Movements and Feeding of Arctic char (Salvelinus alpinus) Relative to Summer Ice-Off in an Arctic Embayment

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Movements and Feeding of Arctic char (*Salvelinus alpinus*) Relative to Summer Ice-Off in an Arctic Embayment

By

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University of New England, 2018

THESIS

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ABSTRACT

Seasonal fluctuations in environmental conditions drive ecosystem processes across the globe, particularly at the earth’s poles. Seasonality in Arctic marine systems is exemplified by an annual summer ice-off that promotes primary productivity blooms and provides nutrients for upper trophic level consumers who often migrate to these productive areas. Arctic char \((Salvelinus alpinus)\) are an economically and culturally important salmonid that migrate from freshwater spawning locations into the marine environment, presumably to feed. In this thesis, I describe two studies investigating the movement and feeding of Arctic char within Tremblay Sound, Nunavut, Canada, a newly designated National Marine Conservation Area (Tallurutiup Imanga). Through the combination of acoustic telemetry and ice data, I found Arctic char migrating into Tremblay Sound before ice-off began in the marine environment, which validates visual observations from the 1950’s and 1970’s. I found potential evidence of multiple populations of Arctic char utilizing Tremblay Sound in the summer or ontogenetic shifts in migration distance. Stomach content analysis suggested that char consume high rates of food during the ice-off season within Tremblay Sound. The frequency of occurrence certain prey items, notably Arctic cod \((Boreogadus saida)\) and \(Onisimus spp.\), changed between years, and was likely related to local ice conditions and differences in sampling time between years. Collectively, this thesis expands our understanding of the interactions between movement and feeding during the marine component of Arctic char migration. The results have important implications for management and the potential resiliency of Arctic char in an ever-changing high Arctic.
CHAPTER 1: Introduction

1.1 Dynamic Seasonal Change

Seasonal change is widespread across the globe and represents a strong driver of variation in natural systems (Boyce 1979). Seasonality can result in changes in temperature, precipitation, daylength, and a host of other variables. These predictable changes support key biological processes such as migration (Dingle 2014) and predator-prey dynamics (Scheffer et al. 1997). Further, rapid change can induce ephemeral resource pulses that are important for many animal communities (Yang et al. 2008). The degree of this seasonality typically increases with latitude, with the most pronounced seasons observed at the earth’s poles (MacArthur 1972, Lisovski et al. 2017). As such, high-latitude Arctic ecosystems provide unique opportunities to study the impacts of seasonal change and resource pulses on animal ecology.

1.2 Arctic Ice-Off

The Arctic experiences some of the most dynamic seasonal changes, including an annual summer ice-off that occurs in marine systems. Prior to ice-off, production of ice algae begins in response to increased light levels, eventually providing a significant proportion of overall primary productivity (Horner & Schrader 1982). As the sea ice melts, sympagic amphipods feed on the abundant and accessible algae (Gradinger & Bluhm 2010). The elevated abundance of amphipods attracts species in higher trophic levels such as Arctic cod (*Boreogadus saida*), an important link in many Arctic food webs (Bradstreet & Cross 1982), as well as other charismatic migratory megafauna into aquatic systems in search of food (Melnikov 1997). As such, the ice-
off drives the flow of energy from primary production to higher trophic levels. However, Arctic waters are currently experiencing the fastest warming on the planet (Intergovernmental Panel on Climate Change 2013) and the duration and extent of seasonal sea-ice cover is decreasing (Johannessen et al. 2004, Yurkowski et al. 2018). It is critical to understand how species respond to and use the ice-off event to provide clues towards the potential consequences of climate-related changes in sea-ice phenology.

1.3 Arctic Char

The Arctic char (Salvelinus alpinus) is an economically and culturally valuable species, particularly in the Arctic where this species is targeted by subsistence fisheries (Kristofferson & Berkes 2005). In fact, Arctic char accounts for 86% of the total catches of small-scale fisheries in the Canadian Arctic (Booth & Watts 2007). In addition, char are targeted in recreational and commercial fisheries in the Arctic as well as in sub-Arctic regions of North America (Kristofferson & Berkes 2005, Day & Harris 2013). Thus, this species is significant throughout its range, and it is important to understand the potential effects of continued climate change on char ecology.

Arctic char exhibit substantial variability in life history patterns among regions and populations (Beddow et al. 1998, Jensen & Rikardsen 2008, Moore et al. 2017). Like many other salmonids, Arctic char exhibit two life history strategies: freshwater residency and anadromy (Nordeng 1983). In some cases, a single population can express both strategies (Finstad & Hein 2012), a phenomenon known as partial migration (Lack 1943, Berthold 1999, Kerr et al. 2009). Anadromous Arctic char are born in fresh water, undergo migrations to marine systems, and return to fresh water to spawn. Char are an iteroparous species, spawning multiple times throughout their adult life (typically every two to three years; Johnson 1980). As such,
anadromous char can make multiple seaward migrations, which are thought to be driven by high productivity in marine systems relative to freshwater habitats at temperate and high latitudes, where anadromous life histories dominate among fishes (Gross et al. 1988). Feeding migrations of Arctic char typically begin in June or July (Gyselman 1984, Bégout Anras et al. 1999, Spares et al. 2015, Moore et al. 2016), and are thought to match the timing of river ice-off (Dempson & Green 1984, Gyselman 1984, Gilbert et al. 2016). However, early studies (1950’s-1970’s) suggested that char could enter the sea before river ice-breakup (Grainger 1953, Moore 1975), and thus, current information on char migration timing is conflicting. Once char have entered the marine environment, residency lasts between one and four months (Johnson 1980, Gyselman 1984, Gulseth & Nilssen 2000), after which, most anadromous char return to fresh water to spawn (Moore 1975, Dempson & Kristofferson 1987; but see Jensen & Rikardsen 2008), often to their natal rivers or lakes (Nordeng 2009). However, char can travel to and overwinter in non-natal rivers (Moore et al. 2013, 2016), occasionally for multiple years (Moore et al. 2017). Although this phenomenon is less likely (but still possible) in spawning years (Moore et al. 2013, 2014), straying behavior leads to population mixing during the overwintering and marine residency periods (Moore et al. 2013, 2017).

Regardless of the variability in migration patterns, marine feeding is a constant among anadromous Arctic char populations, and is critical to growth and survival (Gyselman 1984, Jensen et al. 2018). While intense feeding can last for several months, daily consumption is greatest immediately after the ice-off, and steadily decreases until feeding ceases in accordance with migration to fresh water (Amundsen & Klemetsen 1988). Arctic char typically fast throughout the winter (Boivin & Power 1990), and as such, food consumed during the summer must support metabolism as well as the costs of reproduction in spawning years. Therefore, char
must be able to maximize short-term consumption rates, which may explain rapid weight gain seen in char during the summer (Gyselman 1984).

Maximizing short-term consumption is likely important for char to amplify the benefits of marine residence. However, having a large digestive capacity is costly and not advantageous during periods of low food abundance (Armstrong & Schindler 2011, Norin & Clark 2017). Thus, fishes who exploit short-term resource pulses demonstrate behavioral and physiological adaptations to maximize consumption, including seasonal plasticity in digestive machinery (Armstrong & Bond 2013) and binge-feeding (Furey et al. 2016). Binge-feeding occurs when a fish consumes well beyond normal daily consumption, or what could be digested in a day (Furey et al. 2016). Binge-feeding has been observed in many species, including a close relative of the Arctic char, the bull trout (*Salvelinus confluentus*; Furey et al. 2016). Binge-feeding capacity in a close relative, along with increased digestive capacities in another (Dolly Varden; *Salvelinus malma*; Armstrong & Bond 2013), make similar adaptations likely in Arctic char, particularly populations that experience pulsed resources. However, this has not been explored in Arctic char.

The diets of Arctic char have been studied previously (Rikardsen et al. 2000, Dempson et al. 2002, Rikardsen & Amundsen 2005, Spares et al. 2012). Arctic char are opportunistic feeders in marine systems, feeding on a wide variety of potential prey types (Johnson 1980, Dempson et al. 2002, Rikardsen & Amundsen 2005, Spares et al. 2012). Diets vary both spatially and temporally, which might reflect changes in the availability of different prey types (Dempson et al. 2002, Rikardsen & Amundsen 2005). As an opportunist, diets can be quite broad, including fish, mollusks, annelids, crustaceans, insects, and worms (Dempson et al. 2002). The relative importance of prey types in char diets also varies through space and time. For example, char consumption of *Gammarus* amphipods in Norway increased from June to July, and decreased
until October (Amundsen & Klemetsen 1988). Furthermore, previous studies have found certain prey items (e.g., fish, or crustaceans) to be dominant prey species (Rikardsen et al. 2000, Rikardsen & Amundsen 2005, Spares et al. 2012), while others have found a mix of prey items to be important (Dempson et al. 2002). The observed spatial variability in diet demonstrates that it is difficult to generalize feeding across large spatial scales and suggests the need for site-specific diet information.

1.4 Study Location and Aims

Tremblay Sound, Nunavut, Canada is a high Arctic ecosystem that provides habitat for Arctic char and other charismatic species such as narwhal (Monodon monoceros) and Greenland sharks (Somniosus microcephalus; Heide-Jørgensen et al. 2002, Barkley et al. 2020, Walmsley et al. 2020). A rapid seasonal ice-off in late June or July likely provides pulsed resources that these organisms exploit. Arctic char in this region are targeted by subsistence fisheries that provide food for local communities. As a high Arctic ecosystem, Tremblay Sound is an example of a region that could be impacted by climate change and provides an ideal environment to study climate-related impacts on migratory fishes.

In this thesis, I aim to investigate the movement and feeding ecology of Arctic char in Tremblay Sound, Nunavut, Canada. Chapter 2 characterizes the migration timing and seasonal movements of Arctic char in and out of Tremblay Sound in relation to the ice-off using acoustic telemetry, a powerful tool in the field of movement ecology (Cooke et al. 2004, Hussey et al. 2015). Chapter 3 assesses char diet during the ice-off period, including evaluating the degree of relative consumption, the importance of specific prey taxa, and annual variability in prey consumed. Char diets were quantified using traditional diet indices (Hyslop 1980). Finally, Chapter 4 summarizes and synthesizes the findings of both studies, provides opportunities for
future investigations, and discusses conservation and management implications for char fisheries in a changing Arctic.
CHAPTER 2: Arctic Char (*Salvelinus alpinus*) Movement Dynamics

Relative to Ice-Off in a High Arctic Embayment, Tallurutiup Imanga National Marine Conservation Area

2.1 Introduction

The Arctic experiences dramatic seasonal changes in environmental conditions, including the annual ice-off that occurs each summer in marine ecosystems. Ice-off, in conjunction with increased light levels, facilitates a primary productivity bloom that provides key nutrients and resources for many Arctic consumers (McMeans et al. 2015). In response, ice-off is followed closely by an influx of migratory fauna that seasonally exploit these newly abundant resources (Melnikov 1997). Not only does ice-off drive the ingress of species, but the subsequent ice-on can drive species’ emigration to more suitable environments (Hauser et al. 2017) defining their migration dynamics relative to the period of heightened prey availability. The duration and extent of sea-ice cover across the Arctic, however, is decreasing primarily as a result of increasing temperatures (Johannessen 2004, Yurkowski et al. 2018). Climate-induced changes in sea-ice phenology may impact species who rely on the precise timing and duration of ice-off. Consequently, defining species’ relationships with sea ice is required to predict their future resilience to continued change.
The Arctic char (*Salvelinus alpinus*) inhabits Arctic waters and exhibits two life history strategies: fresh water residency and anadromy (Johnson 1980, Nordeng 1983). It is presumed that marine migrations of anadromous Arctic char are used to exploit feeding opportunities (Johnson 1980, Nordeng 1983, Gyselman 1984, Gross et al. 1988). In fact, char can experience mean weight gains of 42% during the marine migration (Gyselman 1984). For these anadromous fish, the seaward migration occurs around the timing of ice-off, and char remain in the estuarine or marine environment for a period of one to four months (Klemetsen et al. 2003). Although it is widely believed that ice-off initiates migration, a quantitative linkage between ice-off timing and specific migration timing is lacking. Furthermore, migration patterns of anadromous char can be complex and region-specific (Beddow et al. 1998, Jensen & Rikardsen 2008, Moore et al. 2017). Specifically, the ability for char to travel to and even overwinter in non-natal rivers may facilitate interactions between multiple populations in specific areas (Moore et al. 2013, 2017). This straying behavior coupled with declining ice conditions has the potential to increase population mixing, subsequently decreasing genetic diversity (Post et al. 2013). Maintaining healthy Arctic char populations is important as it is the dominant species (~86%) in Canada’s Arctic marine fish catches (Booth & Watts 2007). Thus, if these complex migratory histories are common, it is important to manage populations as metapopulations, which account for population spatial structure and interactions (Ying et al. 2011).

