita et al., 2010). In salmonids, the optimal temperature for growth is known to decrease with increasing body size, with larger and older individuals utilizing cooler temperatures and smaller and younger individuals preferring warmer temperatures (Morita et al., 2010; Jonsson & Jonsson, 2011). The growth of larger individuals is likely enhanced in cooler conditions as a result of the bioenergetics advantage gained by size (Morita et al., 2010). Thus, temperatures utilized by adult Arctic charr in the wild are typically lower than commonly cited laboratory-derived optima for juveniles, varying from 6 to 12 °C in surface waters (Rikardsen, Diserud, et al., 2007; Spares et al., 2012), and averaging 3.7 °C for individuals undertaking deep subtidal dives (Spares et al., 2012). Although the gills are an effective heat exchanger, most heat (70-90%) transfers through the body wall (Elliott, 1981) and there is a time lag in reaching the thermal equilibrium which depends on fish mass. Small fish, therefore, are more susceptible to fluctuations in water temperature than larger fish (Elliott, 1981; Rikardsen, Diserud, et al., 2007) and may be expected to differentially utilize available thermal habitats as a result of the physiological constraints placed on them by body size.

Here we explore relationships between body size and temperature and their effects on activity patterns in anadromous Arctic charr when feeding in the marine environment. Using a combination of acoustic and archival telemetry data from southern Labrador, Canada, we test the following hypotheses: [i] – temperature use depends on body size with larger individuals utilizing cooler water temperatures; [ii] – temperature use is related to diel period with [a] fish utilizing cooler temperatures at greater depth during the day, and [b] displaying increased vertical activity during daylight hours; [iii] – diving activity depends on temperature and body size, with [a] increased vertical activity occurring at warmer body temperatures, and [b] dive duration being positively correlated with both ambient water temperature and body size.

5.2 Methods

5.2.1 Study area

Data on depth and temperature use by Arctic charr were collected at two locations along the Labrador coast, Canada. The first site (52.58°N, 56.02°W) comprised the areas defined by Gilbert and Alexis Bays, hereafter referred to as Gilbert Bay (GB; Figure 5.1). Both bays are narrow coastal inlets, covering an area of approximately 330 km^2 (Morris & Green, 2012), and are generally less than 30 m in depth with maximal water depths of ~100 m occurring near the outer headlands (Copeland et al., 2012). Anadromous Arctic charr using the area for summer feeding are known to overwinter in Shinneys Pond and enter Gilbert Bay in late May/early June following ice breakup (Morris & Green, 2012; Mulder et al., 2018a). Surface water temperatures are sub-zero from December until May, but increase rapidly once ice retreats from the bay areas (early-mid May) (Morris & Green, 2002).

The second site, Sandwich Bay (SB; 53.64°N, 57.21°W) is located about 130 km north of Gilbert Bay (Figure 5.1) and covers an area of ~350 km^2. The bay is generally 30-40 m deep but contains a deeper basin (max. 80 m) near the middle of the bay. The entrance to the bay is shallow (12-21 m) with strong tidal currents (personal observation). Five major rivers (North River, Eagle River, White Bear River, Paradise River and Muddy Bay Brook) empty into the bay, with each contributing a significant inflow of freshwater during the spring thaw. Anadromous Arctic charr are known to overwinter only in the Muddy Bay Brook system and enter Sandwich Bay in late May/early June immediately after ice breakup (Mulder et al., 2018a).

5.2.2 Tagging and tracking

Monofilament gill nets (63-89 mm stretched mesh size, 25 m long), set within a 13 km radius from the mouths of Shinneys River and Muddy Bay Brook were used to capture Arctic charr in the marine environment. Additional sampling occurred at a Fisheries and Oceans Canada operated fish counting facility at Muddy Bay Brook (Reddin et al., 2005). Captured individuals were implanted with temperature-sensing acoustic Vemco (Halifax, NS, Canada) V9T (36 x 9 mm, 2.2 g in water, random delay: 55-85 s, accuracy ± 0.5°C, resolution 0.1°C), V13T (48 x 13 mm, 6.5 g in water, random delay: 55-85 s, accuracy ± 0.5°C, resolution 0.1°C) or data storage tags (DST; described below). The number of fish captured, fork length (cm), tag type and tagging dates are given in Table 5.1. At Muddy Bay Brook, an external Floy tag having a unique number was also attached for ease of identification of all DST or acoustic tagged fish at the Fisheries and Oceans Canada counting fence or by local fishers.

The DSTs (LAT2810ST) were light-based geolocation tags (38 x 11 mm, 3.5 g in water, 60 s sampling interval, LOTEK Wireless Inc., St. John’s, NL, Canada), designed to be implanted in the peritoneal cavity of the fish with a sensor stalk protruding outside. The tag recorded internal temperature (°C) and depth (dbar), and external temperature (°C) through the external stalk in relation to time. The tag temperature range was -5 to 30°C, with an accuracy of less than 0.2°C and a resolution of 0.05°C. Pressure (dbar), a proxy for depth, was measured to a maximum of 50 dbars. Pressure recordings had an accuracy and resolution of 1 and 0.05% of the full scale, respectively. A single unit dbar is equivalent to approximately 1 m in depth (Saunders & Fofonoff, 1976). The data stored on the DSTs were retrieved after fish recapture by connecting the tag to an upload box linked to a computer.

Surgical procedures for acoustic and DST implants followed standards of practice as described in Mulder, Morris, et al. (2018b) and Wagner et al. (2011). Tagging procedures further followed standards and guidance provided by the Canadian Council on Animal Care (protocol # 14-12-IF) and were approved by the Northwest Atlantic Fisheries Centre animal care committee protocol (NAFC 2013-05).

In Gilbert Bay, networks of 32 (2012) and 38 (2014) omnidirectional hydro-acoustic receivers (model VR2W, 69 kHz, Vemco) were used to determine temperature use of the tagged Arctic charr (Figure 5.1 - GB). Similarly, a network of 31 omnidirectional hydro-acoustic receivers (model VR2W, 69 kHz, Vemco) was deployed in Sandwich Bay in 2015 (Figure 5.1 - SB). Each receiver was attached to a buoyed line and suspended approximately 2-6 m above the sea floor. Data were downloaded in October 2012, October 2014 and August 2015. Temperature loggers were deployed near the surface (2-3 m depth) and bottom (11-13 m depth), one kilometer from the river mouth of Shinney's River in 2012 and 2014. Similarly, one temperature logger was deployed in the mid-water column (11 m depth), one kilometer from the river mouth of Muddy Bay Brook.

5.2.3 Data analyses

Temperature and depth time series plots were used to detect and eliminate fish from the dataset whose temperature and/or depth use did not change throughout the study period or showed abnormal behaviour, and were thought to have died, shed their tag or been preyed upon. In addition, to reduce the likelihood of false detections in the acoustic data, detections were only used in statistical analyses if a tag was detected ≥2 times per 24-hr period (Heupel, Semmens, & Hobday, 2006). As year was not found to be a significant predictor of temperature use in Gilbert Bay ($F_{1,69.56}$=0.278, p>0.050), data from both years (2012, 2014) were combined for further analyses. Owing to the differences in frequency and accuracy of temperature recordings between tag types, data were modelled separately by tag type. Marine entry and departure timing by Arctic charr implanted with DSTs were determined by examining the temperature and depth time series plots as the species showed diving behaviour in the marine environment only and temperatures increased when fish entered freshwater. The entrance and departure dates calculated as a result were similar to the individuals implanted with acoustic tags and, therefore, the DST data were considered to correctly reflect the marine migration period and to be comparable with the acoustic data. The diel period was calculated following methods described by Mulder, Morris, et al. (2018a) using computational methods for determining day length provided by the NRC Herzberg Institute of Astrophysics in Canada considered accurate to ±2 minutes for the period 1900-2100 (www.nrc-cnrc.gc.ca/eng/services/sunrise/accuracy.html). A subset of the acoustic data from the marine residency period (mid June-July) was used to test for the effects of tide (incoming versus outgoing tide) on temperature use, in both Gilbert (2012) and Sandwich Bays (2015) using linear mixed models. Although statistical evidence indicated that Arctic charr utilized warmer waters during the rising tide in Gilbert ($F_{1,78829}=246.68$, $p<0.050$) and Sandwich Bays ($F_{1,14804}=54.26$, $p<0.050$), the difference of <0.14°C was less than the measurement precision of the tag and, therefore, considered biologically insignificant. As a result, tidal influence was not considered further in any analyses.

