

Depth and temperature preference of anadromous Arctic char *Salvelinus alpinus* in the Kitikmeot Sea, a shallow and low-salinity area of the Canadian Arctic

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ABSTRACT: The Arctic climate is changing rapidly, yet predicting how aquatic species will respond to these changes remains challenging given the lack of empirical data for most high-latitude taxa. Acoustic telemetry has recently emerged as an important methodology for understanding horizontal and vertical space-use patterns in fishes. Here, we used acoustic telemetry to document marine habitat use and depth/temperature preference of 26 anadromous Arctic char *Salvelinus alpinus* within the Kitikmeot Sea region of the Canadian central Arctic over 4 yr (2013–2016). Most detections (~70 %) were within the top 3 m of the water column, and most were in estuarine (72.6 %) vs. marine (27.4 %) habitats. Arctic char preferred deeper waters later in the summer, but the temperature they occupied remained relatively constant throughout the marine feeding season (~5–8°C). Most Arctic char exhibited some degree of repetitive diving behavior, with individuals diving to 35 m. Diving activity increased later in the summer marine feeding season and is likely a response to the seasonal transition of their preferred prey to deeper waters as the season progresses. Finally, Arctic char preferred deeper waters with less ice cover and during the day, the latter suggesting potential diel patterns to marine habitat use. Finally, year-to-year variation in Arctic char depth and temperature use was very modest despite differences in climatic and ice conditions. This result suggests that habitat use is relatively fixed and may reflect their thermal and osmoregulatory physiology, which has important implications for forecasting the impacts of a changing Arctic on this economically valuable species.

KEY WORDS: Acoustic telemetry · Anadromy · Habitat use · Arctic char

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1. INTRODUCTION

Acoustic telemetry has emerged as a powerful tool for studying the environmental and biological drivers of fish habitat use while providing crucial data to managers tasked with understanding and mitigating the negative impacts of changing environmental con-

ditions on aquatic biota (Cooke et al. 2008, Hussey et al. 2015, Lennox et al. 2017). Anadromous salmonids are especially susceptible to the influences of a changing climate (Reist et al. 2006a,b), and studies incorporating acoustic telemetry have already contributed major advances to our collective understanding of the key drivers of habitat use and migrations in

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this group of fishes. For example, thermal and depth preferences during ocean migrations (Welch et al. 2014, Arostegui et al. 2017), the abiotic and biotic variables driving marine habitat use (Spares et al. 2012), the timing of anadromous migrations between marine and freshwater environments (Bégout Anras et al. 1999, Moore et al. 2016) and the overall spatial extent of marine habitat use (Spares et al. 2015, Moore et al. 2016) have all been documented through the use of acoustic telemetry. Understanding these aspects of fish biology and ecology have important management implications (Crossin et al. 2017) and provide the baselines necessary for assessing changes in aquatic populations and the ecosystems critical to their survival (Hussey et al. 2015).

The Arctic climate is changing faster than anywhere on the planet (Prowse et al. 2006, Pithan & Mauritsen 2014)—a phenomenon known as Arctic amplification (Serreze & Barry 2011), which has major consequences for biota at these latitudes (Post et al. 2009, Barry et al. 2013, Descamps et al. 2017). However, predicting how Arctic species will respond and adapt to these changes remains challenging given the paucity of long-term data sets that are critical for assessing and monitoring climate change impacts on high-latitude populations (Reist et al. 2006a,b, Dey et al. 2018). The anticipated climatic and environmental shifts in aquatic environments at northern latitudes will most notably include temperature increases across marine, estuarine and freshwater habitats as well as alterations to fluvial regimes (Jonsson & Jonsson 2009, Serreze & Barry 2011, Poesch et al. 2016). The impacts of Arctic climate change on the circumpolar Arctic char *Salvelinus alpinus* could be especially pronounced (Power et al. 2012, Connor et al. 2019), and they are widely considered a model species for monitoring responses to abiotic changes across the Arctic (e.g. Lehnherr et al. 2018). Behavioral modifications or adaptations are anticipated as warming waters will impact their migrations and survival (Reist et al. 2006b, Gilbert et al. 2016), but the ability of char to respond to rapid changes remains unclear. Throughout their range, anadromous Arctic char also contribute substantially to the Northern economies through commercial fisheries (Roux et al. 2011, 2019, Day & Harris 2013) and are vitally important to the culture, livelihood and food security of Arctic Indigenous peoples (Friesen 2002, Nuttall et al. 2005).