Biotelemetry technology allows for characterizing movements of individual animals to understand population level processes (Cooke et al. 2004, Hussey et al. 2015) that can form the basis for management (Crossin et al. 2017, Brooks et al. 2019). Acoustic telemetry in particular is ideal for elucidating movement behaviors of species in aquatic and marine environments (Donaldson et al. 2014, Crossin et al. 2017), with deployment of fixed receivers in grids or a
series of gates allowing for the monitoring of individual tagged fish over large areas (Heupel et al. 2006). In addition, receivers/gates deployed in adjacent systems (i.e., neighboring river mouths) can determine the level to which tagged individuals use multiple systems. For example, receivers deployed in multiple systems near Cambridge Bay, Nunavut, Canada recorded complex movements of Arctic char (Moore et al. 2016) that directly informed management recommendations (Harris et al. 2016). Furthermore, the addition of receiver gates at entry or exit points within a system allows for the estimation of migration timing and duration (Lacroix et al. 2005), which can be further correlated to environmental variables such as the timing of ice formation/breakup.

The current study aimed to characterize the movement ecology of Arctic char within Tremblay Sound, Nunavut, Canada. Tremblay Sound is a model ecosystem for investigating the impacts of sea ice phenology on consumer movements; the spring ice-off draws not only char but high biomass of other top-level consumers such as narwhal (*Monodon Monoceros*) and Greenland sharks (*Somniosus microcephalus*) into the system (Heide-Jørgensen et al. 2002, Barkley et al. 2020, Walmsley et al. 2020). Moreover, Char are abundant in Tremblay Sound in the summer and harvesting by local communities provides an important subsistence resource. By integrating acoustic telemetry with sea ice phenology data and additional abiotic/biotic variables, our objectives were to 1) determine if inter-annual Arctic char movements are consistent with seasonal migrations, 2) determine if timing of movements or migration match sea-ice phenology, 3) assess if movements are consistent with a single population or multiple populations utilizing the Sound, and 4) assess correlations between movement behaviors and fish size (total length; TL) and condition.
2.2 Methods

2.2.1 Fish Capture and Telemetry

Arctic char were captured at the Ecosystem Approach to Tremblay Sound (EAT) camp (72.357089, -81.107421) using ~15 cm mesh gillnets between July and September of 2017 and 2018. Before tagging, char were anesthetized using either a Portable Fish Electroanesthesia System (PES; Smith-Root, Vancouver, WA, USA) or a 0.1 g L$^{-1}$ concentration of Tricaine mesylate (MS-222). For the PES system, the optimal system settings delivered a shock of 40 volts at 100 Hz for 8 seconds using a 25% duty cycle. After char ($n = 110$) were anesthetized, acoustic transmitters (VEMCO Ltd., Nova Scotia, Canada) were surgically implanted into the body cavity of each fish. VEMCO V13 tags (69 kHz, 36 mm x 12 mm, 6 g in water; $n = 29$) were implanted in fish $< 60$ cm TL (mean tag burden = 0.90%), while VEMCO V16 tags (69 kHz, 68 mm x 16 mm, 10.3 g in water; $n = 81$) were used for larger fish (mean tag burden = 0.79%). Approval for the above methods was received from the University of Windsor (AUPP:#17-12) and the University of New Hampshire (IACUC:#180602). All tagged fish were measured for TL, fork length (FL), and weighed before being returned to an aerated bin (~130-L) for recovery. Between the two years, the average TL and mass of tagged fish was 67.6 cm (SE = 1.04 cm) and 2.99 kg (SE = 0.13 kg), respectively (Table 2.1). A Fulton’s condition factor ($K = \frac{W}{L^2}$; where $W =$ weight and $L =$ length; Ricker 1975) was calculated for each fish.

Throughout the study period, movements of fish were monitored by a stationary array of 36 acoustic receivers (VEMCO VR2AR-69 kHz, and VEMCO VR2W-69 kHz) arranged in a series of gates (North to South A – G) along the southern section of the Sound (Figure 2.1). Receivers in each gate were located ~500 m apart to maximize detection efficiency to improve
confidence in capturing movements of all fish transiting between gates. In 2018, five additional receivers (VEMCO VR2W-69 kHz) were deployed to obtain information on potential broad-scale movements and connectivity. One was deployed near the mouth of a river at the southern end of Tremblay Sound suspected to be a key transition route from traditional Inuit knowledge, while four others were deployed at the mouths of two rivers (Satut to the north and Robertson to the south) outside the Sound (Figure 2.1). At these latter two rivers, one receiver was placed at either side of the river mouth to capture if these were the locations for freshwater transitions of fish captured and tagged in Tremblay Sound. Receivers were deployed continuously for one-year increments (July 2017 – July 2018 and July 2018 – August 2019), with data download, servicing and redeployment occurring between the two time periods (time to undertake servicing and deployment ranged from 2 to 48 hours [mean = 4 hours]).

2.2.2 Sea Ice Data

Sea ice data were collected from the “Approaches to Resolute” images within the Canadian Ice Service Ice Chart Archives (Ice Archives 2020). The format of these data is .gif images color-coded using the World Meteorological Organization’s Total Concentration Color Code (Table 2.2). The range of values that correspond to each color code represents an estimate of how much area is covered with ice. Daily images were compiled from the beginning of ice-off (~July) until complete ice cover (~October) for both 2018 and 2019. Images were then imported into ArcGIS 10.5 (ESRI, Redlands, CA) and georeferenced to a Lambert Conformal Conic projection. Once georeferencing was complete, images were clipped to match the region of Tremblay Sound using a defined shapefile (Data source: Environment and Climate Change Canada, cis_SGRDAEA_20191015T1800Z_pl_a, [2019]) from the Canadian Ice Service.
Borders between areas of different ice coverage within sea ice images resulted in areas of no data. Using the “set null” and “nibble” functions in ArcGIS, areas of no data were replaced with the ice area color code that was closest in distance. The area of each color code was calculated using the “zonal geometry as table” function in ArcGIS. These areas were then weighted by the median color code definition values (1, 0.95, 0.75, 0.5, 0.2, 0.1; Table 2.2) and summed to obtain an estimated total area of sea ice within Tremblay Sound. Due to gaps in the available sea ice data, the “beginning” of ice-off was determined as the first day open water was visible in Tremblay Sound from EOSDIS worldview imagery (NASA 2020). The number of tagged char detected in the Sound per day was calculated from March 1st, 2018 until August 22nd, 2019 and visualized in relation to estimates of total sea ice area (Figure 2.2).

2.2.3 Migration Chronologies

All tagged fish showed a distinct seasonal presence within the Sound; fish left the Sound prior to ice up, with most reentering before the ice-off in consecutive years (see Results). Day of exit and subsequent entry for each fish were determined based on first or last known detections within the receiver array in Tremblay Sound. Exit dates were established for 2017, 2018, and 2019 while natural entry dates were determined for 2018 and 2019. Residency times were calculated for each fish in each year as the number of days present in Tremblay Sound from their first to last detection. These residency times were only calculated for return migrants (fish that returned to Tremblay Sound in the year(s) after tagging) due to our inability to accurately estimate residency for a fish in the year it was tagged (i.e., char were already in Tremblay Sound for an unknown duration before tagging occurred). All fish were subsequently grouped into three defined migration chronologies based on their migration patterns among years. A fish that
consistently migrated to/from the river at the southern end of Tremblay Sound between or among years (i.e., first and last detected at any of the five southern receiver lines in all years detected; Figure 2.1) was considered a “resident.” Likewise, fish that consistently migrated to a river system outside of Tremblay Sound between or among years (first and last detected at gate A or on additional receivers deployed at external river mouths; Figure 2.1) were considered “external” migrants. Finally, fish that switched their migration direction during any year of the study (e.g., entered and exited from the southern receiver lines in one year, but then exited via gate A the following year) were labelled as “transient” migrants. In 2019, acoustic receivers deployed within Tremblay Sound were retrieved between August 3rd and August 8th, which would normally occur during the middle of the return migration (see Results). However, because < 10% of tagged fish were present in the system on August 8th, we assume that a fish’s final position was indicative of its chosen migration route in that year.

### 2.2.4 Home Ranges and Centroids

To summarize broad space use of char within Tremblay Sound, short-term centers of activity (COAs; Simpfendorfer et al. 2002) were calculated for each fish at six-hour intervals throughout the study period using the VTrack package (Campbell et al. 2012) in R (R Core Team 2019). COAs provide estimates of area use based on weighted means of detection frequency among receivers over the specified time interval (Simpfendorfer et al 2002). COA estimates were then used to generate 50% monthly home ranges using a lattice-based density estimator within the latticeDensity (Barry & McIntyre 2011) package for R (R Core Team 2019). The lattice-based approach was used because it accounts for boundaries (i.e., islands, inlets, points) to ensure that the calculated home range lies within available habitat; this was necessary to ensure
home ranges did not occur on land given the narrow geography of Tremblay Sound (Barry & McIntyre 2011; Figure 2.1). From the generated 50% home ranges, mean monthly centroids (latitude and longitude) were calculated. Because Tremblay Sound is longer in the north-south direction (~48-km) and narrow (~2 km-wide) in the east-west direction (Figure 2.1), only the latitude of each centroid was used in subsequent analyses.

2.2.5 Total Monthly Distances Traveled and Average Monthly Movement Rates

Total monthly distances traveled were calculated using COA positions, and were only calculated for repeat migrants, as these fish were detected for the entire duration of their residency (i.e., represents a natural event without tagging bias). Movement rates were calculated using COA positions rather than individual detections because COAs use a consistent time interval (six hours), which reduces bias introduced by variations in times between successive detections (i.e., shorter time intervals can result in faster movement rates). However, we recognize this approach likely underestimates absolute movement rates, given that we are summarizing over multiple detections. Rates were calculated for each fish by dividing the distance between subsequent COA locations by the six-hour interval between the two COA estimates. These rates were then transformed to body lengths per second (bl s\(^{-1}\)) based on the TL of each fish and averaged for the seasonal period present within Tremblay Sound. It is important to note that COA estimates were calculated using only the gate receiver array within Tremblay Sound and did not incorporate detections on the four receivers located outside of the Sound. This ensured our analyses focused on seasonal space use within the Sound environment.

2.2.6 Statistical Analyses
To assess whether biotic factors were driving differences among the three migration chronologies (resident, transient, external), TL and Fulton’s condition factor (Ricker 1975) were compared using multivariate analysis of variance (MANOVA) followed by individual analysis of variance (ANOVA) tests. Multiple comparisons were conducted for significant ANOVA’s using Tukey’s honestly significant difference tests.

A series of generalized linear mixed models (GLMMs) were then used to determine correlations between movement behaviors and calculated metrics of Arctic char movement within the lmerTest package (Kuznetsova et al. 2017) in R (R Core Team 2019). Four GLMMs were used to assess factors influencing migration timing (entry and exit dates) and duration of residency, which were entered as explanatory variables. Entry date was analyzed in two separate models, expressed as either Julian day of fish entry or days between fish entry and ice-off start date. These two models allowed for the comparison of migration consistency based on calendar date versus ice-off timing. The global model for each of the four GLMMs included year, migratory chronology, and total length as fixed explanatory variables. Due to repeated measures for return migrants, the identity of each char’s tag (FishID) was included in the model as a random effect. A second set of GLMMs were then used to assess factors influencing movement metrics: average monthly centroid latitude, monthly home range size, monthly distance traveled, and average monthly movement rate. The global model for each of these GLMMs included the movement metric as the response variable, with month, year, total length, and migratory chronology as explanatory variables and fish identity as a random effect. To rank candidate models, all subsets regression model selection was performed, using Akaike Information Criterion for small sample sizes (AICc) using the dredge function in the MuMIn package (Bartoń
2019) in R (R Core Team 2019). The model with the lowest AICc was selected as the best fit in each case.

2.3 Results

A total of 759,321 detections were recorded by the acoustic receiver array throughout the three-year period (Table 2.1; Figure 2.3). Two fish tagged in 2017 (1665 and 1677) were considered mortalities as they did not exit the system and were detected consistently on two receivers throughout the year. Thus, 133,839 detections from these fish were removed from analyses, leaving a total of 625,482 detections.

Movements of tagged char were consistent with seasonal migrations and were timed with ice occurrence (Figure 2.2). Tagged fish typically exited the system in mid-August and returned the following June or July (Figure 2.2). No detections of fish occurred between the months of October and May (i.e., the ice on period), with only 75 detections recorded in September among all years. Throughout the duration of the study, 67 fish were last detected near Tremblay Sound’s southern river systems (gate G) consistently each year and were classified as “residents,” 35 fish used Tremblay Sound in the summer, but migrated to/from other systems and were classified as “external” migrants, while eight fish exhibited both behaviors (i.e., transient migrants). All eight transient migrants began their chronologies by exiting to one of Tremblay Sound’s southern river systems (matching the behavior of a resident fish), but subsequently migrated out of the Sound via gate A to the broader marine environment (matching the behavior of an external migrant). It is important to note that all fish were not detected each year and some chronologies are determined from a single year of data (Figure 2.3). Biological (TL and fish condition) differences were investigated among the migratory chronologies (MANOVA; $F_{(2,107)} = 15.3; P < 0.001$; Figure 2.4); individual ANOVA tests revealed that TL significantly varied among the three
chronologies (ANOVA; $F_{(2,107)} = 36.15; P < 0.001$), but not condition (ANOVA; $F_{(2,107)} = 2.512; P = 0.086$). External migrants were on average ~14 cm larger than both resident (pairwise comparison; $P < 0.001$; Figure 2.4) and transient (pairwise comparison; $P = 0.001$; Figure 2.4) migrants. Although there was no significant difference in TL between resident and transient migrants ($P = 0.99$), transient fish were of an intermediate size between resident and external migrants (Figure 2.4).