5.2.4 Model details

All hypotheses were tested using linear mixed model (LMM) methods (Gelman & Hill, 2007; Zuur et al., 2009), with models fit using the lme4 package (Bates et al., 2015) in the statistical software R (R Core Team, 2015). For all models, hierarchical random intercepts were fitted including: individual Arctic charr (Ind) and the nested level *series*, a combination of individual and day (or individual and week) to account for the temporal autocorrelation in the data (Gelman & Hill, 2007; Araya-Ajoy, Mathot, & Dingemanse, 2015). The continuous fixed effects were mean centred, and all two-way interactions with fixed effect variables were considered.

To test the temporal and spatial constancy of temperature use (H1 and H2a) across varying time scales (days, years) and body size, temperature use (°C) was modelled (Model 1) as a function of the fixed effects: diel period (DP: day, night), location (LOC: GB, SB), fork length (FL: cm) and a random error term (e_0), using the acoustic data only as follows:

$$y_{ijk} = \left(\beta_0 + Ind_{0j} + series_{0jk}\right) + DP_{ijk} + LOC_{ijk} + FL_{ijk}$$
$$+DP \cdot LOC_{ijk} + DP \cdot Fl_{ijk} + LOC \cdot FL_{ijk} + e_{0ijk}$$

A second test (Model 2) of H1 and H2a was completed using the DST data with temperature use (°C, mean temperature per diel period per fish) as a response variable with fixed effects of diel period, year (2015, 2016), fork length and a random error term (e_0) as follows:

$$y_{ijk} = \left(\beta_0 + Ind_{0j} + series_{0jk}\right) + DP_{ijk} + Year_{ijk} + FL_{ijk}$$
$$+ DP \cdot Year_{ijk} + DP \cdot FL_{ijk} + Year \cdot FL_{ijk} + e_{0ijk}$$

Where y_{ijk} in both Model 1 and 2 is equivalent to temperature use at instance i, for individual fish j, during the tracking series k.

To further test H2a, depth (m, mean depth per diel period per fish) use was modelled (Model 3) as a function of the fixed effects: diel period, year, fork length and a random error term (e_0), using DST data only as follows:

$$y_{ijk} = (\beta_0 + Ind_{0j} + series_{0jk}) + DP_{ijk} + Year_{ijk} + FL_{ijk}$$
$$+ DP \cdot Year_{ijk} + DP \cdot FL_{ijk} + Year \cdot FL_{ijk} + e_{0ijk}$$

Where y_{ijk} is equivalent to depth use at instance i, for individual fish j, during the tracking series k.

The relationship between vertical movement activity and temperature on a small temporal scale (H2b, H3a) was modelled (Model 4) with diel vertical activity (DVA) equalling the sum of change in depth divided by the detection duration per diel period in meters per hour, using DST data and methods described by Harrison et al. (2013). DVA was modelled as a function of diel period, body temperature (T_b in °C), fork length and a random error term (*e₀*) as follows:

$$y_{ijk} = (\beta_0 + Ind_{0j} + series_{0jk}) + DP_{ijk} + T_{b_{ijk}} + FL_{ijk}$$
$$+ DP \cdot T_{b_{ijk}} + DP \cdot FL_{ijk} + T_b \cdot FL_{ijk} + e_{0ijk}$$

Where y_{ijk} is equivalent to rate of vertical movement at instance i, for individual fish j, during the tracking series k. Dive duration (in minutes, using DST data) was calculated for each dive made below 3 m depth using the diveMode package (Luque, 2007) in R.

To test H3b, dive duration was modelled (Model 5) as a function of fork length, the external temperature (T_E in °C) recorded at the end of the descent of each dive and a random error term (e_0) as follows:

$$y_{ijk} = (\beta_0 + Ind_{0j} + series_{0jk}) + FL_{ijk} + T_{E_{ijk}} + FL \cdot T_{E_{ijk}} + e_{0ijk}$$

Where y_{ijk} is equivalent to dive duration at instance i, for individual fish j, during the tracking series k. The response variable depth was cube-root transformed, whereas DVA and dive duration were log transformed to achieve normality and to ensure variance homogeneity across the fixed effects (Zuur et al., 2009).

Backwards selection was used for all random and fixed effect component estimates as implemented in the ImerTest package (Kuznetsova, Brockhoff, & Christensen, 2015) in R. The p-values for the fixed effects were calculated from the F-test based on Sattethwaite's approximation, whereas the p-values for the random effects were based on likelihood ratio tests (Kuznetsova, Brockhoff, & Christensen, 2015).

5.3 Results

Tagged Arctic charr used a variety of mean depths (0.79-1.30 m) and mean temperatures (7.25-10.25°C), with use varying by diel period. Detailed characteristics of the acoustic and DST tagged fish that were detected and/or recovered in this study and the corresponding means of individual fish length, temperature (°C) and depth use (m) per diel period, and year are reported in Table 5.2. Significant correlations were found when the mean of average daily temperature use of individual fish was regressed against mean daily sub-surface temperatures, or against mean daily bottom temperatures for all sites ($R^2 \geq 0.366$, $p \leq 0.001$; Figure 5.2).

5.3.1 Temperature use Arctic charr (H1, H2a)

In the model relating temperature use (°C) to diel period, location, fork length and its interactions (Model 1) estimated using 189,633 post-filtered temperature detections, the interactions diel period and fork length and diel period and location were found to be significant predictors of temperature use ($p<0.001$, Table 5.3). Model predictions at 0.05, 0.5 and 0.95 quantiles of fork length revealed that smaller individuals generally used warmer water temperatures compared to larger individuals in both Gilbert and Sandwich Bays (Figure 5.3). Moreover, a strong diel pattern in temperature use was found in Gilbert Bay (LS Means, $p<0.001$) with Arctic charr utilizing cooler water temperatures during the day (Figure 5.3). No such general pattern was observed in Sandwich Bay (LS Means, $p=0.040$).

In the second test (Model 2) using DST data in which temperature use (°C) was related to diel period, year, fork length and its interactions, fork length was not found to be a significant predictor of temperature use ($F_{1,45.72}=0.109$, $p=0.742$) and was removed through backwards selection. As with the acoustic data, temperature use differed significantly with diel period ($p=0.017$, Table 5.3), although in contrast to the acoustic data temperature use was marginally higher at night than during the day (difference day-night: 0.2°C; Figure 5.4). Temperature use also varied significantly between years ($p<0.001$, Table 5.3), with N=5 tagged fish in 2015 using generally cooler waters than the N=3 tagged fish in 2016.

5.3.2 Depth and vertical activity (H2, H3a)

In the model relating depth use (m) to diel period, year, fork length and its interactions (Model 3), the interactions between year and fork length and year and diel period were found to be significant predictors of depth use ($p<0.001$, Table 5.3). Back-transformed model predictions indicated that Arctic charr resided at deeper depths during the day and moved to shallower waters at night (Figure 5.5), particularly in 2015. In 2015 smaller individuals showed a clear pattern of shallower depth use during both day and night as compared to larger individuals

(Figure 5.5). Although sample size was limited, in 2016 significant differences in diel depth use were maintained (LS Means, $p<0.001$), although in contrast to 2015 larger fish were resident at shallower depths during all diel periods than smaller fish.

The mean of individual fish average vertical movement activity per hour was 25.67 ± 18.56 m during the day and 5.97 ± 3.14 m at night. Diel period and body temperature were found to be significant predictors of vertical activity ($p<0.001$, Model 4, Table 5.3). Back-transformed model predictions indicated vertical activity in Arctic charr was significantly greater during the day than at night (LS means, $p<0.001$, Figure 5.6). Moreover, model predictions also showed that vertical activity was positively correlated with body temperature ($p<0.001$, Table 5.3, Figure 5.6) in both diel periods.

5.3.3 Diving behaviour (H3b)

Over the study period a total of 7522 individual dives were made below 3 m, with an average of 34 ± 33 dives made per day by each of the eight DST tagged fish. Although individual differences in diving patterns were evident (Figure 5.7), the majority (85.8%) of the dives did not descend below the 5m mark (Figure 5.8). Moreover, the majority (73.5%) of the dives were of short duration (i.e., between 1-2 min), with duration depending significantly on the interaction between external body temperature and fork length ($p<0.001$, Table 5.3). The back-transformed model predictions indicated that Arctic charr performed shorter dives at cooler ambient water temperatures (external temperature), with smaller individuals performing shorter dives in colder water temperatures compared to larger individuals (Figure 5.9). At temperatures above 13 °C, smaller individuals begin to perform longer dives than their larger conspecifics.