The anadromous migrations of high-latitude populations of Arctic char differ from those of other anadromous salmonids in several unique ways. After smolting, Arctic char undertake a downstream migration to

the marine environment in late-June/early-July typically around 7 yr of age (although a wide range of age-at-first-migration has been documented; Gyselman 1994, Gilbert et al. 2016, Harris et al. 2020). They spend the summer feeding in marine habitats (Moore et al. 2016), and unlike other anadromous salmonids at more southerly latitudes, they must return to fresh water every fall to overwinter in order to avoid sub-zero water temperatures of high-latitude marine waters (Dutil 1984, Klemetsen et al. 2003). Adult anadromous Arctic char are not suspected to feed when in fresh water, which means that they must accumulate their yearly energy reserve during the short summer marine feeding season: typically 30–45 d in high latitude populations, although as little as 6 d has been documented (Dutil 1986, Gyselman 1994, Moore et al. 2016). The marine phase is therefore crucial to the survival and production of this species, and even small variations in the summer climatic and environmental conditions have been shown to impact reproduction and growth (Dutil 1984, Power et al. 2000, Murdoch et al. 2015). Thus, understanding the ecology of anadromous Arctic char during the marine phase of their life cycle, including depths and temperatures preferred while at sea, is crucial for predicting how these fish will respond as climate change influences ocean waters (Tallman et al. 2013).

Depth preference of anadromous Arctic char in the marine environment is shaped by temperature, prey availability and salinity (Spares et al. 2012). In ectotherms, ambient temperature largely dictates all physiological rates (e.g. activity, metabolism, food consumption, digestion and growth), and these rates are limited at high and low temperature extremes (Fry 1947, 1971, Larsson et al. 2005, Farrell 2009). As such, Arctic char should preferentially select depths at which temperatures are optimal for these physiological processes (Jobling 1981, Farrell 2016). Evidence from laboratory studies suggests that preferred and optimal temperatures for growth in this species are between 11 and 18°C (Larsson & Berglund 1998, Larsson 2005, Larsson et al. 2005, Mortensen et al. 2007), but temperatures occupied in nature are lower (5–9°C; Rikardsen et al. 2007, Spares et al. 2012, Jensen et al. 2016), as is the optimal temperature for aerobic metabolic capacity (~7°C; Hansen et al. 2017). However, Arctic char can clearly maintain adequate physiological performance over much broader thermal ranges (Gilbert et al. 2016, Gilbert & Tierney 2018). In the Arctic marine environment, such temperatures (5–9°C) occur near the surface (<5 m), and we therefore expect Arctic

char to preferentially swim in that region (Bégout Anras et al. 1999, Rikardsen et al. 2007, Spares et al. 2012). As the temperature of marine surface water warms throughout the summer, we would also expect Arctic char to access and use deeper water as it warms to levels that permit higher metabolic capacity, activity levels and growth rates.

The spatial distribution of prey items is known to influence 3-dimensional habitat use in the marine environment (Dempson & Kristofferson 1987, Spares et al. 2012), and this is especially true for Arctic char that have a narrow temporal window for locating prey and foraging in marine habitats (Dutil 1982, Moore et al. 2016). Available data suggest that Arctic char feed on small fish (mostly Arctic cod *Boreogadus saida*, capelin *Mallotus villosus* and northern sand lance *Ammodytes dubius*) and zooplankton (e.g. amphipods [Amphipoda] and mysids [Mysidacea]; Dempson & Kristofferson 1987, Gyselman 1994, Dempson et al. 2002, Spares et al. 2012). Many marine prey items move to deeper waters after sea-ice melt and exhibit diel vertical migration (DVM) as the day–night cycle returns at higher latitudes (Benoit et al. 2010, Berge et al. 2014). Accordingly, the mean depth used by Arctic char in the region should increase as the summer feeding season progresses, and they should also display some degree of DVM as they track marine prey items throughout the summer feeding season.