The timing of migration entry into the system was directly linked to the timing of ice-off (Figure 2.2 and Figure 2.5). The start of ice-off occurred on July 2\textsuperscript{nd} in 2018 and June 28\textsuperscript{th} in 2019 (Figure 2.2). Both models characterizing char entry dates (response variables of Julian day of fish entry and days between fish entry and ice-off date) retained all explanatory variables of year and migratory chronology, and TL. These models had high model weights ($w = 0.994$ for both; Table 2.3), indicating that year, migratory chronology, and TL were consistently important variables explaining timing of entry. Resident and transient fish consistently arrived ~7.5 days before the start of ice-off with an average Julian entry date of June 23\textsuperscript{rd} and June 22\textsuperscript{nd}, respectively (Figure 2.5). The mean Julian date of entry was ~9 days earlier for resident and transient fish in 2019 compared to 2018, corresponding to an average entry date of ~3 additional days before ice-off start. The consistency in migration timing related to the start of ice-off suggests that char migration may be more tightly linked to this process than day of the year (Figure 2.5). Although entry data for external fish were only available in 2019, these fish entered much later than their resident and transient counterparts (mean entry date of July 19, ~21 days after ice-off start). In addition, large fish (~75 cm TL) also entered the system ~10 days earlier (~5 additional days before ice-off start) than their smaller (~40 cm) counterparts, at least within the resident and transient groups (Figure 2.5).
When considering fish emigration from the Sound, the same variables (migration chronology, total length, and year) were retained within the model (Table 2.3; Figure 2.6). On average, resident and transient fish exited the system around the same time (~August 6th), while external migrants exited 9 days later (~August 15th). The earliest exits occurred in 2019 (~16 days earlier than 2017), with exits in 2018 occurring ~6.6 days earlier than those in 2017 (Figure 2.6). In addition, large resident fish exited ~20 days later than smaller residents (Figure 2.6). While a moderate negative relationship between exit date and TL for transient fish was observed, the sample size was too small (n = 8) to substantiate this result (Figure 2.6).

In terms of the duration of seasonal residency within the Sound, migration chronology and year were retained in the model as explanatory variables (Table 2.3; Figure 2.7). One external fish was removed from this analysis in 2018, given it was the only returning fish of that chronology in that year. The majority of fish stayed in Tremblay Sound between 27 (25th percentile) and 44 (75th percentile) days (mean = 33.5 days) before exiting. Among migratory chronologies, external fish exhibited the shortest residencies (mean = 21.5 days), followed by resident fish (mean = 35 days), and transient fish (mean = 40.7 days; Figure 2.7). Although on average, transient fish had higher residency times than resident fish, this was only true in 2019 (Figure 2.7). Average residency times among all fish were approximately four days longer in 2019 (mean = 37.6 days) than in 2018 (mean = 33.4 days; Figure 2.7).

To investigate temporal space use of char and overlap in migration chronologies within the Sound, the model investigating average monthly centroid (latitude) as the response variable retained migratory chronology, month, total length, and year as key factors (Table 2.3; Figure 2.8). External migrators occupied the most northern centroids, which were ~4-km further north than for transient fish and ~5.5-km further north than for resident fish (Figure 2.8). During the
ice-free season, the three migratory groups appeared to converge within the Sound. The average monthly centroid for resident and transient migrants was the most southern in June and moved northward through August (Figure 2.8). In direct contrast, external migrators moved southward through time, with their northernmost centroids calculated in July and southernmost centroids in August (Figure 2.8). Among all years, transient and external migrants appeared to occupy their most northern centroids in 2019 (2-4 km further north than previous years for transient fish, 7-10 km for external fish; Figure 2.8). Resident fish exhibited their most southern centroids in 2019, however, these fish showed very little (<1-km) variability in centroid position among years (Figure 2.8). For absolute space used by char in the Sound, the model examining home range size retained month and migration chronology variables (Table 2.3; Figure 2.7). In July, fish occupied home ranges that were ~6 km² larger than in June or August regardless of chronology (Figure 2.7). In general, external migrators occupied the largest home ranges (~11.5 km² larger than transient fish and ~8 km² larger than resident fish; Figure 2.7). Transient fish, however, occupied the largest home ranges by about 4 km² in July (Figure 2.7).

Examination of the average movement rates of char found that year and month were important explanatory variables (Figure 2.7). Movement rates appeared to decrease from 2017 through 2019 (means = 0.26 bl s⁻¹, 0.16 bl s⁻¹, 0.10 bl s⁻¹ for 2017, 2018, and 2019, respectively; Figure 2.7). On average, movement rates were lowest in June and increased moderately throughout the ice-free season (monthly means = 0.09 bl s⁻¹, 0.15 bl s⁻¹, 0.22 bl s⁻¹ for June, July, and August, respectively; Figure 2.7). Month, year, TL and direction of migration were retained in the model where total monthly distance was the response (Table 2.3; Figure 2.7). On average, total monthly distance traveled for all fish among years was the highest in July (127 km, ~100
km more than in June or August; Figure 2.7). Regardless of chronology, fish traveled about 30-km further in 2019 than in 2018 (Figure 2.7).

2.4 Discussion

Understanding the movement dynamics of Arctic char is of particular importance given the propensity for interactions among populations (Moore et al. 2017) as well as their seasonal dependence on ice-associated prey pulses to maximize fitness and survival (Gyselman 1984, Jensen et al. 2018). To date, little is known regarding the specific dynamics of char migration phenologies relative to ice-off/formation while in the region of Tremblay Sound. Consequently, knowledge of char movements in this high Arctic region is required in order to inform stock dynamics for effective management. This is particularly important given the recent designation of the region as the Tallurutiup Imanga National Marine Conservation Area. Moreover, given char undertake region-specific movement behaviors (Beddow et al. 1998, Jensen & Rikardsen 2008, Moore et al. 2017), increasing our understanding of their movement dynamics with latitude builds on previous work in the central Arctic (Cambridge Bay; Moore et al. 2013, 2016, 2017) and low Arctic (Frobisher Bay; Spares et al. 2012, 2015).

Arctic char migrations in Tremblay Sound were directly related to ice-off timing, but most fish entered the Sound before the start of ice-off. Resident and transient fish consistently arrived ~5-15 days before ice-off even though the actual ice-off date varied by ~4 days between years. While entry dates into the marine environment (mid-June) were consistent with other studies (Gyselman 1984, Bégout Anras et al. 1999, Spares et al. 2015, Moore et al. 2016), much of the available literature suggests that migration occurs just after ice-off or that char follow the ice edge as it retreats (Johnson 1980, Bégout Anras et al. 1999, Gilbert et al. 2016). These studies, however, did not directly quantify ice phenology. While the current study was able to
quantify ice phenology in the system, these data are coarse in spatial resolution. In fact, we were unable to determine the ice dynamics occurring in the river near gate G, from which resident fish migrate. Thus, our estimates of the ice-off start date might be inaccurate. However, it is unlikely that potential inaccuracies are enough to dramatically change our findings, and it is clear that char are migrating before the ice-off in this system. The fact that the arrival of char occurs well before the beginning of marine ice-off suggests that these fish may be responding to other cues such as terrestrial ice melt (Heim et al. 2015), increased daylength (Finstad et al. 1989, Arnesen et al. 1992), or increased temperatures (Ellis & Vokoun 2009, Brodersen et al. 2011) in order to anticipate marine ice-off rather than directly reacting to it. This may suggest it is important for char migration in Tremblay Sound to precede the ice-off and resulting productivity bloom (McMeans et al. 2015), such that char experience the greatest benefits of exploiting the marine prey pulse for their growth and survival (Gyselman 1984, Jensen et al. 2018).

Although char migration into Tremblay Sound appears to be related to ice-off timing, our results for emigration and marine residence time are likely related to food availability rather than the timing of ice-on. In fact, char exited Tremblay Sound soon after the completion of ice-off; this was particularly evident in 2019, however, this result may have been affected by the earlier timing of receiver retrieval (August 4, 2019 – August 6, 2019), which overlaps the timing of emigration from the Sound. Earlier receiver retrieval may have artificially decreased the number of tagged fish present in the marine environment. The number of char in the system, however, had steadily decreased since its peak in early July, so it is unlikely that this result had an appreciable effect. In addition, the average exit date for 2018 fish (August 8th) was well before the start of ice-on and the mean duration of residency was actually five days shorter in 2018 (~33 days) than in 2019 (~38 days). Regardless, these residency times in the marine environment are
short (~35 days) and are similar to ranges reported in other studies (Johnson 1980, Gyselman 1984, Gulseth & Nilssen 2000). This short residency time identifies that the pulse of food that presumably regulates char migration and residency in Tremblay Sound must be ephemeral. Once the short period of enhanced food availability is over or reaches a certain threshold, the benefits of marine residency decrease, driving char to return to their freshwater habitats. Examples of migratory coupling, by which predators migrate to feed on rapid pulses of migratory prey are ubiquitous across terrestrial and aquatic taxa (Glenn & Miller 1980, Tsipoura & Burger 1999, Furey et al. 2018). Through matching their migration timing to prey phenologies, predators can maximize energetic gain (Reed et al. 2009) with implications for long term fitness and reproductive success (Gyselman 1984, Jensen et al. 2018).

In addition to sea-ice phenology, char migration timing was also related to fish TL, migration chronology, and year of migration. Large individuals entered the marine environment before smaller fish, a finding consistent with other char studies in the Arctic, albeit in different regions (Grainger 1953, Gilbert et al. 2016). However, in contrast to other findings (Gulseth & Nilssen 2000), smaller fish exited the system earlier than larger fish, suggesting their residence time in the marine environment is shorter than for large individuals. These combined results may be related to difference in consumptive capacity associated with fish size. Typically, relative consumption rates are highest for small fish and decrease with predator size (Furey et al. 2016). Thus, small char may be able to consistently exploit the summer prey pulse, repleting their energy reserves quicker than large char. Similarly, large fish may require more time to regain lost energy reserves from overwintering and/or spawning (Dutil 1986), and benefit from a longer marine residence phase. This size-based variation in migratory timing could have potential implications for management in terms of subsistence harvesting by communities who are known
to target specific char runs (Roux et al. 2011). Char migrating from freshwater systems outside of Tremblay Sound entered the system later than those migrating from freshwater systems within the Sound. This trend is to be expected due to the additional distance (in some cases estimated to be 80+ km) that external fish need to travel before they arrive in the Sound. Their late arrival (mean entry date of July 19th) likely means that these external fish are not present for the entire period of the resource pulse in Tremblay Sound, and may be feeding elsewhere first and/or en route to Tremblay Sound. Further investigation of the factors driving external migrant char movements into Tremblay Sound is required to fully understand why subpopulations exhibit such different movement dynamics (in terms of scale of directed movement). Alternatively, a South to North gradient in ice-off timing (i.e., Southern areas are ice-free first) in Tremblay Sound and the surrounding systems may indicate that fish migrating from external systems face the barrier of sea-ice in Eclipse Sound prior to reaching Tremblay Sound, which might explain their late arrivals. The difference in migration timing among years provides further evidence of how these fish time their migrations to ice phenology. Ice-off began on July 2nd, 2018 and on June 28th, 2019, with migration occurring ~9 days earlier in 2019. Johnson (1980) reported that the duration of marine residency of Arctic char correlates with the timing of ice breakup (i.e., longer marine residency in years with earlier ice-off dates. Our data do not substantiate this point, with only a three-day difference in residency between 2018 and 2019 (despite ~9-day difference in migration timing). Thus, as climate change continues to alter ice phenologies, we might expect to see char migrating to marine systems earlier to maximize feeding opportunities, with little to no effect on overall duration of residency.