5.4 Discussion

Data collected on the two anadromous Arctic charr populations in this study were consistent with the hypothesized temperature and depth use and its relation to activity patterns during the marine residency period. Arctic charr temperature and depth use were dependent on body size and diel period, although the effects varied between locations. Vertical activity was positively correlated with body temperature and related to diel period with increased vertical activity during daylight hours. Dive duration was positively correlated with both ambient water temperature and body size, with smaller individuals performing shorter dives in cooler temperatures.

Arctic charr showed evidence of size-dependent temperature use with larger individuals utilizing cooler water temperatures compared to smaller individuals. While the pattern was not evident in DST tagged fish, the limited size range and number of fish tagged precluded a strong test of the effect. Size-dependent thermal preferences have been reported previously in laboratory studies with other fish species including: turbot *Scophthalmus maximus* (Imsland et al., 1996), Atlantic halibut *Hippoglossus hippoglossus* (Hallaråker, Folkvord, & Stefansson, 1995; Björnsson & Tryggvadóttir, 1996), Atlantic cod *Gadus morhua* (Lafrance et al., 2005), rainbow trout *Oncorhynchus mykiss* (Kwain & McCauley, 1978) and Pacific salmon *Oncorhynchus spp* (Morita et al., 2010), where optimal growth temperatures decreased with increasing body size

(Lafrance et al., 2005; Morita et al., 2010). For example, juvenile turbot in the size range 25-75 g achieved optimal growth at temperatures between 16 and 19°C, whereas optimal temperatures for growth in 100 g turbot were between 13 and 16°C (Imsland et al., 1996). Similarly, older and larger Atlantic salmon at sea inhabited colder waters (>40 cm fish generally utilized < 5-6°C) compared to younger and smaller individuals (<40 cm fish generally utilized > 5-6°C) (Jákupsstovu et al., 1985; Morita et al., 2010). The shift in temperature use with body size has been suggested to be linked to ontogenetic changes in thermal habitat and represent an adaptive behaviour to maximize growth (Morita et al., 2010; Jonsson & Jonsson, 2011). Moreover, in some species, early life stages have been observed to have a narrow thermal window that widens with the rising physiological performance capacity with body size (Pörtner, 2006; Rijnsdorp, 2009). Larger individuals, however, become more thermally sensitive as oxygen demands increase (Pörtner & Farrell, 2008), with warming water temperatures known to increase both active and routine metabolic rates (Eliason & Farrell, 2016). Warmer temperatures also affect organismal physiological functions, such as activity, growth and reproduction (Pörtner et al., 2008) as metabolic rate appears to increase with gonad development (Eliason & Farrell, 2016) and would favour use of cooler temperatures by larger, maturing fish. Although other factors such as food availability and competition (Magnuson, Crowder, & Medvick, 1979; Elliott, 1994) cannot be ruled out, the size-dependent temperature patterns observed in Arctic charr in this study are suggestive of ontogenetic changes in thermal habitat use for the purposes of maximizing growth.

In addition to size-dependent temperature patterns, diel patterns in temperature use were evident in Gilbert Bay Arctic charr, though not in Sandwich Bay. While the temperature data from both the acoustic and DSTs in Sandwich Bay showed little evidence of diel temperature variation, the depth data showed evidence of rapid and repeated dives up to depths of 12 m (one fish up to 26 m) during the day. Diving patterns similar to those observed in this study have been noted for anadromous Arctic charr populations in Norway (Rikardsen, Diserud, et al., 2007) and northern Canada (Spares et al., 2012). Olfactory orientation, bioenergetic gain, foraging opportunity optimization and predator avoidance have all been suggested to drive vertical movement (Rikardsen, Diserud, et al., 2007; Mehner, 2012; Spares et al., 2012). V-shaped scarring on the upper dorsal area suggested some diving activity may be driven by bird attacks, although the development of consistent, repeated patterns of diving to avoid bird attacks seems unlikely given the probable stochastic nature of bird encounters and the repeatability of the diving pattern across time. Although predation by larger marine mammals cannot be ruled out, the evolution of diving behaviour as an effective means of predator avoidance was ruled out in northern waters where marine mammal densities and predation opportunities are considerably higher (Spares et al., 2012). Given the short duration of the dives and their repeated nature, it is more likely that diving behaviour is related to foraging. Arctic charr is an opportunistic feeder, known to prey on pelagic and benthic fish, crustaceans and surface insects (J. W. Moore & Moore, 1974; Dempson, Shears, & Bloom, 2002; Rikardsen, Dempson, et al., 2007; Spares et al., 2012). Spares et al. (2012), in particular, noted that Baffin Island Arctic charr made rapid and repeated short duration dives to deeper (10-58 m) depths for foraging purposes, with Arctic charr feeding on large pelagic crustaceans and benthic fishes.

Although other salmonids species such as Dolly Varden, Atlantic salmon and chum salmon (*Oncorhynchus keta*) move further offshore compared to Arctic charr, similar diving behaviour driven by food availability has been noted (Tanaka et al., 2005; Reddin et al., 2011; Courtney et al., 2016). Therefore, we suggest that Arctic charr in this study dive to seek benthic prey and then return to warmer surface waters which support higher overall physiological function, such as digestion efficiency and, as a result, growth (Elliott, 1994; Angilletta, Niewiarowski, & Navas, 2002). As a combination of factors (e.g., bioenergetic gain and foraging opportunity optimization) is thought to drive vertical movement, the importance and strength of each factor may differ from system to system depending on available environmental conditions and the spatial and temporal availability of food (Dempson & Kristofferson, 1987; Mehner, 2012). The variation in patterns observed between locations and years in this study might therefore be bounded to some degree by the specifics of the study sites, e.g. bathymetry and prey resources.

Diving activity showed a clear diurnal pattern with more frequent and deeper dives during the day than at night. Similar patterns have been reported for other salmonids with fish occupying warmer waters at night with more frequent and deeper dives occurring during the remainder of the day (Tanaka et al., 2005; Reddin et al., 2011; Courtney et al., 2016). For example, Pacific salmon are known to dive below the thermocline to feed on high-caloric fish that leave the surface waters during the day (Tanaka et al., 2005). At night, they adapt a different, low-cost feeding strategy during which they feed on dense patches of slow-moving zooplankton that move to the upper water column at night (Walker et al., 2000; Tanaka et al., 2005). The common phenomenon of diel vertical migration by zooplankton (De Meester et al., 1999), directly affects the foraging behaviour of predators at higher trophic levels such as fish (Shepard et al., 2006; Davoren et al., 2007), seabirds (Regular et al., 2010) and marine mammals (Croxall et al., 1985), that may modify their behaviour to optimise the exploitation of their prey (Hays, 2003). Labrador Arctic charr are also known to feed on zooplankton (e.g., amphipods and mysids) and fish species that closely match the vertical distribution of zooplankton such as capelin (*Mallotus villosus*) (Dempson, Shears, & Bloom, 2002). The diurnal patterns observed by Arctic charr in this study might, therefore, reflect the vertical migrations of their prey species. However, Arctic charr do not remain at depth throughout the day. Atlantic salmon have been observed to show a similar pattern of short-term dives during the day, with salmon seeking prey in cooler deeper waters where prey is more abundant, and then return to the surface waters, possibly to re-warm and improve digestion. Dives were believed to be of short duration to prevent the internal body temperature from dropping, thereby maintaining temperature-sensitive metabolic processes and swimming capacity (Reddin et al., 2011). Similar behaviour has been observed in Arctic charr and supports our earlier statement that the species likely feeds in cooler deeper waters, remains for only short periods of time, and returns to surface waters where warmer temperatures enhance physiological functions.

Additionally, the diurnal patterns of diving activity might be related to visual capabilities of Arctic charr (Ali, Klyne, & Einarsson, 1981). Even though Arctic charr are more effective at feeding under low temperature and light levels compared to other salmonids (Elliott, 2011), daytime feeding likely remains more profitable in terms of rapid food acquisition and minimizing energy expenditure (Fraser & Metcalfe, 1997; Watz et al., 2014). A similar strategy has been observed during the freshwater residency period, with anadromous Arctic charr displaying diurnal activity patterns, which were suggested to be linked to opportunistic maintenance feeding throughout the winter months (Mulder, unpublished data). A combination of different prey-capture strategies in which energy expenditure is minimized to maximize rapid growth seems most beneficial, as has been observed in Pacific salmon (Tanaka et al., 2005).