Arctic char tend to be less salinity tolerant than most anadromous salmonids (Bystriansky et al. 2006) and can have impaired osmoregulation, feeding rate and growth at high salinities (35 ppt; Arnesen et al. 1993). As such, Arctic char may require longer, more gradual acclimation periods when transitioning from freshwater to seawater environments and vice versa (Bystriansky et al. 2006, 2007). Thus, we would anticipate estuarine use to be highest in Arctic char during the early- and late-season acclimation periods. Preference for estuarine habitats during the marine phase of Arctic char migrations has previously been documented (see Harwood & Babaluk 2014, Moore et al. 2016). While salinity is widely regarded as an important driver of estuarine use, estuaries also tend to be more productive and warmer (Thorpe 1994, Barbier et al. 2011), adding to their attractiveness. Arctic char typically enter the marine environment from fresh water immediately upon river ice break-up, but before the sea ice is entirely melted (Bégout Anras et al. 1999, Moore et al. 2016). Melting sea ice in the spring results in the formation of a lower-salinity meltwater layer at the surface (Rudels 2016), which may also be favorable to Arctic char (e.g. Spares et al. 2012). It can therefore also be predicted

that while this surface melt layer persists, Arctic char may have an affinity to surface water, as it would serve as a low-salinity refuge relative to the higher salinity waters at greater depths.

In this study, we aimed to characterize the environmental drivers of the vertical and horizontal distribution of Arctic char while at sea. We used acoustic telemetry to track 26 Arctic char throughout the duration of their summer marine migrations over 4 yr (2013–2016) in the Kitikmeot Sea near the community of Cambridge Bay on Southern Victoria Island, Nunavut, Canada (Fig. 1). This multi-year dataset offers an opportunity to understand how seasonal patterns in depth use are influenced by inter-annual variation in climatic and environmental variables (e.g. air temperature, marine water temperature, ice conditions). These data are combined with a description of the basic oceanography of the Kitikmeot Sea, a unique marine region of the Canadian Arctic characterized by shallow depth and low salinity. Our primary objective was to determine the relative importance of temperature, salinity and, indirectly, prey distribution (indirectly via the frequency of presumed foraging dives) in shaping patterns of depth preference and estuarine use. Our second objective was to describe how seasonal variation in habitat use and depth preference is influenced by inter-annual variation in average air and sea surface temperature (SST), sea ice melt date and timing of spring freshet. Together, these objectives will increase our understanding of the drivers of marine habitat use of Arctic char, and will contribute to predictions of the impacts of a changing climate on this species.

2. MATERIALS AND METHODS

2.1. Study area, fish capture and surgical implantation of tags

This work is part of an ongoing (2013–present) acoustic telemetry research program associated with the Ocean Tracking Network (Cooke et al. 2011) in the Cambridge Bay region of Nunavut. Detailed descriptions of the study area, fish capture and acoustic tagging are provided elsewhere (see Day & Harris 2013, Moore et al. 2016). Briefly, our study focused on the marine environment used by anadromous Arctic char inhabiting river systems near the community of Cambridge Bay, Nunavut, on southern Victoria Island (Fig. 1B). This area currently has 5 active commercial water bodies for Arctic char, the largest of which, the Ekalluk River, has an annual quota of