In addition to variability in migration timing with ice-off and among migrant phenotypes, we also observed variation in apparent migration distance. Upon entering the marine system,
resident fish typically stayed within ~20 km of their river of origin, a finding consistent with the idea that individuals of the *Salvelinus* genus remain close to their natal rivers (Curry et al. 2006, Spares et al. 2015). However, transient and external migrators traveled much further to utilize the Sound. Fish that presumably traveled to/from the Satut River (near northernmost receivers in Figure 2.1) moved an additional ~20 km after entering/exiting the sound (~53 km from tagging location) before reaching their overwintering river/lake. Furthermore, char presumably traveling to the Robertson River (southernmost receivers in Figure 2.1) would have moved an additional ~80 km (~103 km from tagging location) before reaching this system. However, these conclusions rely heavily upon our assumptions of fish overwintering in these habitats. Although it is likely that tagged fish entered the Satut and Robertson Rivers, they could have continued further along the coast to other locals. Future studies could include both marine and freshwater receivers to accurately determine the location of freshwater overwintering habitat. Regardless, the estimated distances travelled by external migrants are comparable to movements described in other studies (Dempson & Kristofferson 1987, Finstad & Heggberget 1993, Moore et al. 2016). Overall variability in the estimated marine migration distances (herein and in previous studies) suggest char exhibit diverse movement strategies among populations and across regions (Dempson & Kristofferson 1987, Finstad & Heggberget 1993, Moore et al. 2016) with consequences for individual and subpopulation fitness. It is possible the marine migration distance of Arctic char in the Arctic is at least partially determined by proximity to preferential summer feeding habitat and abundant resources. For example, the seasonal migrations of Arctic char, narwhal (Heide-Jørgensen et al. 2002, Walmsley et al. 2020), and Greenland shark (Barkley et al. 2020) could suggest that food availability is high within Tremblay Sound. The fact that external migrants enter and remain in Tremblay Sound following an extended migration
(relative to resident fish) identifies further evidence of the potential regional importance of this system in terms of either heightened resource availability or possibly other factors such as providing refuge from predation. Furthermore, shallow coastal regions such as Tremblay Sound provide ideal feeding habitat for char (Spares et al. 2015, Moore et al. 2016), and the quantity of food observed in char stomachs suggests that these fish are readily exploiting available resources (Chapter 3). A directed approach connecting between-system movements and prey densities, however, will be needed to appropriately assess the importance of individual habitats to the marine phase of char migration and how it shapes variation in migration distance.

The existence of three distinct migratory chronologies of char tagged in Tremblay Sound suggest multiple hypotheses for their occurrence in the system. First, these distinct movement patterns could indicate that multiple subpopulations of Arctic char use Tremblay Sound. In fact, mixing among subpopulations (although not necessarily gene flow) may be quite common in this species (Moore et al. 2013). The multi-population hypothesis in Tremblay Sound is further supported by the size differences among groups, with external fish being the largest, residents the smallest, and transients being of intermediate size. However, it is impossible to differentiate between subpopulations without genetic evidence (Moore et al. 2017), which we lack in the current study. Char are known to overwinter in non-natal rivers (Moore et al. 2013, 2017), and in some cases, for multiple years (Moore et al. 2017), which could explain the behavior of transient fish in the current study. It is possible that transient fish are native to external systems, but are tagged in years that they overwinter in a non-natal system (Tremblay Sound rivers) to avoid a harsh return migration (Moore et al. 2017). Under this scenario, fish would have to travel at least an additional ~20-80 km beyond Tremblay Sound to return to their assumed natal river, which could be a significant barrier.
An alternate explanation for the presence of unique migratory chronologies could relate to ontogenetic shifts in migration behavior. Individuals within a population can exhibit varying levels of migratory behavior, a phenomenon termed partial migration, such that both migratory and resident cohorts exist within a single population (Lack 1943, Berthold 1999, Kerr et al. 2009). Arctic char populations are known to exhibit partial migrations (Finstad & Hein 2012), with distinct migratory and resident cohorts present as early as the parr life history stage (Finstad & Hein 2012). But fish can also vary the magnitude or distances traveled during seasonal migrations with ontogeny. For example, oceanic residence of striped bass (*Morone saxatilis*) increases with age and size (Secor & Piccoli 2007). In addition, char can be completely absent from their natal rivers during certain size and age classes (Gilbert et al. 2016). It is therefore possible given size differences among fish (the smaller resident fish only migrated from the rivers to the lower half of Tremblay Sound, while the larger external fish travelled to and from further locales outside of Tremblay Sound), that the migratory chronologies we identified correspond to increases in migration distance with ontogeny. Transient fish (intermediate size) could therefore be in the process of an ontogenetic shift in migration distance over the study period. The fact that behavioral “switches” displayed by transient fish were always unidirectional (i.e., transient fish always start their chronology by behaving like resident fish, then switch to behaving like an external fish) provides compelling evidence for increased migration distance with ontogeny. Additionally, there was no evidence that transient fish eventually return to freshwater systems within Tremblay Sound after transitioning. Long-term monitoring in addition to genetic assessment will be needed to substantiate these conclusions given our data were only from a three-year period. However, similar ontogenetic shifts are ubiquitous among other aspects of fish behavior including habitat use and diet (Werner and Hall 1988, Jones et al. 2003, Grubbs
It also should be noted that our two hypotheses explaining the various migratory chronologies, i.e., presence of multiple subpopulations and ontogenetic changes in migratory distance, are not necessarily mutually exclusive.

Regardless of migration chronology, fish moved toward the center of the Sound throughout the summer (transient and resident fish from the south, external fish from the north). This behavior suggests that char were tracking the seasonal resource pulse as it moved throughout the system or along the ice-edge (Johnson 1980). As in other systems, char may exhibit their highest activity rates (i.e., feeding rates) soon after the migration to sea, with rates decreasing through time (Amundsen & Klemetsen 1988, Rikardsen et al. 2000). For example, home range size and total distance traveled generally were the largest in July, which could represent feeding behavior during the peak of the resource pulse. Movement rates also increased in July relative to June. However, the highest movement rates were calculated in August, most likely reflecting their directed migration out of the marine system. Observed variation in movement speeds among years might be an artefact of our sampling, in which 2017 estimates only included fish tagged that year, while 2018 included both freshly tagged individuals and return migrations, and 2019 only included return migrants. Return migrants likely have lower estimated speeds than freshly tagged individuals because the movement rate calculation captures their entire residency, rather than the week(s) during or leading to return migration when speeds are more directed and therefore faster.

As in all telemetry studies, our ability to characterize the movement behaviors of char is dependent on the assumption that tagged fish behave similarly to non-tagged fish. Although we were unable to measure the effects of tag burden on char behavior, it is unlikely that tagging had an appreciable effect as our burdens (mean = 0.9% for V13 tags and 0.79% for V16 tags) were
well below the “2% rule” (Winter 1983). In addition, the “2% rule” may not apply to all species and life histories (Jepsen et al. 2005), and thus, higher tag burdens may be acceptable (Brown et al. 1999, 2010). Tagged fish, however, may experience long-term tagging effects (Lacroix et al. 2004, Thorstad et al. 2009). Of all fish tagged, 41% (45 of 110) seasonally returned to Tremblay Sound in the subsequent year(s) after tagging. This could indicate a long-term impact of tagging (i.e., mortality through reduced fitness), but is more likely explained by factors including natural mortality, reported and unreported fishing mortality, movements to unmonitored systems, and skipped migrations due to spawning (Johnson 1980, Moore et al. 2013) rather than tagging effects on survival.

Throughout its range, Arctic char have supported subsistence fisheries for centuries (Kristofferson & Berkes 2005, Roux et al. 2011) while commercial fisheries have been operating since the 1960s (Kristofferson & Berkes 2005, Day & Harris 2013). If multiple subpopulations are indeed present and use Tremblay Sound, the current study highlights the importance of managing char populations as metapopulations given the potential for stock mixing (Ying et al. 2011, Moore et al. 2013). As a result, recent studies have advocated for aspects of an area-based management approach rather than traditional plans that governed stocks on a river-by-river basis (Harris et al. 2014, 2016). Ideally, these plans would more accurately account for interactions among populations in the marine environment than river-by-river plans, leading to more effective management that promotes genetic diversity and portfolio effects (Schindler et al. 2015). However, area-based management plans have resulted in collapsed Arctic char fisheries in the past, so any strategy must be approached with caution, taking into account the actual extent of stock mixing and dispersal (Kristofferson & Berkes 2005, Harris et al. 2014, 2016). Current telemetry and genetic evidence highlight the potential utility of quota transfer management
strategies for the commercial harvest of Arctic char (Harris et al. 2014). A quota transfer strategy could sustainably increase yields, allowing an unmet quota to be transferred to a neighboring system (see Harris et al. 2016).

The current study documents the migration dynamics and marine residency behavior of Arctic char tagged within Tremblay Sound, a region recently designated as a conservation area (Tallurutiup Imanga National Marine Conservation Area). As climate change continues to shift the Arctic toward completely ice-free summers (Wang & Overland 2012, Overland & Wang 2013), important questions are arising about the future of Arctic char marine migrations and char flexibility and adaptability to change. The direct link between migration timing and ice-off timing indicates that char can adapt to small-scale changes in sea-ice phenology. However, it is unclear if the observed plasticity will mediate large-scale shifts such as those associated with an ice-free summer (Wang & Overland 2012, Overland & Wang 2013). In addition, as the extreme seasonality of processes in the Arctic become more diluted, prey pulses may become muted or non-existent, altering the risk-reward dynamics of freshwater-marine migrations. Under the extreme scenario of ice-free summers, associated increases in terrestrial productivity may decrease the prevalence of anadromous populations of Arctic char, with potential impacts on commercial and subsistence fisheries across the region (Gross et al. 1988, Reist et al. 2006b). Future work is required to link movements directly to feeding behavior to quantify prey consumed during these seasonal productivity pulses and the rate and extent of foraging. Through conducting these studies across a range of latitudes with varying ice cover and ice on/off dynamics (sub arctic to high Arctic), it will be possible to gain a deeper understanding of the energetic benefits of migrations for Arctic char, and to predict the potential impacts of more severe changes in ice phenology and elevated water temperatures. Overall, the current study
provides important insight for appropriate management of Arctic char in Tremblay Sound and understanding of variation in char movement dynamics in an ever-changing Arctic.
### 2.5 Tables

Table 2.1. Summary information for all Arctic char tagged during 2017 and 2018. Values in parentheses indicate standard error.

<table>
<thead>
<tr>
<th></th>
<th>Year</th>
<th>Tag Type</th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>2017</td>
<td>2018</td>
<td>V13</td>
<td>V16</td>
<td>V13</td>
</tr>
<tr>
<td>Number of char tagged</td>
<td>58</td>
<td>52</td>
<td>28</td>
<td>30</td>
<td>1</td>
</tr>
<tr>
<td>Mean tag burden</td>
<td>0.91% (0.08)</td>
<td>0.71% (0.03)</td>
<td>0.88 (0.15)</td>
<td>0.96 (0.05)</td>
<td>1.51</td>
</tr>
<tr>
<td>Avg TL (cm)</td>
<td>61.88 (1.26)</td>
<td>68.49 (1.22)</td>
<td>58 (2.05)</td>
<td>65.5 (1.18)</td>
<td>42.6</td>
</tr>
<tr>
<td>Avg mass (kg)</td>
<td>2.29 (0.14)</td>
<td>3.13 (0.16)</td>
<td>1.77 (0.16)</td>
<td>2.79 (0.19)</td>
<td>0.73</td>
</tr>
</tbody>
</table>
Table 2.2. Ice concentration ranges for color codes given by the World Meteorological Organization (WMO) along with the concentrations used for calculations of total ice area within Tremblay Sound.

<table>
<thead>
<tr>
<th>WMO Color Code - Concentration</th>
<th>Median Concentration Used</th>
</tr>
</thead>
<tbody>
<tr>
<td>&lt; 1/10</td>
<td>1/10</td>
</tr>
<tr>
<td>1-3/10</td>
<td>2/10</td>
</tr>
<tr>
<td>4-6/10</td>
<td>5/10</td>
</tr>
<tr>
<td>7-8/10</td>
<td>7.5/10</td>
</tr>
<tr>
<td>9-10/10</td>
<td>9.5/10</td>
</tr>
<tr>
<td>Fast Ice</td>
<td>1</td>
</tr>
</tbody>
</table>
Table 2.3. Generalized Linear Mixed Models (GLMM) with model weight $\geq 0.10$ determined via all subsets regression. The response variables and best-fit models are presented in bold. Additional models for a given response variable fall below the best-fit model, and the response variable is not shown.