The use of short duration dives prevents the internal body temperature from equilibrating with the ambient water temperature (e.g., Rikardsen, Diserud, et al., 2007; Reddin et al., 2011). By maintaining its core temperature Arctic charr are able to conserve burst speed abilities and gain advantage over potential prey. In brown trout (*Salmo trutta*), capture probability and capture manoeuvre time are significantly reduced at colder temperatures, with probability of prey capture decreasing from 96% at 14°C to 53% at 5.7°C (Watz & Piccolo, 2011). In Arctic charr (mean fish size: 31.6 cm), the minimum critical swimming speed is known to decrease with temperature from 68.0 cm/s at 10°C to 47.0 cm/s at 5°C (Beamish, 1980; Peake, 2008). For Arctic charr to maintain rapid and efficient food acquisition at deeper and colder temperatures, dive duration is dictated by ambient water temperatures, with smaller individuals performing shorter dives than larger individuals. During diving activity, Arctic charr sometimes descended to temperatures close to 0°C, but avoided decreasing their body temperature below 0°C (Table 5.2, Spares et al., 2012). The time it takes to reach thermal equilibrium is dependent on body mass with smaller fish reaching thermal equilibrium faster (Elliott, 1981). Thus, smaller Arctic charr spend less time in colder waters before the core temperature changes. Lowering internal temperature might affect locomotory capacity (Bennett, 1990), possibly making fish more susceptible to predation and reducing foraging efficiency.

In contrast, at temperatures above ~13 °C, smaller individuals in this study begin to perform longer dives than their larger conspecifics. Temperatures within the 6-12°C range were noted to optimize larger fish physiology (Rikardsen, Diserud, et al., 2007; Spares et al., 2012). Therefore, smaller fish may have a metabolic advantage in temperatures above 13°C, as foraging costs will rise for larger individuals, possibly reducing energetic gains and growth potential as has been observed by Michaud, Dempson, & Power (2010).

5.5 Conclusion

This study provides some of the first observations of size-dependent temperature and depth use in wild anadromous Arctic charr while foraging in the marine environment. Results suggested that Arctic charr utilized warmer ambient water temperatures available in the upper water column, possibly to aid physiological processes such as digestion, and utilized deeper depths for feeding purposes. Size-dependent thermal preferences were evident, where size segregation was suggested to be linked to ontogenetic changes in thermal habitat use for the purposes of maximizing growth. The diurnal diving activity observed may reflect the vertical migration of prey items and/or be related to the visual capabilities of Arctic charr as daytime feeding likely remains more profitable in terms of rapid food acquisition and minimization of foraging costs. Dive duration was also dependent on body size with smaller individuals performing shorter dives to avoid significant decreases in body temperature that would reduce activity levels and capacity. Study results also highlight that climate-driven increases in water temperatures may affect Arctic charr size-classes differently. To improve our understanding of how a changing climate may affect anadromous Arctic charr populations, further studies should be undertaken to develop a more complete picture of size-dependent thermal preferences and determine the generality of the results reported here for more northernly and European populations of Arctic charr.

Table 5.1. Tagging specifications for Arctic charr tagged in Gilbert, Alexis and Sandwich Bays.

Location	Year	Tagging dates	Tag type	No. fish	Mean fork length ± SD (cm)
Gilbert Bay	2012	9-13 June	V9T	10	34.9 ± 4.5
			V13T	40	38.7 ± 3.2
	2014	3 - 4 June	V13T	35	40.8 ± 3.1
Sandwich Bay	2015	4 June - 6 July	V9T	21	34.3 ± 5.2
			V13T	20	40.5 ± 3.4
		4 June - 14 August[†]	DST	64	44.1 ± 4.4

[†] N=10 fish tagged in the marine environment and N=54 tagged at the Fisheries and Oceans Canada operated fish counting fence in Muddy Bay Brook during their ascend.

Table 5.2. Characteristics of the acoustic and DST tagged Arctic charr detected and recaptured in this study. Means are given as the average of the means for each fish for depth and internal (IT) and external (ET) body temperatures ± SD per diel period and location. Near-surface (S), bottom (B) and mid-water column (M) temperatures were recorded by the temperature loggers are indicated by location and year.

Data	Location/ Year	No. fish	Mean fork length ± SD (cm)	Mean ambient water temp, °C	Diel period	Mean IT °C (range)	Mean ET, °C (range)	Depth, m (range)
Acoustic	GB 2012	39	39.8 ± 4.5	S: 11.81 ± 3.05 B: 7.69 ± 2.69	Day	9.09 ± 0.36 (0.71 – 19.24)		
					Night	10.25 ± 0.37 (3.90 – 19.34)		
	GB 2014	31	42.8 ± 5.0	S: 10.63 ± 3.67 B: 4.14 ± 3.74	Day	8.86 ± 0.41 (2.96 – 18.77)		
					Night	10.21 ± 0.41 (3.43 – 19.05)		
	SB 2015	37	39.2 ± 4.9	M: 5.82 ± 1.59	Day	9.05 ± 0.40 (3.43 – 16.33)		
					Night	9.03 ± 0.40 (2.87 – 15.76)		
DST	SB 2015	5	40.5 ± 5.2	M: 5.82 ± 1.59	Day	8.89 ± 0.45 (2.54 – 17.72)	8.64 ± 0.49 (1.06 – 18.42)	1.19 ± 0.31 (0.01 – 12.76)
					Night	9.34 ± 0.51 (2.48 – 17.24)	9.13 ± 0.57 (0.28 – 17.72)	0.79 ± 0.30 (0.01 – 26.16)
	SB 2016	3	43.7 ± 2.1		Day	7.25 ± 0.16 (3.36 – 14.29)	7.09 ± 0.15 (2.72 – 14.42)	1.30 ± 0.45 (0.48 – 5.48)
					Night	7.54 ± 0.43 (3.95 – 13.89)	7.34 ± 0.37 (3.52 – 14.03)	1.09 ± 0.29 (0.49 – 3.81)

Table 5.3. Estimated model coefficients for the linear mixed effects models of temperature use (°C; H1, H2a), depth (m, H2a), diel vertical activity (m/hr; H2b, H3a) and dive duration (min; H3b). Marginal (R^2_m) and conditional (R^2_c) fit values were calculated using the methods described by Nakagawa & Schielzeth (2013). Parameter significance is shown, displaying F values, degrees of freedom (ndf, ddf), and P values calculated from F-tests based on Sattethwaite's approximation (Kuznetsova, Brockhoff, & Christensen, 2015).

Models	Hypotheses tested	Fixed effect parameters	F value	P value
Model 1	*H1, H2a*	*Fork length*	$F_{(1,90.86)} = 3.39$	0.069
(R^2_m=0.351,		*Diel period*	$F_{(1,188398.30)} = 9709.42$	<0.001
R^2_c=0.616)		*Location*	$F_{(1,93.20)} = 6.59$	0.012
		Diel period:Fork length	$F_{(1,188437.94)} = 962.86$	<0.001
		Diel period:Location	$F_{(1,188400.50)} = 9705.80$	<0.001
Model 2	*H1, H2a*	*Diel period*	$F_{(1,539.95)} = 5.74$	0.017
(R^2_m=0.139,		*Year*	$F_{(1,46.46)} = 12.47$	<0.001
R^2_c=0.640)				
Model 3	*H2a*	*Fork length*	$F_{(1,45.84)} = 7.37$	0.009
(R^2_m=0.351,		*Diel period*	$F_{(1,541.46)} = 109.24$	<0.001
R^2_c=0.616)		*Year*	$F_{(1,46.00)} = 21.71$	<0.001
		Fork length:Year	$F_{(1,45.84)} = 21.73$	<0.001
		Diel period:Year	$F_{(1,541.46)} = 27.57$	<0.001
Model 4	*H2b, H3a*	*Body temperature*	$F_{(1,553.68)} = 68.52$	<0.001
(R^2_m=0.392,		*Diel period*	$F_{(1,576.24)} = 967.68$	<0.001
R^2_c=0.776)				
Model 5	*H3b*	*External temperature*	$F_{(1,5572.61)} = 130.78$	<0.001
(R^2_m=0.048,		*Fork length*	$F_{(1,4.95)} = 4.17$	0.097
R^2_c=0.187)		*External temperature:Fork length*	$F_{(1,5116.45)} = 28.78$	<0.001