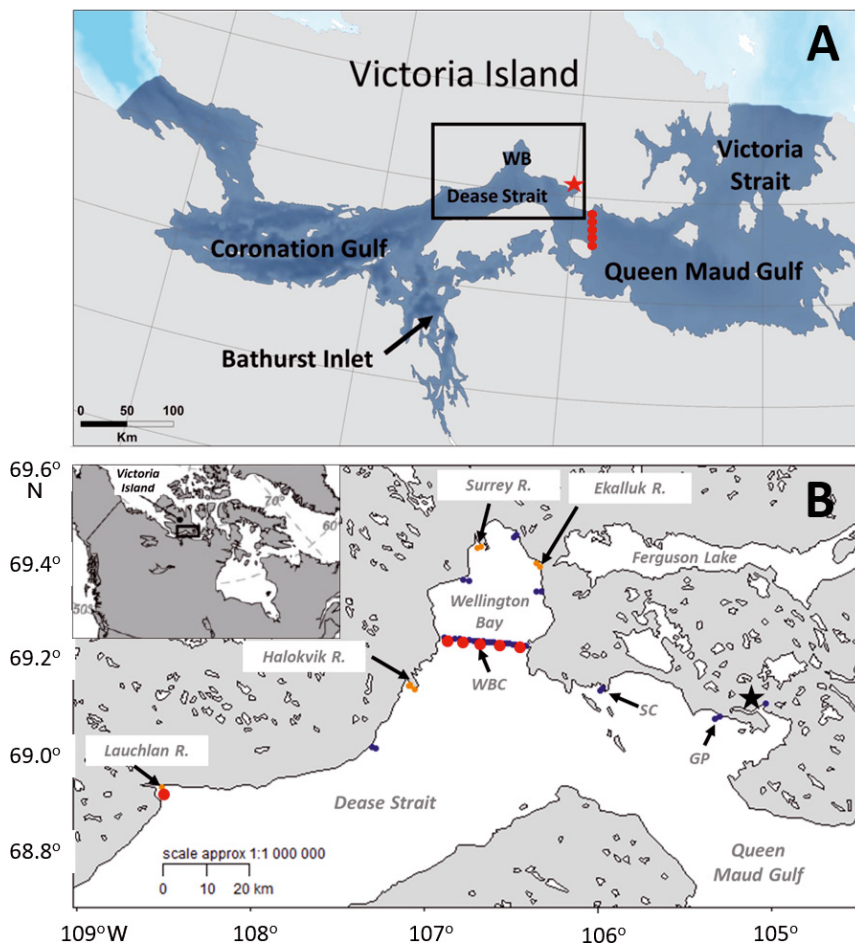


Fig. 1. (A) Kitikmeot Sea (dark blue) in context with our primary study area (black rectangle). The Kitikmeot Sea includes Coronation Gulf, Dease Strait, Bathurst Inlet, Queen Maud Gulf, Victoria Strait and Chantry Inlet (not shown). The community of Cambridge Bay, Nunavut (NU), is indicated by the red star. WB: Wellington Bay. The CTD sampling locations for the chlorophyll maxima assessment are shown with red circles. (B) Immediate study area on southern Victoria Island, NU. Yellow (estuary stations) and blue (marine stations) circles indicate the locations of the individual receivers used across all study years. Slight modifications to the design of the acoustic array in each year of the study are shown in Fig. S1. The four active commercial waterbodies within our study area are the Lauchlan, Halokvik, Surrey and Ekalluk Rivers. All Arctic char in this study were acoustically tagged at the Ekalluk River. Shown also are the Wellington Bay curtain (WBC) and the areas locally known as Starvation Cove (SC) and Gravel Pit (GP). Red circles indicate the oceanographic data collection locations along the WBC and in the Lauchlan River estuary.

The community of Cambridge Bay is indicated by the black star

20 000 kg (Day & Harris 2013). The Ekalluk River is located ~60 km northwest of the community of Cambridge Bay and drains an area of approximately 5835 km² including Ferguson Lake at the outlet, the largest lake on Victoria Island (Kristofferson 2002). This lake is thought to be especially important for overwintering Arctic char in the region from all Arctic char-bearing rivers (Moore et al. 2017).

This region located along the southwestern waterways of the Northwest Passage is unofficially referred to as the 'Kitikmeot Sea' by oceanographers. The Kitikmeot Sea is relatively shallow, with depths exceeding 300 m in Coronation Gulf and parts of Queen Maud Gulf, but rarely exceeding 100 m in the central Kitikmeot Sea near Cambridge Bay (Fig. 1A). It is bounded by sills (<30 m depth) to the west at Dolphin and Union Strait and to the north in Victoria Strait that restrict circulation of higher-salinity marine waters that are typically found in deeper channels of the Northwest Passage. At the same time, the Kitikmeot Sea is heavily influenced by river discharge, such as from those systems described above. As a result of restricted inflowing marine water and excessive river runoff, the Kitikmeot Sea has relatively low salinity throughout the water column (maximum of ~29 PSU at depth), especially near the surface (Bouchard et al. 2018). The lowest salinities are found near large river mouths (i.e. estuaries) and along the nearshore regions which are influenced by smaller rivers. Salinity typically increases offshore due to mixing with marine waters. These freshwater-marine interactions create a heavily stratified vertical structure in the region composed of warm, fresher water in a shallow layer (~10–30 m deep) overlying cooler, saltier water below this. Because the rivers of this region are nutrient-poor, the surface water layer of the Kitikmeot Sea is typically nutrient limited, and very low surface chlorophyll *a* (i.e. phytoplankton biomass) is typically observed (Ahmed et al. 2019). Deep chlorophyll maxima, however, have been observed in the Kitikmeot Sea at depths ranging from 30–60 m (Martin et al. 2010), suggesting that much of the biological activity may be happening well below the surface.