<table>
<thead>
<tr>
<th>Response</th>
<th>Model</th>
<th>loglik</th>
<th>AICc</th>
<th>Wi</th>
</tr>
</thead>
<tbody>
<tr>
<td>Entry Date (Julian day)</td>
<td>Year + Chronology * TL + (1</td>
<td>Transmitter)</td>
<td>-123.854</td>
<td>269.8</td>
</tr>
<tr>
<td>Entry Date (Days from ice-off)</td>
<td>Year + Chronology * TL + (1</td>
<td>Transmitter)</td>
<td>-123.854</td>
<td>269.8</td>
</tr>
<tr>
<td>Exit Date</td>
<td>Year + Chronology * TL + (1</td>
<td>Transmitter)</td>
<td>-607.412</td>
<td>1236.3</td>
</tr>
<tr>
<td>Residency Time</td>
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2.6 Figures

Figure 2.1. A map of the study area in Tremblay Sound, Nunavut, Canada. The black circles represent receiver locations within Tremblay Sound. Receiver gates are labelled by letters on the right-hand side of the Sound. The four grey triangles in the inset to the right represent additional receivers, which were added near the Robertson and Satut River mouths. The grey star on the map and the black box within the left inset designate the approximate location of capture. Bathymetry is represented in greyscale, with dark colors representing deep water. Sources: Esri, HERE, Garmin, © OpenStreetMap contributors, and the GIS User Community, GEBCO Compilation Group (2020) GEBCO 2020 Grid (doi:10.5285/a29c5465-b138-234d-e053-6c86abc040b9).
Figure 2.2. The number and timing of occurrence of tagged Arctic char present in Tremblay Sound relative to interpolated ice area (km²) throughout the study period. Black dots indicate the number of tagged fish in Tremblay Sound. The grey line and grey confidence intervals show interpolated ice area within the sound. The dotted grey lines represent an estimated start of ice-off from EOSDIS Worldview imagery (NASA 2020). Black horizontal lines and associated labels indicate the duration of the ice-free season.
Figure 2.3. Detection histories for all Arctic char tagged throughout the study period (2017 to 2019). Tagging dates are represented by open circles for each individual. Detections are separated into three columns based on year and are colored and ordered by migration chronology (see Methods and Results). Shaded regions represent periods when Tremblay Sound was completely covered in ice.
Figure 2.4. Boxplots showing differences in total length (A) and condition (B) between the three migratory chronologies of Arctic char. Each point indicates an individual fish. Mid lines in each boxplot represent median values and the hinges represent the first and third (25th and 75th) percentiles. Whiskers extend 1.5 * the interquartile range from each hinge. The asterisk above the external chronology in the first panel indicates a significant (P < 0.05) difference in TL from the other two chronologies.
Figure 2.5. A two-panel plot of day of entry in Julian day (A) and days between entry and ice-off date (B) by total length of Arctic char. Points represent individual fish and lines indicate predicted values from the model while holding year and chronology constant. Points and lines are colored by migration group. Point shape and line type indicate year.
Figure 2.6. Day of exit from Tremblay Sound by Arctic char size (total length). Points represent the individual entry dates for each fish and are separated into three columns based on migratory chronology. Lines indicate predicted values from the model while holding year and chronology constant. Squares and dotted lines indicate 2017 data, triangles and solid lines indicate 2018 data, and circles with dashed lines represent 2019 data.
Figure 2.7. Total residency (A), monthly home range size (B), mean monthly speeds (C), and total distance traveled (D) by Arctic char tagged in Tremblay Sound. Points within all plots indicate calculations for each metric for individual fish. In the residency, home range, and distance panels, points are colored by migratory chronology. Shapes in the mean monthly speed plot indicate the year. In all plots, the mid-line indicates the median value, the hinges indicate the first and third (25th and 75th) percentiles, and whiskers extend to 1.5 * IQR from each hinge.
Figure 2.8. Average monthly centroids for individual char that constitute the three migratory chronologies (circles within the Sound; resident, transient and external migrants), month-chronology combination-specific latitude of centroid (left side, outside of Sound – color coded Xs), and year-chronology specific latitude of centroid (right side, outside the Sound – color coded shapes). X positions of summary shapes on the left-hand and right-hand side of the Sound are selected arbitrarily for visualization (only the mean latitude is shown). Sources: Esri, HERE, Garmin, © OpenStreetMap contributors, and the GIS User Community
3.1 Introduction

Seasonal changes in environmental conditions are ubiquitous among ecosystems across the globe, with seasonal variability most pronounced at the earth’s poles (MacArthur 1972, Lisovski et al. 2017). Among the most dynamic changes in these regions is an annual summer ice-off, which is responsible for driving many ecosystem processes in the Arctic. In particular, this ice-off along with increased light levels, promotes primary productivity blooms that provide nutrients for consumers (McMeans et al. 2015). In the spring, before the ice-off begins, ice algae production increases in response to increased light levels, providing a significant proportion of total spring primary productivity (Horner & Schrader 1982). As the ice begins to melt, amphipods feed on the abundant algae causing an increase in biomass (Gradinger & Bluhm 2010). The abundance of amphipods draws species in higher trophic levels such as Arctic cod (*Boreogadus saida*) into the system (Bradstreet & Cross 1982), and the flow of energy continues to higher trophic levels. However, the timing and magnitude of this event has been shifting due to climate change (Johannessen et al. 2004, Yurkowski et al. 2018). In fact, models predict that the Arctic summer could be nearly ice-free within the foreseeable future (Wang & Overland 2012, Overland & Wang 2013). These impending changes may have direct consequences for human and animal communities throughout the Arctic who rely on ecosystem processes that have persisted for centuries.
The Arctic char (*Salvelinus alpinus*) is an important consumer that provides food for indigenous communities throughout the Arctic (Booth & Watts 2007). Anadromous populations of this species undergo seasonal migrations to marine systems in the summer, presumably to feed on abundant prey items (Johnson 1980, Nordeng 1983, Gyselman 1984, Gross et al. 1988). In many cases, residency within Arctic marine systems is short, only lasting a few weeks or months (Johnson 1980, Gyselman 1984, Gulseth & Nilssen 2000, Chapter 2). It is likely that char residency times in Arctic systems approximately match the duration of the prey pulse, with char entering systems during (Johnson 1980, Bégout Anras et al. 1999, Gilbert et al. 2016) or before (Chapter 2) the onset of ice-off.

The diets of Arctic char have been explored previously (Rikardsen et al. 2000, Dempson et al. 2002, Rikardsen & Amundsen 2005, Spares et al. 2012), however, this information is likely region- and population-specific (Dempson et al. 2002, Rikardsen & Amundsen 2005). Regardless, the feeding during marine residency is critical for growth and overwinter survival (Gyselman 1984, Jensen et al. 2018). Due to cold temperatures and low prey availability, Arctic char typically undergo a period of fasting during the winter (Boivin & Power 1990). Thus, food consumed during the summer must support winter metabolism and reproduction during spawning years. Therefore, the ability to maximize short-term consumption is important, and may explain how char can double in weight over a one-month period in the summer (Gyselman 1984).

Binge-feeding occurs when an organism eats more than a theoretical maximum daily consumption value (Furey et al. 2016). Bull trout (*Salvelinus confluentus*), a closely related char, is capable of binge-feeding (Furey et al. 2015, 2016). In addition, the Dolly Varden (*Salvelinus malma*; another char) seasonally exhibits an increase in digestive capacity required to binge-feed
when food is abundant (Armstrong & Bond 2013). While the ability to binge-feed can provide benefits (Furey et al. 2016), maintaining high capacity for food processing can be taxing during periods of food scarcity (Armstrong & Schindler 2011). In addition, increases in assimilative capacity increase the energetic costs of maintenance metabolism and locomotion (Armstrong & Schindler 2011, Norin & Clark 2017). Thus, species demonstrate behavioral and physiological adaptations to seasonally regulate digestive capacity (Armstrong & Bond 2013). As a close relative of bull trout and Dolly Varden, Arctic char may possess similar adaptations. Furthermore, Arctic char live in dynamic systems where food availability is highly seasonal, and they likely would benefit from the ability to regulate their digestive capacity.

Tremblay Sound, Nunavut, Canada is a high Arctic ecosystem that supports at least one anadromous population of Arctic char (Chapter 2). In addition to migratory char, this system serves as summer habitat for tertiary consumers like narwhal (*Monodon monoceros*) and Greenland sharks (*Somniosus microcephalus*; Heide-Jørgensen et al. 2002, Barkley et al. 2020, Walmsley et al. 2020). The seasonal presence of these charismatic migratory species suggests that primary productivity is high, and the rapid ice-off suggests that these resources become available in distinct pulses. By studying Arctic char feeding ecology in relation to this important, but fleeting prey pulse, my objectives were to 1) assess the degree of relative consumption during summer feeding, 2) quantify the importance of specific prey taxa to char diets, and 3) evaluate factors related to within and among year variability in diet.

3.2 Methods

3.2.1 Fish Capture and Stomach Content Removal
Arctic char were collected in Tremblay Sound (72.357089, -81.107421) at the Ecosystem Approach to Tremblay Sound (EAT) field camp using ~15 cm mesh gillnets between July and September in 2017, 2018, and 2019. To understand temperature conditions near the location of capture, a temperature logger (HOBO UTBI-001 TidbiT version 1.09; Onset Computer Corporation; Bourne, MA, USA) was placed on a nearby fyke net in 2019. Once captured, all char were measured for mass and total length (TL). Additionally, a Fulton’s condition factor \( K = 100 \frac{W}{L^3} \) (where \( W \) = weight and \( L \) = length; Ricker 1975) was calculated for each fish.

Captured char were then dissected and their stomachs were removed. All capture and dissection methods were approved by the University of Windsor (AUPP:#17-12) and the University of New Hampshire (IACUC:#180602). Stomach processing differed slightly by year. In 2017, stomach contents were identified in the field, but only the present taxa were recorded. In 2018, whole stomachs were frozen in WHIRL-PAK bags (ULINE; Pleasant Prairie, WI, USA) for sorting at a later date. In 2019, stomach contents were removed from the stomach prior to freezing. In addition to a full stomach weight, 2019 stomachs were also weighed without content.

After 2018 and 2019 field seasons, samples were transported to the University of Windsor (Windsor, Ontario, Canada). In the lab, 2018 stomachs were thawed and then stomach contents were removed. The collective mass of all stomach contents was measured. Stomach contents were then sorted to the lowest taxonomic level, and each taxa present was enumerated and massed. Unfortunately, 2019 stomach contents were not quantified due to COVID-19-related travel restrictions between the United States and Canada.

3.2.2 Relative Consumption and Diet Composition
Relative consumption was measured as the percentage of total bodyweight occupied by stomach contents. Total stomach content mass was either calculated as the sum of all diet items (2018) or the difference between the mass of the full stomach and empty stomach (2019). The total stomach content mass was then divided by fish mass to obtain relative consumption.

Frequency of occurrence of each prey type (lowest taxonomic level) was calculated for each year as the proportion of char stomachs that contained any of the given prey categories. These values could only be calculated for 2017 and 2018 data, as 2019 samples were not assessed due to COVID-19. The contributions of prey items were also quantified using percent abundance both numerically and by mass for each year (Hyslop 1980). Numeric abundance of a prey type was calculated as the numeric frequency of a given taxa divided by the total number of organisms among all diet samples in a given year. Percent mass was calculated in a similar fashion. Both metrics were also calculated for each individual char.

### 3.2.3 Analyses

To investigate differences in the biological characteristics (TL and mass) of sampled char among years, ANOVA tests were conducted with either TL or mass as the response variables and year as an explanatory variable. Multiple comparisons were conducted using a Tukey’s honestly significant difference test. An alpha level of 0.05 was used to determine significance of all ANOVA and Tukey tests. All tests and post-hoc analyses were conducted in R (Version 3.6.2; R Core Team 2019). To assess temporal differences in relative char abundance, catch per unit effort (CPUE) was determined for 2018 and 2019, and was calculated as the number of char captured per hour for each gear deployment. CPUE could not be calculated prior to July 28th, 2018 due to missing effort data. Temporal differences (among years and across days of the year)
in CPUE were evaluated using a generalized linear model (GLM). First, a global model included CPUE as the response variable, with year and Julian day as explanatory variables. All subsets regression model selection was performed, with models ranked via Akaike Information Criterion for small sample sizes (AICc) using the ‘dredge’ function in the ‘MuMin’ (Bartoń 2019) package in R (R Core Team 2019). The model with the lowest AICc was selected as the best fit model.

To assess variability in feeding rates among years, a t-test was performed with relative consumption as the response variable and year as an explanatory variable. An alpha value of 0.05 was used to determine significance of the t-test. To determine important predictors of relative consumption within years, a single generalized linear mixed model (GLMM) was created using the ‘lmerTest’ package (Kuznetsova et al. 2017) in R (R Core Team 2019). The global model included relative consumption as the response variable, with month and char mass as explanatory variables. Year was entered into the model as a random effect to account for the effects of interannual variability within the model. All-subsets regression model selection was performed, with models ranked via Akaike Information Criterion for small sample sizes (AICc) using the ‘dredge’ function in the ‘MuMIn’ package (Bartoń 2019) in R (R Core Team 2019). The model with the lowest AICc was selected as the most parsimonious model. The likelihood (weight) of each model was also examined and was calculated as: \( W_i = e^{-0.5*\Delta \text{AICc}} \cdot \sum (e^{-0.5*\Delta \text{AICc}})^{-1} \), where \( W_i \) is equal to the weight of a model.