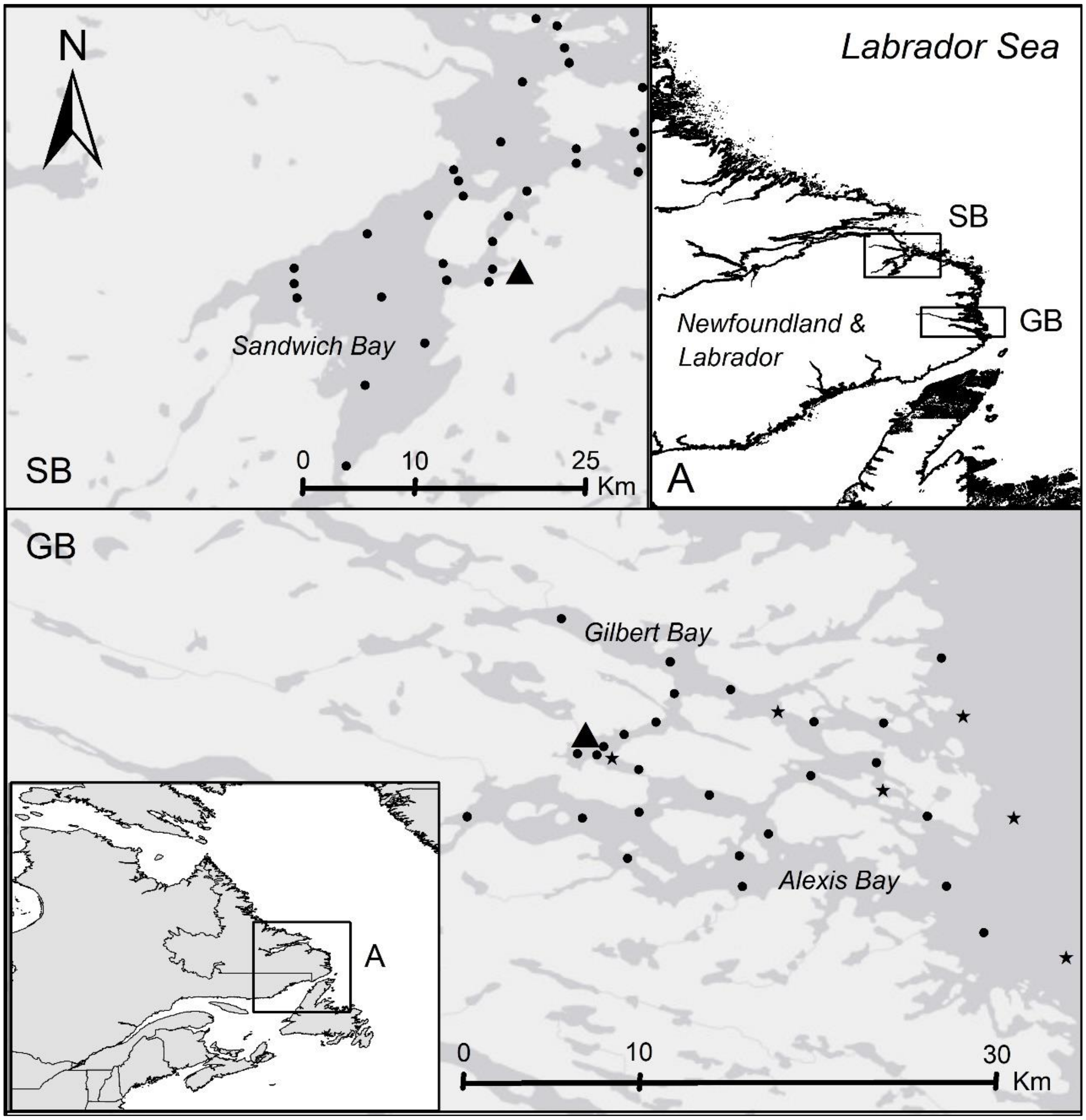

Figure 5.1. Location of Gilbert, Alexis (GB) and Sandwich (SB) Bays with respect to the Labrador coast, showing the location of receivers deployed in SB 2015 (*closed circle*), GB 2012 (*closed circle*) and GB 2014 (*closed circle and star*). The entrance to Shinneys River (GB) and Muddy Bay Brook (SB) are indicated by triangles.

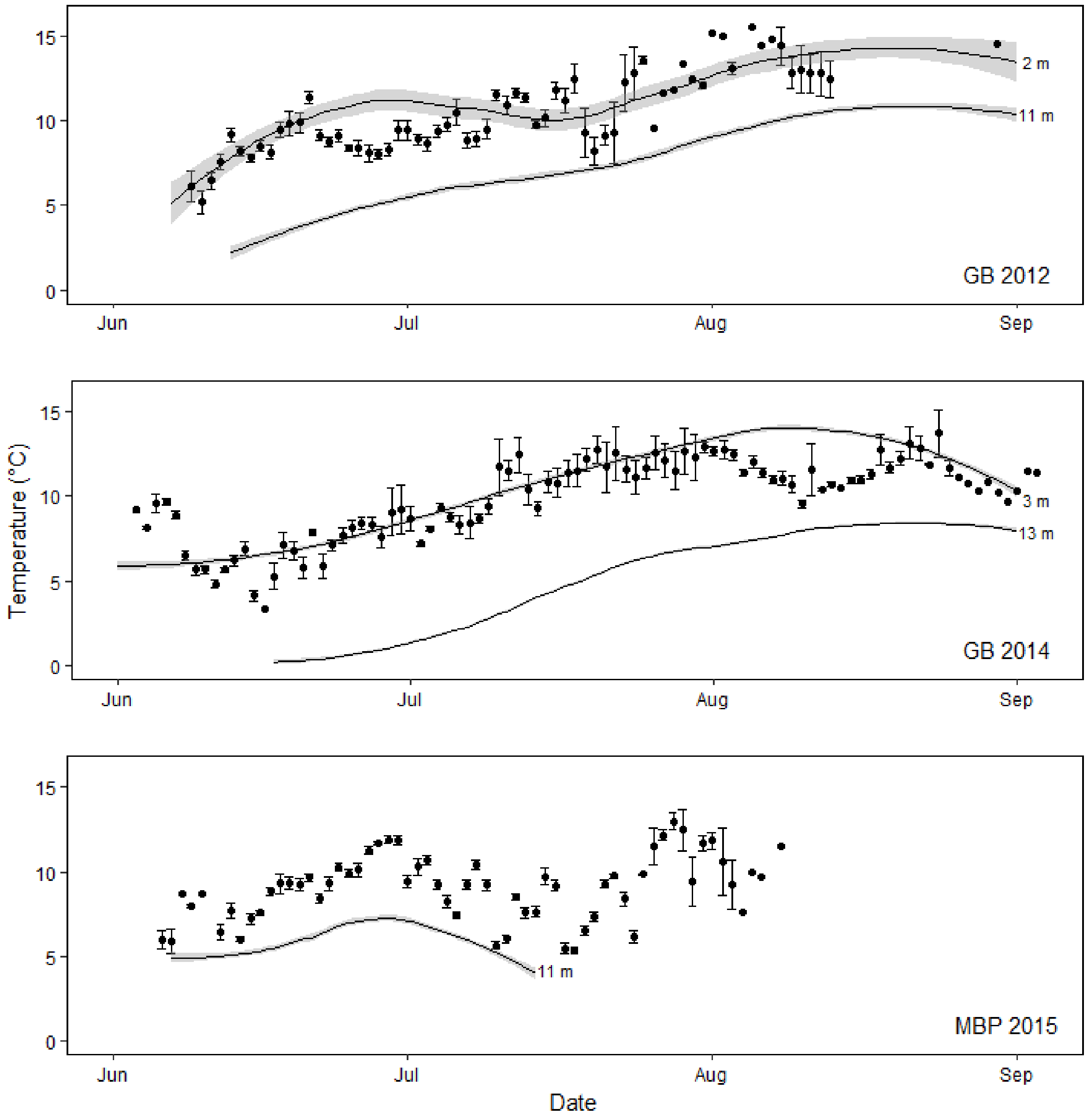

Figure 5.2. Daily temperature averages of individual fish means (°C, closed circles (±SE)) recorded for acoustically tagged Arctic charr during the marine migration period in Gilbert (2012 - top, 2014 - middle) and Sandwich (2015 - bottom) Bays. The lines plot the average temperatures (°C, ±SE) at various depths recorded by temperature loggers deployed near the mouths of Shinneys River (2012, 2014) and Muddy Bay Brook (2015) throughout the study period.