Non-metric Multidimensional Scaling (NMDS) ordination was used to assess variability among char diet samples. Presence-absence data for prey types found in > 5% of stomachs (among years) were input into the ordination, which used a Bray–Curtis distance measure and was created using the vegan package (Oksanen et al. 2019) in R (R Core Team 2019). Stress values (the goodness-of-fit between data and ordination) were investigated to choose the fewest
number of dimensions necessary to appropriately report the data. To detect variability in prey community among years, multiple response permutation procedure (MRPP) was used with year as an explanatory variable. Subsequent indicator species analysis (ISA) was conducted to assess which prey items were potentially responsible for differences highlighted in the MRPP analysis. Within year variability was investigated by creating separate NMDS ordinations for both years (2017 and 2018). Ordination axes were related to variables of interest using further MRPP tests for categorical variables (year, week, and fortnight) and penalized spline regression for continuous variables (TL and mass). An alpha level of 0.05 was used to determine significance for all tests (i.e., MRPP, ISA, penalized spline regression).

3.3 Results

Ninety-one char were sampled among the three years of the study (Table 3.1). One stomach from a char captured in 2018 was lost during storage, and its stomach content was not analyzed. The average TL and mass of all fish was 62.2 cm (SE = 1.67 cm) and 2.6 kg (SE = 0.2 kg) respectively. The TL of sampled fish differed significantly among years (ANOVA; $F_{(2,85)} = 7.103; P = 0.001$). Fish captured in 2018 were the largest (mean = 70.1 cm, SE = 3.48 cm) and were ~15 cm larger than 2017 fish (mean = 55.4 cm, SE = 2.83 cm; $P = 0.001$; Table 3.1; Figure 3.1). Individuals from 2017 were the smallest and were ~9 cm smaller than 2019 fish (mean = 64.2 cm, SE = 1.67 cm; $P = 0.046$), which were of an intermediate size (Table 3.1; Figure 3.1).

Although there was not a significant difference in length between 2019 and 2018 fish ($P = 0.34$), 2018 fish were ~6 cm larger (Table 3.1; Figure 3.1).

There were similar differences in fish mass among years (ANOVA; $F_{(2,85)} = 6.737; P = 0.002$). The largest fish were captured in 2018 (mean = 3.19 kg, SE = 0.4 kg) and were ~1 kg heavier than 2017 fish (mean = 1.96 kg, SE = 0.2 kg; $P = 0.005$), which were the lightest.
captured in 2019 (mean = 2.97 kg, SE = 0.2 kg) were also ~1 kg heavier than 2017 fish ($P = 0.01$). Fish from 2018 were only 0.22 kg heavier than 2019 fish, which was not significant ($P = 0.84$). Fulton’s condition factor also significantly differed among years (ANOVA; $F_{(2,83)} = 48.29; P < 0.001$) with the highest conditioned fish observed in 2019 (mean = 1.06, SE = 0.02) and less conditioned fish in 2018 (mean = 0.79, SE = 0.03) and 2017 (mean = 0.86, SE = 0.03; Table 3.1; Figure 3.1). Fish condition differed significantly between 2019 and 2017 fish ($P < 0.001$) and between 2019 and 2018 fish ($P < 0.001$). CPUE of char were explained by Julian day and year variables, along with their interaction (Table 3.2). Pooled across both years, CPUE decreased by 0.05 char/hour each day, but decreased much quicker (-0.24 char/hour each day) in 2019 (Figure 3.2). Average catch per unit effort in 2019 (0.96 char/hour) was double that of 2018 (0.51; Table 3.1), however peak CPUE was higher in 2018 (2.92 char/hour) than 2019 (1.86 char/hour). For the 11 days that the temperature logger was deployed in 2019, average daily temperature ranged from 8.1 °C to 9.81 °C.

Relative consumption was calculated for 54 char (from 2018 and 2019) and varied significantly between years (t-test; $t = -3.74$; df = 46.8; $P < 0.001$; Figure 3.3). Consumption in 2019 (mean = 2.42%) was more than double that of 2018 (mean = 1.15%; Figure 3.3). Although consumption was not quantified in 2017, only two char (~5.4%) had completely empty stomachs. Similarly, only one char captured in 2019 (~3.2%) had a completely empty stomach, with the highest relative consumption (4.63%) recorded just three days prior. GLMMs revealed that month and char mass were not strong predictors of relative consumption, with an intercept-only model (with year as a random effect) resulting in the lowest AICc (Table 3.2) and 58.7% of the AICc weight. However, month was included in the second-ranked model that contained the remaining 41.3% of AICc weight (Table 3.2).
Prey taxa information was collected from 59 individuals (37 in 2017 and 22 in 2018). The number of unique prey items was consistent between 2017 and 2018 with eight unique and identifiable prey items found in stomachs in both years (Table 3.3; Figure 3.4). Prey items included copepods, multiple species of amphipods and fish, krill, and jellyfish (Table 3.3). Although the types of prey remained consistent between years, the frequency of occurrence of some prey items changed between years (Table 3.3; Figure 3.4). For example, *Onisimus spp.* amphipods were found in 21.6% of stomachs in 2017 but occurred in 77.3% of stomachs in 2018 (Table 3.3). In contrast, Arctic cod was found in 24.3% of stomachs in 2017 and only 4.5% of stomachs in 2018 (Table 3.3). With the exception of copepods (29.7% in 2017 and 13.6% in 2018), the frequency of occurrence of the remaining taxa did not change by more than 9% between years (Table 3.3).

In 2018, the only year prey type, abundance, and mass data are available, *Onisimus sp.* was the most numerically abundant (66.1%) prey among all char (Figure 3.5). Krill comprised 30.1% of samples by number, and *Gammarus sp.* added an additional 2.6% (Figure 3.5). All other prey types combined accounted for < 2% of the overall numeric abundance. It is important to note that the number of copepods, unidentified amphipods, and other unidentified organisms could not be counted due to the poor condition of samples. As such, these taxa could have represented a significant proportion of abundance. However, *Onisimus spp.* was also the most abundant organism by mass (47.5%; Figure 3.4). Arctic cod accounted for 15.5% by mass, followed by unidentified amphipods (11.9%), sand lance (8.6%), unidentified organisms (6.4%), krill (5.2%), copepods (2.2%), and *Gammarus spp.* (1.3%) (Figure 3.5). All other prey items combined accounted for < 2% of the overall abundance by mass.
When calculating the numeric abundance of prey items among individual fish in 2018, *Gammaracanthus spp.* made up the smallest percent number (mean = 13.6%, SE = 11.4) while *Onisimus spp.* represented the largest (mean = 63.8%, SE = 8.72; Table 3.3). Arctic cod was only found in one stomach, and that species was the only identifiable prey present, so it represented 100% of the numeric abundance for that individual char (Table 3.3). Krill accounted for an average numeric abundance of 62.6% (SE = 13.8), and jellyfish 40.5% (SE = 32.2). The only other identified fish species (sand lance) occupied an average numeric abundance of 44.5% (SE = 29.4), and other unidentified fish occupied an average of 41.4% (SE = 22.2). The other identified amphipod (*Gammarus spp.*) occupied 15.4% (SE = 5.52) of the average numeric abundance. This breakdown was slightly different when considering mean percent mass. Copepods made up the largest percent mass (mean = 93%, SE = 7.01), followed by unidentified organisms (mean = 69.6%, SE = 9.02) and sand lance (mean = 68.3%, SE = 30; Table 3.3). Arctic cod made up 56.6% (SE = 0) of the mean percent mass, followed by jellyfish (mean = 50.8%, SE = 45.6), unidentified amphipods (mean = 43.4%, SE = 0), krill (41.5%, SE = 14.2), and *Onisimus spp.* (mean = 31.7%, SE = 8.41; Table 3.3). *Gammaracanthus spp.* accounted for 16.3% (SE = 8.39) of the percent mass with unidentified fish contributing 14.4% (SE = 10.9) and *Gammarus spp.* with 8.35% (SE = 3.61).

The two-dimensional NMDS ordination was chosen as it provided ease of interpretation and an adequate stress level (0.088). Diet samples (presence/absence data of each prey type within stomachs) significantly differed between 2017 and 2018 (MRPP; *P* < 0.001; Figure 3.6). Indicator species analysis suggested that an increased abundance of Arctic cod (ISA; *P* = 0.01) and unidentified amphipods (ISA; *P* = 0.02) in stomachs was responsible for the differences in 2017, while the presence of *Onisimus spp.* (ISA; *P* < 0.001) was responsible for differences in
2018 (Figure 3.6). Since the MRPP of the ordination that included both years suggested that year was significant, the remaining variables were analyzed separately for each year. Total length was a significant predictor of diet samples in 2018 (penalized spline regression; $F = 1.081; P = 0.04$; Figure 3.7), but not in 2017 (penalized spline regression; $F = 0.197; P = 0.26$). The significant relationship appears to be largely based off of one small (41.4 cm) char that consumed krill, copepods and fish (Figure 3.7). None of the other explanatory variables (mass, ice concentration, week, and fortnight) input into either an MRPP or penalized spline regression were significant.

3.4 Discussion

Char body size and condition varied across the three-year study. The differences in TL and mass may indicate the presence of multiple char populations, which has been suggested previously in the Tremblay Sound area (Chapter 2). However, there are other potential explanations for these differences in size and condition. For example, size differences could be representative of multiple age-classes from the same population of char (i.e., presence of different age-classes, sampling effects, etc.). Differences in condition were more apparent among years. Mean Fulton’s condition factor was below one in 2017 (mean = 0.86) and 2018 (mean = 0.79) and above one in 2019 (mean = 1.06). Anadromous Arctic char are thought to fast throughout the winter, depending on the energy reserves gained during summer feeding for survival (Jobling et al. 1993, Jørgensen et al. 2013, Jensen et al. 2018). Thus, compared to the emaciated nature of seaward migrating Arctic char, high condition is expected during and after marine feeding and indicates the importance of this phase to char life history. As such, differences in fish condition may be related to the timing of sample collection among years, with samples collected later likely having a higher condition. Fish from 2017 and 2019 were captured late in the season (August 7th – August 15th) and exhibited higher condition than 2018 fish,
which were captured earlier (July 28th – August 8th). Differences in condition among years may also relate to the abundance and quality of prey types available during the annual prey pulse and might explain why condition was higher in 2019 compared to 2017 despite samples being collected at similar times of the year.

Changes in char CPUE may be related to variations in the prey pulse. CPUE had a negative relationship with Julian day, suggesting that more char utilized the system early in the ice-free season as opposed to the end of the ice-free season. Anadromous Arctic char typically enter Arctic marine systems in June or July (Gyselman 1984, Bégout Anras et al. 1999, Spares et al. 2015, Moore et al. 2016) so variations in CPUE align with migratory phenologies elsewhere and in Tremblay Sound (Chapter 2). Similarly, the decline in CPUE towards the end of the summer likely corresponds to a decrease in food availability and a reduction in the overall benefits of marine residence. Average CPUE in 2019 was double that of 2018, which may indicate a more productive system or a prolonged prey pulse in 2019. However, it is more likely that time and duration of sampling had an effect on average CPUE. CPUE in 2019 was only calculated over a period of 10 days during the middle of char residence (Chapter 2). In contrast, 2018 CPUE was calculated for a five-week period, with half of the data obtained a week after the average outmigration date (August 8th) for char in Tremblay Sound that year (Chapter 2). Thus, low abundance after August 8th likely lowered the average CPUE of 2018 data compared to 2019. In fact, peak CPUE was actually higher in 2018 (2.92) than in 2019 (1.86). However, CPUE in both years may not represent maximum abundance as both years did not include many early measurements in June or July when abundance (and thus CPUE) may have been higher.

Arctic char in Tremblay Sound are capable of consuming over four percent of their bodyweight (mean = 1.92%), which is higher than previously reported values (max of 1.1% in
Amundsen & Klemetsen 1988; mean of 1.56% in Rikardsen & Amundsen 2005). The low levels of relative consumption in Amundsen & Klemetsen (1988) may be related to low food availability, as the population focused on in that study exhibited stunted growth (Amundsen & Klemetsen 1988). Rikardsen & Amundsen (2005) described food availability as high in their study system, although the relative difficulties of capturing fish prey in the pelagic zone (as opposed to more stationary, benthic prey in bay or sound) may have accounted for the low relative consumption in that study (Rikardsen & Amundsen 2005). Additionally, char in the current study exhibited a small proportion of empty stomachs (3.3%). A similar value (3.4%) was observed for char in Spares et al. (2012), but much higher frequencies are common in char (11%; Malmquist et al. 1992, 11%; Rikardsen & Amundsen 2005; Spares et al. 2012), and across fishes generally (Arrington et al. 2002). The rarity of empty stomachs combined with high relative consumption confirms that feeding occurs at high rates in Tremblay Sound.