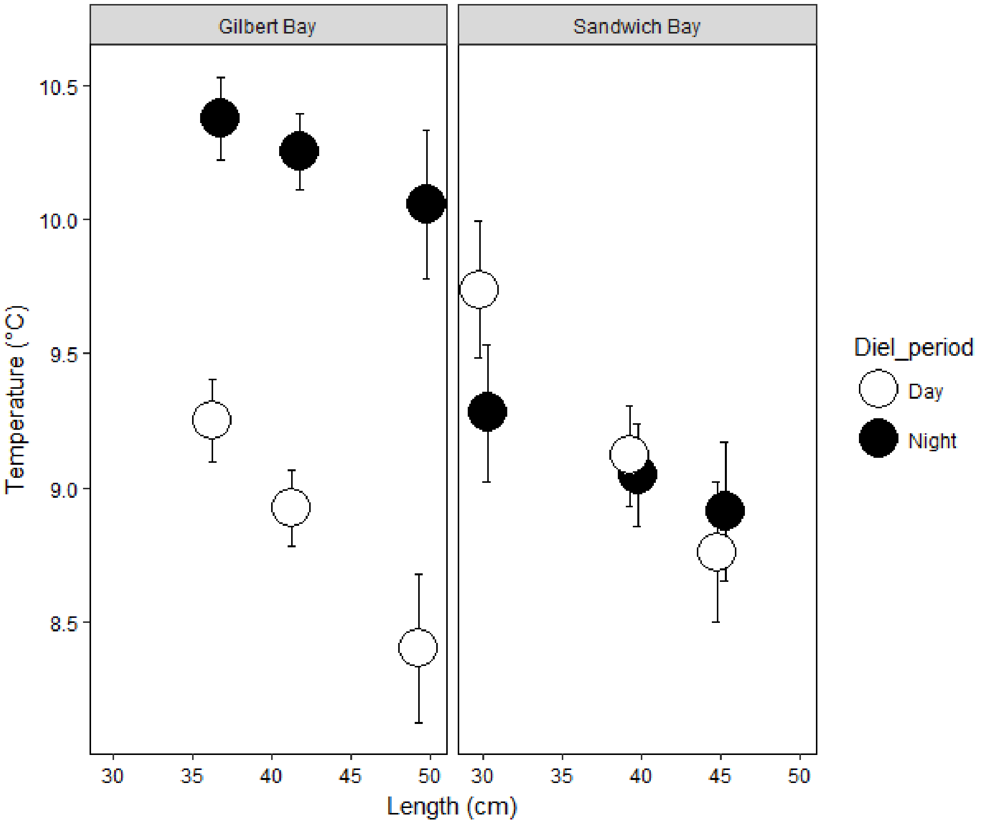

Figure 5.3. Back-transformed reduced linear model (Table 5.3) estimates of temperature use (°C) in Arctic charr at 0.05, 0.5 and 0.95 quantiles of fork length among locations (Gilbert Bay, Sandwich Bay). Error bars represent standard errors. Open circles represent daytime temperature use, and closed circles represent nighttime temperature use. Model estimates based on acoustic data only.

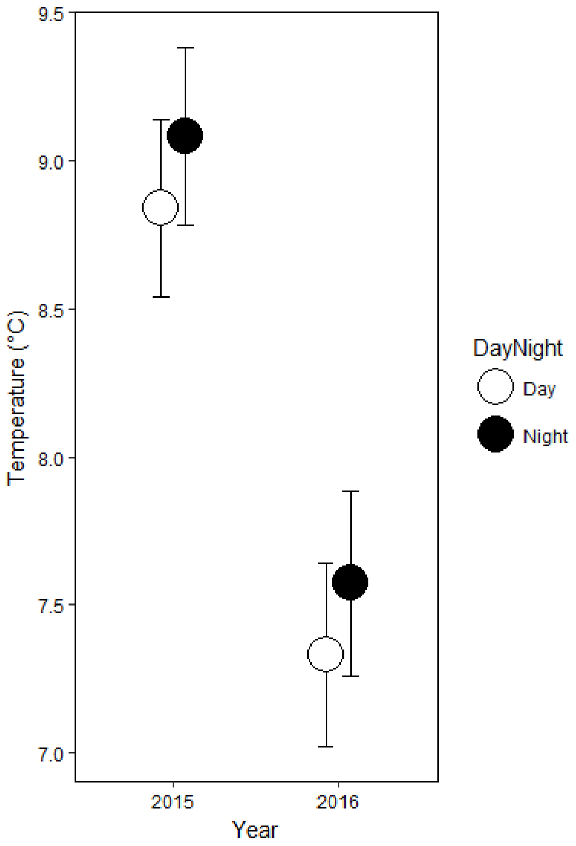

Figure 5.4. Back-transformed reduced linear model (Table 5.3) annual estimates of temperature use (°C) by Arctic charr in Sandwich Bay. Error bars represent standard errors. Open circles represent daytime use, and closed circles represent nighttime use. Model estimates based on data storage tag data only.

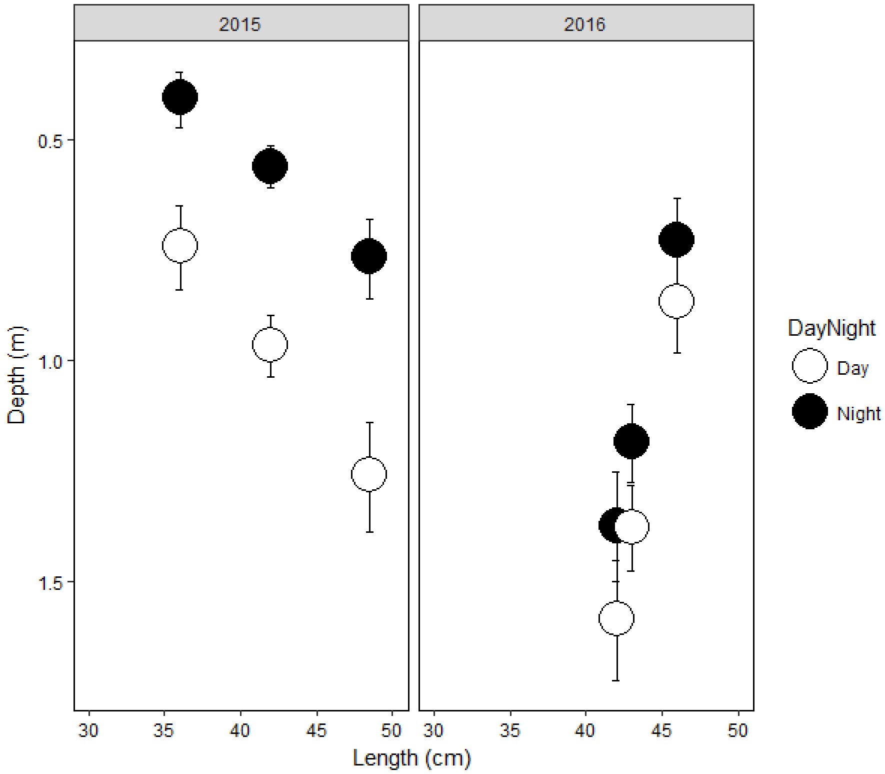

Figure 5.5. Back-transformed reduced linear model (Table 5.3) estimates of Arctic charr depth (m) estimates at 0.05, 0.5 and 0.95 quantiles of fork length among years in Sandwich Bay. Error bars represent standard errors. Open circles represent daytime depth use, and closed circles represent nighttime depth use. Model estimates based on data storage tags only.

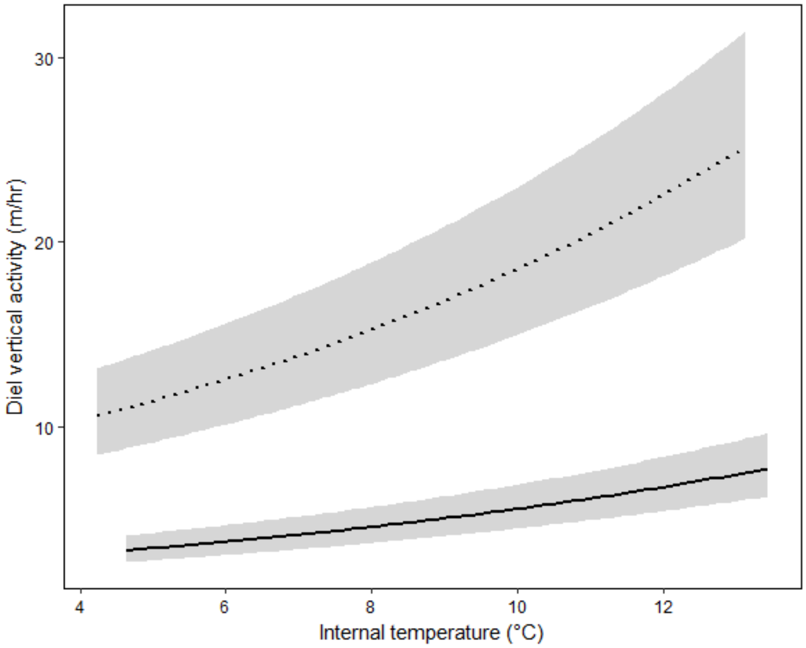

Figure 5.6. Back-transformed reduced linear model (Table 5.3) estimates of vertical activity (m/hour) for Arctic charr (N=8) as a function of diel period and body temperature (°C) in Sandwich Bay. Error bars represent standard errors. The dotted line represents daytime vertical activity, and the solid line represents nighttime vertical activity. Model estimates based on data storage tag data only.

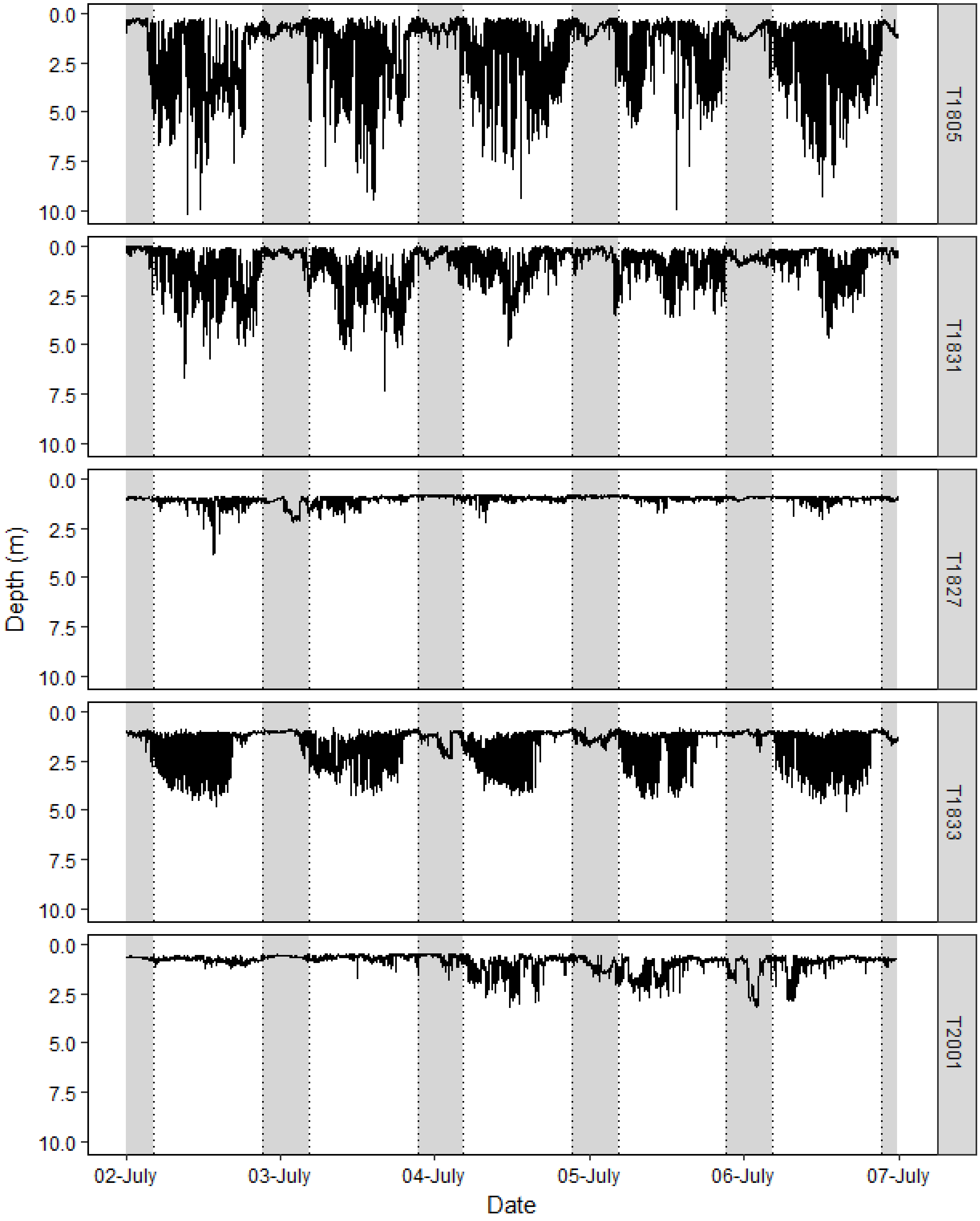

Figure 5.7. Depth use for five DST tagged Arctic charr collected over a five-day period (2-7 July) in 2015 (T1805, T1831) and 2016 (T1827, T1833, T2001). Data are plotted at minute intervals. Shaded areas indicate night time, i.e. the diel period between sunset and sunrise.

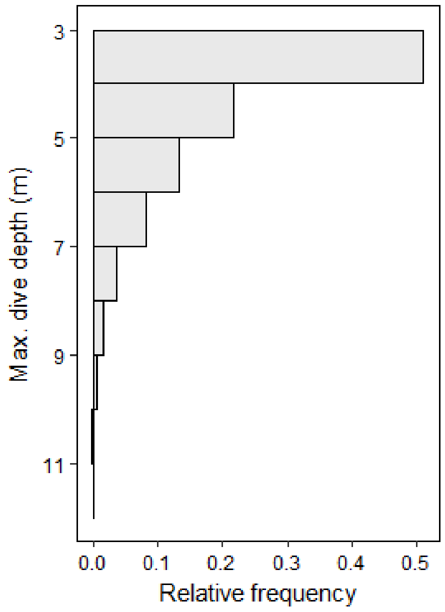

Figure 5.8. Relative frequency of diving depth (m) of N=8 DST tagged Arctic charr in Sandwich Bay.

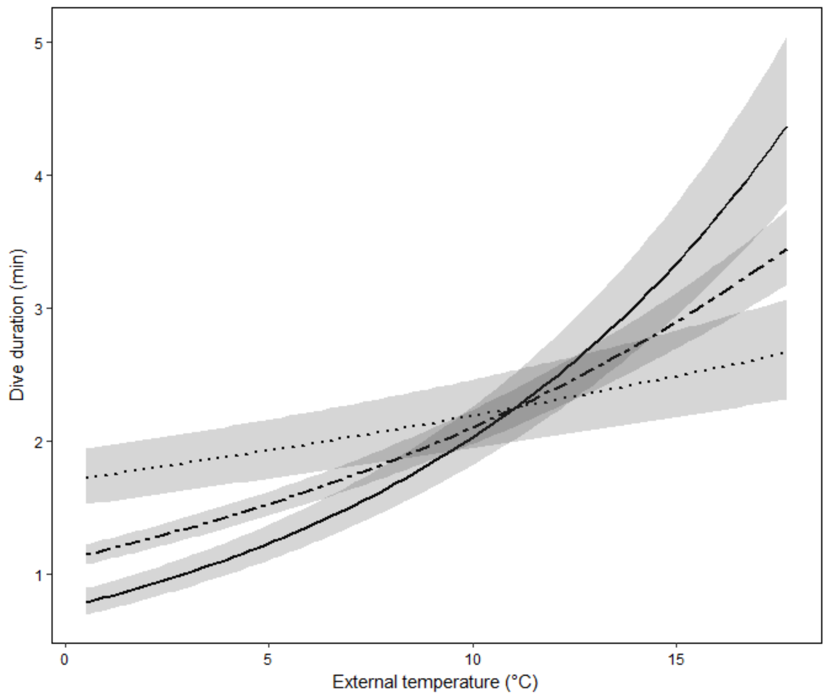

Figure 5.9. Back-transformed reduced linear model (Table 5.3) predictions of Arctic charr (N=8) dive duration (minutes, ± SE). Estimates are provided for the 0.05 (36.0 cm, solid line), 0.5 (42.0 cm, dashed line) and 0.95 (48.5 cm, dotted line) quantiles of fork length and plotted as a function of recorded external body temperature (°C) in Sandwich Bay. Model estimates based on data storage tag data only.

Chapter 6: General Conclusions

Research presented in this thesis has addressed several knowledge gaps in the literature on the winter ecology and marine migration of anadromous Arctic charr (*Salvelinus alpinus*) populations near the southern end of the species' distributional range, and has considerably advanced our understanding of Arctic charr winter ecology and behaviour. In addition to providing some of the first species-specific observations of movement activity and thermal habitat use by Arctic charr while overwintering in freshwater, the study has focussed on (environmental) factors that figure prominently in the determination of these patterns in adult fish. An improved understanding of their behaviour in both freshwater and the marine environment will improve our understanding of how a cold-water specialist, such as Arctic charr, may respond to a changing climate, given the predicted and observed climate changes and existing hypotheses about its likely consequences for northern fishes (Reist et al., 2006). The thesis comprises four chapters, three of which aimed to address different aspects of winter ecology including seasonal and daily movement patterns and thermal habitat use during the ice-covered period using acoustic and archival telemetry methods. In chapter 4, similar methods were used to investigate diel patterns of temperature and depth use and its relation to activity patterns during the marine residency period.