Although relative consumption in Arctic char (mean = 1.92%) was not as high as observed in the closely related bull trout (mean = 3.5%; Furey et al. 2015, 2016), it is likely that at least some of these fish are binge-feeding. Bull trout in Furey et al. (2015) were captured near a government-run counting fence that concentrates migrating sockeye salmon (*Oncorhynchus nerka*) smolts, which may have provided ideal conditions for binge-feeding (Furey et al. 2016). Furthermore, large fish typically consume less food in one sitting relative to their body size (Budy & Luecke 2014), and the majority of the fish captured in the current study were slightly larger (mean = 66.7 cm) than those in Furey et al. (mean = 62.6 cm; Furey et al. 2015), and thus, relative consumption values in the current study might still represent binge-feeding. Assessing whether a fish is binge-feeding is straightforward if a bioenergetics model has been parameterized for the species, such as for bull trout (Mesa et al. 2013). Unfortunately, the
development of such models is resource intensive and generally requires laboratory experiments, which is difficult or unfeasible for fishes living in remote ecosystems such as Arctic char. In addition to bioenergetic investigations, further research could identify if char exhibit other physiological adaptations to maximize feeding rates, such as the ability to seasonally regulate digestive capacity to exploit abundant resources (Armstrong & Bond 2013). This phenomenon exists in a closely related char, the Dolly Varden (Armstrong & Bond 2013) and is likely important for other cold-water fishes such as Arctic char that experience temperature-dependent constraints on consumption and digestion (Thornton & Lessem 1978, Sweka et al. 2004). Regardless, it is beneficial for fishes to exhibit an increased digestive capacity, particularly in regions that experience dramatic prey pulses (Armstrong & Schindler 2011). While these adaptations have not been investigated in Arctic char, it is possible that char possess such them.

In addition to eating a high quantity of food, char also consumed a wide range of prey taxa. In general, the most important prey taxa included copepods, amphipods, krill, and fish. Arctic char are opportunists, feeding on a wide variety of prey species (Johnson 1980, Amundsen & Klemetsen 1988), and that is reflected in Tremblay Sound char; their diet at sea is likely based upon what is available in the system, and is therefore location-specific. For example, studies in other systems have found fish (Rikardsen & Amundsen 2005), or crustaceans (Rikardsen et al. 2000, Spares et al. 2012) to be the dominant prey species, while others have found a mix of prey species to be important (Dempson et al. 2002).

Variability in annual sea-ice conditions is likely important in determining what char consume and at what rates. Sea-ice dynamics drive ecosystem processes in the Arctic and changes in ice dynamics can be reflected in the prey population (Melnikov 1997, McMeans et al. 2015). Ice conditions differed among years in Tremblay Sound, particularly between 2018 and
2019 and are reflected in the approximate ice-off start dates among years (July 3rd 2017, July 2nd 2018, June 28th 2019; see Chapter 2). Based on observation, ice-off occurred early in 2019, and the weather was warm and sunny. In contrast, 2018 was cold and although ice-off began on July 2nd 2018, northerly winds blew sea-ice into Tremblay Sound, covering much of the area by the end of July, and remained for about two weeks until ~August 10th. Although models relating consumption and diet to ice concentrations did not show any correlation, the effect of year is likely related to changes in annual ice conditions. There were marked dissimilarities in the relative amounts of prey consumed between years, particularly for *Onisimus spp.* and Arctic cod. For example, in 2017, Arctic cod were found in one quarter of char stomachs, while in 2018, cod were only found in 4% of diets. In contrast, *Onisimus spp.* was found in only 20% of stomachs in 2017 but almost 80% of stomachs in 2018. *Onisimus spp.* are ice-associated amphipods (Gradinger & Bluhm 2004) so their increased occurrence in stomachs in 2018 may be due to the additional ice present in Tremblay Sound during that summer. Although it is unclear why Arctic cod were less abundant in 2018, their absence might be related to low numbers of narwhal within Tremblay Sound in that year (L.J. Hammer, personal observation, Bradstreet & Cross 1982). As the Arctic summer becomes increasingly ice-free, char may switch to a more piscivorous diet community based on prey availability.

Total length was a significant predictor of diet community in 2018. It appeared that large char fed upon larger organisms (fish and amphipods) than small char (copepods). However, this result was marginally statistically significant, and largely based on one small (41.4 cm) char that ate fish, copepods, and krill. The importance of larger prey increasing with predator size is not unusual in char (Moore & Moore 1974, Dempson et al. 2002). Although a similar trend was observed in this study, the lack of strong significance cautions interpretations. The majority of
char captured in 2018 were between 60 cm and 90 cm TL, with only two individuals below ~55 cm. It is unlikely that prey preference changed drastically at sizes larger than ~50 cm because gape width is not limiting. Moore & Moore (1974) determined that as char grow from 4 cm to 85 cm, the minimum prey size only increases 4-fold. Thus, much of the available food in 2018 (mostly small amphipods and krill) would have been accessible among size classes, and diet communities may not have shifted with fish size in any substantial way.

Apart from differences associated with char TL, there was no evidence of within-year variability in diet community or relative consumption, likely due to the opportunistic feeding strategies of Arctic char (Johnson 1980, Amundsen & Klemetsen 1988) as well as their capacity to move. Char are quite mobile (e.g., Chapter 2), which could allow them to track prey pulses, or move to areas with abundant prey. Therefore, it is plausible that char exploit the most abundant prey items in the system and substantial deviations away from those items are rare. The lack of variability might also be explained by the limited temporal scope of samples collected during the study. In 2017 and 2018, all samples were collected within a period of 1.5 months, with samples collected across four subsequent days in 2019, and thus, only captured a small portion of char marine residency (late June to mid-August; Chapter 2). This is particularly important during the first few weeks of residency during which consumption may be higher (Amundsen & Klemetsen 1988, Berg & Berg 1989). Lack of sampling before mid-July limits our understanding of the importance of feeding during early marine residence. Thus, it is recommended that future studies intentionally spread sampling efforts across the entire residency period, with a large enough sample size to detect potential temporal (weekly, biweekly) differences in diet metrics. In addition, inconsistent methods were used among years in the current study. For example, consumption was not assessed in 2017 and the majority of prey items within stomachs were not
enumerated or massed. This prevented comparisons across the entire study period and limited analyses to two-year comparisons (2017–2018 or 2018–2019). Thus, consistency should be observed throughout data collection. However, it is important to maximize the amount of data collected, particularly in remote or challenging systems, so additional data can be included as new questions arise.

Analyses of diet were also limited by a high occurrence of unidentifiable items in char stomachs. At least one unidentifiable organism (i.e., Unidentified, Unidentified amphipods, and Unidentified Fish) was present in ~70.3% of stomachs in 2017 and in ~72.7% of 2018 stomachs. The high number of unidentifiable organisms in 2018 was partially due to the storage method, by which stomach contents were stored inside the stomach, leading to additional degradation after storage. Difficulty in visual identification of digested taxa is widespread across diet studies regardless of storage method. Genetic techniques have emerged as a reliable method of diet identification (Symondson 2002) and are more precise than visual inspection, even when prey items have lost all physical characteristics (Carreon-Martinez et al. 2011). Thus, combining visual assessment with genetic methods to identify stomach contents is recommended when logistically possible.

This study investigates the feeding behavior and diet of anadromous Arctic char in Tremblay Sound, with high levels of relative consumption demonstrating the importance of ephemeral prey pulses that occur during and after summer ice-off in the Arctic. Summer feeding opportunities likely provide the bulk of the annual energetic budget of Arctic char (Swanson et al. 2011) and thus, these resources are directly related to overwinter survival (Jensen et al. 2018). However, climate change is shifting the Arctic towards an entirely ice-free summer (Wang & Overland 2012, Overland & Wang 2013) with implications for predator-prey dynamics. In an
ice-free Arctic, Arctic char might shift away from sympagic prey items toward pelagic or benthic taxa if migration (and thus marine feeding) remains at all beneficial to them (Gross et al. 1988, Reist et al. 2006a). Overall, this study provides insight into the importance of marine feeding for Arctic char, how annual variability in environmental conditions influences this stage, and implications for future Arctic change.
### 3.5 Tables

Table 3.1. Summary information for all fish dissected during the study. Values to the right of the ± sign indicate standard error. Numbers within parentheses represent minimum and maximum values in that order. An NA represents values that were not calculated or assessed.

<table>
<thead>
<tr>
<th></th>
<th>Year</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>2017</td>
<td>2018</td>
<td>2019</td>
</tr>
<tr>
<td>Number of char sampled</td>
<td>37</td>
<td>23</td>
<td>31</td>
</tr>
<tr>
<td>Avg TL (cm)</td>
<td>55.4 ± 2.8</td>
<td>70.1 ± 3.5</td>
<td>64.2 ± 1.7</td>
</tr>
<tr>
<td></td>
<td>(16.0 – 81.3)</td>
<td>(16.4 – 90.8)</td>
<td>(42.4 – 80.2)</td>
</tr>
<tr>
<td>Avg mass (kg)</td>
<td>1.96 ± 0.2</td>
<td>3.2 ± 0.37</td>
<td>3.0 ± 0.20</td>
</tr>
<tr>
<td></td>
<td>(0.008 – 5.6)</td>
<td>(0.03 – 6.6)</td>
<td>(0.7 – 5.1)</td>
</tr>
<tr>
<td>Fulton’s Condition Factor</td>
<td>0.86 ± 0.03</td>
<td>0.79 ± 0.03</td>
<td>1.06 ± 0.02</td>
</tr>
<tr>
<td></td>
<td>(0.02 – 1.09)</td>
<td>(0.60 – 1.15)</td>
<td>(0.90 – 1.25)</td>
</tr>
<tr>
<td>Avg diet contribution to body mass</td>
<td>NA</td>
<td>1.15% ± 0.22</td>
<td>2.42% ± 0.24</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(0.06% – 3.13%)</td>
<td>(0% – 4.63%)</td>
</tr>
<tr>
<td>Catch per unit effort</td>
<td>NA</td>
<td>0.51 ± 0.13</td>
<td>0.96 ± 0.25</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(0 – 2.9)</td>
<td>(0 – 1.86)</td>
</tr>
</tbody>
</table>
Table 3.2. GLM and GLMM models of CPUE and relative consumption (response variables) of Arctic char. The best-fit model (determined via best subsets regression) is shown in bold, with additional models with model weight ($W_i$) ≥ 0.10 shown below. Marginal ($R^2_m$) and conditional ($R^2_c$) coefficients of determination are shown for the best-fit model.

<table>
<thead>
<tr>
<th>Model</th>
<th>Loglik</th>
<th>AICc</th>
<th>$W_i$</th>
<th>$R^2_m$</th>
<th>$R^2_c$</th>
</tr>
</thead>
<tbody>
<tr>
<td>CPUE ~ Day * Year</td>
<td>-30.306</td>
<td>72.3</td>
<td>0.531</td>
<td>0.57</td>
<td>0.57</td>
</tr>
<tr>
<td>CPUE ~ Day</td>
<td>-33.208</td>
<td>73</td>
<td>0.362</td>
<td>0.52</td>
<td>0.52</td>
</tr>
<tr>
<td>CPUE ~ Day + Year</td>
<td>-33.196</td>
<td>75.5</td>
<td>0.108</td>
<td>0.51</td>
<td>0.51</td>
</tr>
<tr>
<td>Relative Consumption ~</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intercept + (1</td>
<td>Year)</td>
<td>-85.196</td>
<td>176.9</td>
<td>0.587</td>
<td>0.03</td>
</tr>
<tr>
<td>Relative Consumption ~</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Month + (1</td>
<td>Year)</td>
<td>-84.369</td>
<td>177.6</td>
<td>0.413</td>
<td>0.02</td>
</tr>
</tbody>
</table>
Table 3.3. The number of char stomachs containing each observed taxa in 2017 and 2018. Percentages in the third and fifth columns indicate frequency of occurrence. The sixth and seventh columns represent numeric abundance and average percent mass of each observed taxa in 2018. Values are calculated for each individual and averaged among individuals. Numbers in parentheses indicate standard error and NA’s indicate values which could not be calculated.