6.1 Summary

The analyses in chapter 2 provided observations of movement activity in anadromous Arctic charr while overwintering in freshwater lakes. Results showed that movement activity declined markedly during the ice-covered period, with low movement activity suggesting only opportunistic maintenance feeding as an energy conservation strategy. Fall and spring movement was correlated with daylight hours, and ice breakup had a significant effect on the timing of outmigration. Movement activity was negatively correlated with body length, with smaller individuals being more active than larger conspecifics. Although general movement activity patterns were evident, there were significant differences among individuals, particularly in the spring immediately prior to lake departure. Lake size and individual differences in metabolic rate may account for some of this variation. Photoperiod strongly influenced the decline in movement activity in late autumn and, in combination with ice breakup, the increase in movement activity in spring. As populations in this study originate from the southern end of the distributional range of anadromous Arctic charr, further investigations are needed, such as provided by this chapter, to determine the generality of the results for more northerly populations.

The findings presented in chapter 3, provided a detailed data set on the thermal overwintering of anadromous Arctic charr. Results showed that individuals utilized a narrow temperature window (0.5-2°C) during the ice-covered period and used cooler temperatures available within the middle to upper water column. Use of the selected lower temperatures is indicative of a strategy to reduce metabolic costs and minimize energy expenditure, preserving stored lipids for overwinter survival and the energetic costs of preparation for seaward migration. As Arctic charr are visual feeders, use of the upper water column is thought to aid foraging efficiency by increasing the likelihood of prey capture.

Chapter 4 examined the diel variation in activity patterns in overwintering wild anadromous Arctic charr. The species displayed diurnal activity patterns throughout the overwinter residency period, likely driven by prey and light availability in the upper water column where daylight facilitates foraging efficiency by increasing the likelihood of prey capture. Movement activity increased as a function of temperature, except during winter, where cold-water temperatures associated with increased activity were likely a by-product of (opportunistic) feeding behaviour immediately below the ice. The utilization of warmer water temperatures when activity was reduced was thought to occur for the purpose of improving assimilation efficiencies in winter and preparing for outmigration during the ice breakup period. Body size did not have an effect on activity patterns, although the result may have been an artefact of the limited size ranged of tagged fish used in this study.

Chapter 5 suggested that during the marine migration, Arctic charr utilized warmer ambient water temperatures available in the upper water column, possibly to aid in physiological processes such as digestion, whereas deeper depths were used for feeding purposes. Size-dependent thermal preferences were evident, with larger individuals utilizing cooler water temperatures compared to smaller individuals, a pattern of temperature use suggestive of ontogenetic changes in thermal habitat use for the purpose of growth maximization. Diurnal patterns of diving activity were interpreted to reflect the vertical migration of prey items and/or to be related to the visual capabilities of Arctic charr as daytime feeding likely remains more profitable in terms of rapid food acquisition and minimization of foraging costs. Dive duration was dependent on body size with smaller individuals performing shorter dives to maintain their core temperature and abilities to both effectively capture prey and avoid predation.

6.2 Study significance

To the author’s knowledge this thesis is the first study to provide observations of movement activity and thermal habitat use in adult anadromous Arctic charr while overwintering in freshwater lakes located near the southern end of the species distributional range. Chapter 2 provided the first database on seasonal movement patterns in migratory Arctic charr and looked at environmental factors, such as photoperiod and timing of ice-breakup, that may figure prominently in the determination of these patterns. Chapter 4 continued to build on this information by focussing on diel activity patterns and their correlation with temperature use. Chapter 3 provided the first detailed dataset on the thermal overwintering during the ice-covered period showing that Arctic charr utilized cooler temperatures available in the upper water column. Restricted winter movement and use of selected lower temperatures are indicative of a strategy to reduce metabolic costs and minimize energy expenditure. Chapter 2, 3 and 4 have demonstrated how the species utilizes the cold-water environment to its advantage, seasonally and on a daily basis, thereby highlighting the potential vulnerability of Arctic charr to increasing temperatures, particularly at the southern end of the range where winter warming may significantly alter ice-cover dynamics (e.g., Reist et al., 2006; Prowse & Brown, 2010). The research performed in these chapters thus lays the foundation for assessing future climate change effects on Arctic charr populations in Canada and elsewhere. For example, this information might prove useful to researchers attempting to predict how changes in ice-cover duration, followed by longer growing seasons and an increase in primary production (Prowse & Brown, 2010) may affect anadromous Arctic charr populations in terms of life-history characteristics (Reist et al., 2006).

Knowledge of temperature and depth use of anadromous Arctic charr while foraging in the marine environment has been expanded in chapter 5, with a particular focus on diel activity patterns and size-dependent thermal habitat use. To the author's knowledge, this is the first study to directly test and observe size-dependent thermal preferences in Arctic charr at sea, with larger individuals utilizing cooler water temperatures compared to smaller conspecifics. These results highlight that climate-driven increases in water temperature may affect Arctic charr size-classes differently. Moreover, this information may be useful for researchers attempting to predict if the geographical range of Arctic charr will shift in response to climate change. Particularly in southern populations, which may be faced with both increasing water temperatures and associated invasion of species from the south (Reist et al., 2006). Thus, this research may be critically important for maintaining Arctic charr stocks and intraspecific biodiversity.

6.3 Future directions

While the results of this thesis offer insight into the winter ecology and marine migration of anadromous Arctic charr, they also highlight a number of areas where future research is needed.

1. The findings in chapter 3 suggested that the diurnal activity patterns observed in adult anadromous Arctic charr were driven by prey and light availability in the upper water

column where daylight facilitates foraging efficiency. To date, gut content analyses have only been performed on northern anadromous populations (Sprules, 1952; Dutil, 1986; Rikardsen, Amundsen, & Bodin, 2003), indicating that Arctic charr do little to no feeding in studied Baffin Island (J. W. Moore & Moore, 1974) and Ungava Bay (Boivin & Power, 1990) populations. Further research should combine biotelemetry with stable isotope analyses or gut content analyses in southern populations to confirm the now suggested link between increased movement activity and opportunistic maintenance feeding in winter (e.g., Harrison et al., 2017).

2. The continuously observed diurnal activity patterns in winter (Chapter 3) suggested that Arctic charr in this study were able to keep track of time under ice and snow cover even at low ambient light levels, as diel activity rhythms were found to be absent in lacustrine Arctic charr living under conditions of continuous darkness (Hawley et al., 2018). As the population in this study originates from the southern end of the distributional range of anadromous Arctic charr, an area characterized by distinct differences in photoperiod between day and night, further investigations are required to determine the generality of the results for more northerly anadromous populations which experience periods of constant darkness.
3. No size-dependent thermal preferences were observed in Arctic charr while overwintering in freshwater (chapter 2), although the results may be been an artifact of the limited size range of tagged fish used in this study. While temperature use in the marine environment has been observed to be dependent on body size (chapter 4),

future studies should include a wider range of body sizes to test if this pattern is present during the freshwater residency period as well.

4. Findings in chapter 4 suggested that Arctic charr utilized warmer ambient water temperatures available in the upper water column and utilized deeper depths for feeding purposes. Previous studies have characterized the spatial and temporal variability of the diet of anadromous Arctic charr (Dempson, Shears, & Bloom, 2002; Spares et al., 2012) but never on an individual level. Chapter 4 indicated that diving behaviour differs among individuals, with some individuals performing deeper dives than others. Future studies could link biotelemetry with stable isotope analyses to determine if variation in diving behaviour may be related to diet, as has been suggested for burbot (Harrison et al., 2017).
5. Most research focusses on single species with little attention being given to studying the competitive interactions among species, which is of increasing importance given climatic changes and associated invasion of species from the south (Reist et al., 2006). For example, little is known about the interaction between resident and anadromous Arctic charr while both residing in freshwater. Moreover, in the marine environment, Arctic charr co-exist with brook trout (*Salvelinus fontinalis*) and Atlantic salmon (*Salmo salar*) but little is known about potential competition for habitat as has been observed in freshwater (Helland et al., 2011). Therefore, future studies should aim to include co-existing populations, to determine potential interactions among species, and determine to which extent these interactions (such as competition) may affect fitness.

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