<table>
<thead>
<tr>
<th>Taxa</th>
<th>2017 (n = 37)</th>
<th>2018 (n = 22)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Number of Stomachs</td>
<td>Frequency of Occurrence</td>
</tr>
<tr>
<td>Copepods</td>
<td>11</td>
<td>29.7%</td>
</tr>
<tr>
<td>Onisimus spp.</td>
<td>8</td>
<td>21.6%</td>
</tr>
<tr>
<td>Gammarus spp.</td>
<td>6</td>
<td>16.2%</td>
</tr>
<tr>
<td>Gammaracanthis spp.</td>
<td>1</td>
<td>2.7%</td>
</tr>
<tr>
<td>Unidentified amphipods</td>
<td>13</td>
<td>35.1%</td>
</tr>
<tr>
<td>Krill</td>
<td>9</td>
<td>24.3%</td>
</tr>
<tr>
<td>Jellyfish</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Sand Lance</td>
<td>2</td>
<td>5.4%</td>
</tr>
<tr>
<td>Arctic cod</td>
<td>9</td>
<td>24.3%</td>
</tr>
<tr>
<td>Unidentified fish</td>
<td>8</td>
<td>21.6%</td>
</tr>
<tr>
<td>Unidentified</td>
<td>6</td>
<td>16.2%</td>
</tr>
</tbody>
</table>
3.6 Figures

Figure 3.1. Biological characteristics (TL, mass, and condition) of Arctic char caught among years. Each point represents an individual fish. Mid lines in each boxplot represent median values and the hinges represent the first and third (25th and 75th) percentiles. Whiskers extend 1.5 * the interquartile range from each hinge. The endpoints on the lines above represent the groups compared using Tukey’s honestly significant difference tests, and the asterisks indicate level of significance (* = < 0.05, ** = < 0.01, *** = < 0.001).
Figure 3.2. The number of char diet samples collected per day across the three years of the study (left) and catch per unit effort measurements by day of the year (right). Dots indicate single sampling events and are colored by year. Lines indicate predicted CPUE values. No CPUE data are available for the 2017 season.
Figure 3.3. Boxplots of relative consumption (percent body weight consumed) between years. Each dot represents an individual stomach. Midlines indicate median values, hinges indicate the first and third (25th and 75th) percentiles, and whiskers extend to 1.5-times the interquartile range from each hinge. Asterisks indicates the level of significance (** = < 0.001).
Figure 3.4. Frequency of occurrence of all taxa found within char stomachs. Bars are colored by year, and yearly sample sizes are shown within the legend. The “Unidentified Amphipods” and “Unidentified Fish” columns represent the frequency of occurrence of unidentified species in those groups.
Figure 3.5. The abundance both numerically and by mass of each taxa among all Arctic char stomach samples in 2018. Portions of each bar are colored by taxa. Percentage values have been added for diet items that make up > 2% of either the abundance or mass of all samples. Categories that constitute < 2% in numeric abundance include: Arctic cod, copepods, fish, *Gammaracanthus* spp., jellyfish, sand lance, and unidentified organisms. Unidentified fish, jellyfish, *Gammaracanthus* spp., and *Gammarus* spp. individually contribute to < 2% by mass.
Figure 3.6. A two-dimensional NMDS ordination showing the relationship between the year of capture and the ordination of Arctic char stomach samples. Circles represent prey communities of individual char and are colored by year. The ellipses indicate 95% confidence intervals for prey communities in either year. Lines indicate the influence of specific taxa on the ordination, with only the important taxa (identified by indicator species analysis) highlighted for each year. Percentages on the axes indicate the amount of variance explained by each axis.
Figure 3.7. A two-dimensional NMDS ordination for the 2018 Arctic char diets showing the relationship between char TL and the ordination of samples. Circles indicate individual diets and text indicates the directionality contributed to the ordination by each taxa. The size of circles indicates the length of fish, with larger circles representing larger fish.
CHAPTER 4: Conclusion

The seasonal migrations of anadromous Arctic char to marine feeding habitats are important for growth and survival (Gyselman 1984, Jensen et al. 2018). In fact, marine prey can account for up to 91% of char diets (Swanson et al. 2011). The success of both spawning events and overwintering depends on the energy gained from these feeding endeavors. Broadly, my thesis combines movement and diet information in order to improve our understanding of Arctic char ecology during the ice-free summer, particularly in relation to resource pulses.

This work identified the importance of the annual summer ice-off to char ecology. Char consistently entered Tremblay Sound ~5-15 days before the start of ice-off (Chapter 2). Although this is not the first evidence of char migration preceding the ice-off (Grainger 1953, Moore 1975), this is the first study to couple char migration timing data with quantified sea ice data rather than just visual observations. However, the available ice data were coarse in spatial resolution - sufficient for quantifying sea ice in Tremblay Sound, but not in associated rivers or lakes. High-resolution ice cover data could provide important information related to migration timing relative to lake or river ice-off as well as migration duration (from overwintering location to sea and vice versa). To my knowledge, no such information has been quantified but is increasingly important in the Arctic as climate change continues to shift ice phenologies.

4.1 Shifting Phenologies

Shifting ice phenologies will likely have profound effects on char ecology. Earlier migration times have been observed in multiple salmonids (Kovach et al. 2013). Additionally,
the migrations of a closely related char (Dolly Varden; *Salvelinus malma*) have remained synchronized to annual prey pulses of Pacific salmon (*Oncorhynchus spp.*) despite substantial changes in prey migration timing (Sergeant et al. 2015). Thus, we might expect char populations to similarly match their movements to earlier ice-off and earlier prey pulses. In the current study, char arrived nine days earlier in 2019 than in 2018, despite only a four-day difference in ice-off date between years, suggesting that char may have matched their migration to changes in the ice-off date. Responses to phenological change may also be expressed in char diets. In Chapter 3, changes in the frequency of occurrence of *Onisimus spp.* amphipods and Arctic cod (*Boreogadus saida*) may have been related to changes in annual ice conditions when samples were collected. *Onisimus spp.* are ice associated amphipods, and these preferences may have been reflected in the diet content of char, with 2018 stomachs containing more *Onisimus spp.* while stomachs from 2017 contained more Arctic cod. Thus, as the amount of summer ice cover decreases, we might expect char to shift their diets toward Arctic cod and other fish prey and away from ice-associated amphipods. However at the very extreme, when the Arctic is completely ice-free (Wang & Overland 2012, Overland & Wang 2013) and terrestrial systems become more productive (Karlsson et al. 2005, Post et al. 2013), the benefits of migration (i.e. feeding) and thus the prevalence of anadromy in Arctic char might decrease (Gross et al. 1988, Reist et al. 2006b, Finstad & Hein 2012).

### 4.2 Adaptive Plasticity

Plasticity will likely be key in determining the effects of shifting phenologies on char populations. Some migratory species have changed mean migration dates by as little as six days earlier (since 1949 [as of 1993]; sockeye salmon; *Oncorhynchus nerka*; Quinn & Adams 1996), while other have shifted as much as 38 days earlier (since 1938 [as of 1993]; American shad;
Char can modify their migration timing in response to small changes in ice-off timing (Chapter 2; four day difference between 2018 and 2019), however, the first day of ice melt has been occurring three days earlier per decade since 1979 (Stroeve et al. 2014) and it is unclear to what degree char will be able to alter their migration phenology in response. Additionally, an earlier marine entrance will likely correspond with an earlier marine exit, with potential implications for return migrations. More specifically, earlier return migrations might expose char to suboptimal temperature and flow regimes that could present challenges to the success of the return migration (Gilbert et al. 2016, Gilbert & Tierney 2018).

If char can modify their migration timing to continually match the ice-off, they will likely be able to withstand changes in prey availability that correspond with an increasingly ice-free summer. Char are opportunistic feeders and have diet elasticity (Johnson 1980, Amundsen & Klemetsen 1988; Chapter 3). In addition, changes in diet composition may be mediated by similarities in the energetic quality of ingested taxa. For example, Onisimus spp. and Arctic cod are of similar energetic quality (Wolowicz & Szaniawska 1986, Britten Harter et al. 2013) so a switch from mainly Onisimus spp. to Arctic cod might not result in an overall loss of energy, provided that char are able to maintain consistent feeding rates and prey availability remains high. However, cod are likely harder to catch than amphipods and would require higher energy expenditure by char to capture them.

### 4.3 Feeding Rates and Binge-Feeding Ability

The arrival of char before the ice-off demonstrates the importance of exploiting the entire resource pulse for maximal energy gains. In this study (see Chapter 3), char fed at higher relative rates than observed in other char studies (Amundsen & Klemetsen 1988, Rikardsen & Amundsen
Similarly, the proportion of empty stomachs was low compared to other char studies (Malmquist et al. 1992, Rikardsen & Amundsen 2005) and across fishes globally (Arrington et al. 2002). These data provide further evidence that char are feeding at high rates, with important implications for energetics. Binge-feeding is the ability to consume well beyond normal daily consumption or what could theoretically be digested in a day (Furey et al. 2015, 2016). These adaptation are particularly important for organisms that experience intense, ephemeral feeding opportunities (Armstrong & Schindler 2011, Furey et al. 2015). Although char can eat large quantities of food, binge-feeding ability could not be assessed in this study due to the lack of a bioenergetics model, as has been developed for bull trout (Salvelinus confluentus; Mesa et al. 2013) and lake trout (Salvelinus namaycush; Stewart et al. 1983), thus, remaining a key knowledge gap for Arctic char. Further, it is important to quantify the proportion of the annual energy budget or growth of char that is attributed to the brief ice-off period. This information would establish an important baseline for char populations that could be integrated with climate models to assess the potential implications of future diet and phenology shifts to char energy budgets and growth. Similar information is particularly key for regions that experience pulsed resources, where marine prey make up the majority of char diets and high prey abundance may attract multiple populations of Arctic char.

### 4.4 Multiple Populations and Ontogenetic Shifts

Potential evidence exists of multiple Arctic char populations within Tremblay Sound or the possibility of ontogenetic shifts in migration behavior (Chapter 2). Population mixing in Arctic char is likely quite common (Moore et al. 2013), and the potential for ontogenetic shifts (certain age classes absent from natal rivers) in this species exists (Gilbert et al. 2016). However, we were unable to validate either pattern due to a lack of genetic evidence, which can provide
important insight into organisms with complex life histories (Shafer et al. 2016, Moore et al. 2017) and should be included in future studies where population interactions are suspected (Moore et al. 2017). Multiple populations and/or ontogenetic shifts likely not only impact movement, but also feeding; however, evaluating potential differences in diet based on migratory chronology was not possible in this study. Traditional stomach content analysis used in the current study captures short-term (days) diet information but gives no indication of food consumed in the weeks prior to capture. Such differences could have been evaluated with the inclusion of stable isotope data, which could have revealed additional diet information from the stomach and liver tissues.

Regardless of potential differences in stomach contents, both hypotheses (ontogenetic shifts and multiple populations) have far-reaching implications for fisheries management. Currently Arctic char fisheries throughout the Arctic are managed on a river-by-river basis under the assumption that each river supports a discrete stock (Kristofferson & Berkes 2005). Recently however, this assumption has been discredited by evidence of extensive stock mixing in marine and freshwater systems (Moore et al. 2013, 2017, Harris et al. 2016). Although char from the Pond Inlet area (Pond inlet, Nunavut, Canada) are not currently fished commercially, an emerging fishery is developing (Wong 2013, Martin et al. 2018, Tallman & Martin 2018), which will benefit from management plans that integrate interactions among populations and systems (Harris et al. 2016). Area-based management plans or quota transfer strategies show great utility for char populations in the Arctic (Harris et al. 2014, 2016).

4.5 Summary

Collectively, this thesis identified the importance of the ice-off transition and ice-free period to Arctic char in Tremblay Sound. My work highlights how seasonal ice conditions and
pulsed resources can shape the migration timing and residency duration of Arctic char in marine systems. Subsequent high rates of feeding suggest potential adaptations to a life of gorging and fasting (Armstrong & Schindler 2011). Future genetic work coupled with telemetry studies (see Moore et al. 2017) could elucidate whether multiple populations of char utilize Tremblay Sound or if char exhibit ontogenetic habitat shifts to other systems. An understanding of potential stock mixing within Tremblay Sound and the Pond Inlet area will be crucial in guiding the development of a sustainable commercial fishery in the region (Wong 2013, Martin et al. 2018, Tallman & Martin 2018). Further, as the climate continues to warm, long-term datasets monitoring migrations, prey communities, and annual climatic variability will become particularly important. These data can provide information to scientists and managers tasked with the conservation and management of important Arctic fishes in complex and ever-changing Arctic socio-ecological systems (Johnson et al. 2002, Huntington et al. 2007, Wang & Overland 2012, Overland & Wang 2013).
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Appendix A: IACUC Approval Letter

University of New Hampshire
Research Integrity Services, Service Building
51 College Road, Durham, NH 03824-3565
Fax: 603-862-3564

29-Jun-2018
Furey, Nathan P
Biological Sciences, Spaulding Hall
Durham, NH 03824

IACUC #: 180602
Project: Arctic Fish Ecology in Tremblay Sound
Approval Date: 19-Jun-2018

The Institutional Animal Care and Use Committee (IACUC) reviewed and approved the protocol submitted for this study under pain or distress category D - Animal use activities that involve accompanying pain or distress to the animals for which appropriate anesthetic, analgesic, tranquilizing drugs or other methods for relieving pain or distress are used.

Approval is granted for a period of three years from the approval date above. Continued approval throughout the three year period is contingent upon completion of annual reports on the use of animals. At the end of the three year approval period you may submit a new application and request for extension to continue this project. Requests for extension must be filed prior to the expiration of the original approval.

Please Note:
1. All cage, pen, or other animal identification records must include your IACUC # listed above.
2. Use of animals in research and instruction is approved contingent upon participation in the UNH Occupational Health Program for persons handling animals. Participation is mandatory for all principal investigators and their affiliated personnel, employees of the University and students alike. Information about the program, including forms, is available at http://unh.edu/research/occupational-health-program-animal-handlers.

If you have any questions, please contact either Dean Elder at 862-4629 or Julie Simpson at 862-2003.

For the IACUC,

[Signature]
Jessica Bolker, Ph.D.
Chair

cc: File