All acoustic tagging of Arctic char in this study was conducted at the Ekalluk River as it enters the

marine environment in Wellington Bay (Fig. 1B), the details of which are clearly described by Moore et al. (2016). Fish were acoustically tagged with V16-TP-4L (2013) or V16-TP-4H (2014 and 2015) transmitters (VEMCO) that are able to measure pressure (converted to depth) and temperature. All tags had a pinging rate of 30 s and life of the transmitters ranged from 1533 d (in 2014) to 2863 d (in 2013) (Table 1), allowing us to track char over multiple feeding seasons. The sex of all fish used in this study was inferred following the genetic-sex determination protocol of Yano et al. (2013). Maturity was inferred based on fork length, where mature individuals were classified as those ≥ 700 mm and immature individuals were classified as those < 700 mm in length (Harris et al. 2020).

Table 1. Biological summary of Arctic char tagged in this study, as well as tag ID, date of tagging (given as year-month-day) and the battery life of each tag. Fulton's relative condition factor (K) was calculated as: $K = [W \times 10^5]/L^3$, where W and L are weight (g) and fork length (mm), respectively. Under sex, M: male, F: female; under maturity, M: mature, I: immature

Tag ID	Date tagged	Tag life (d)	Sex	Estimated maturity ^a	Fork length (mm)	Round weight (kg)	Condition factor
13372	2013-07-11	2863	M	M	776	4.500	0.96
13374	2013-07-11	2863	M	M	730	4.100	1.05
13376	2013-07-11	2863	F	M	720	3.700	0.99
13386	2013-07-11	2863	F	M	780	4.950	1.04
13388	2013-07-11	2863	F	I	668	3.300	1.11
13390	2013-07-11	2863	F	I	680	3.750	1.19
13378	2013-07-12	2863	M	M	721	4.250	1.13
13380	2013-07-12	2863	U	M	756	4.350	1.01
13382	2013-07-12	2863	F	I	676	3.400	1.10
13384	2013-07-12	2863	F	M	804	5.850	1.13
12862	2014-07-11	1757	M	I	661	3.300	1.14
12864	2014-07-11	1757	F	I	665	2.600	0.88
12866	2014-07-11	1757	F	M	768	4.250	0.94
12868	2014-07-11	1757	M	I	581	2.150	1.10
12870	2014-07-11	1757	M	M	753	4.450	1.04
12872	2014-07-11	1757	M	I	630	2.750	1.10
12874	2014-07-11	1757	M	I	608	2.450	1.09
12876	2014-07-11	1757	F	M	748	4.300	1.03
12878	2014-07-11	1757	F	I	614	2.700	1.17
12880	2014-07-11	1757	F	I	647	3.050	1.13
12223	2015-07-09	1533	F	M	712	3.700	1.03
12225	2015-07-09	1533	F	M	650	3.300	1.20
12227	2015-07-09	1533	F	I	767	4.500	1.00
12229	2015-07-09	1533	M	I	749	4.850	1.15
12231	2015-07-09	1533	F	I	786	5.650	1.16
12235	2015-07-09	1533	M	M	669	3.950	1.32
12237	2015-07-09	1533	M	M	778	4.950	1.05
12241	2015-07-09	1533	M	I	644	2.700	1.01

^aGiven the available data on sizes at maturity for Arctic char in the region (i.e. 100 % maturity is attained by a length of 700 mm, Harris et al. 2020), we considered Arctic char > 700 mm to be mature

2.2. Design of the acoustic array

The acoustic array, designed with the intent of inferring dispersal of Arctic char among commercial water bodies and assessing residency within Wellington Bay where 3 of the commercial rivers drain, is described by Moore et al. (2016). The immediate study area is home to 6 known Arctic char-bearing rivers (from east to west: Lauchlan River [Byron Bay], Halokvik River [30 Mile], Paliryaak [Surrey] River, Ekalluk River, Kitaga River and Freshwater Creek), 4 of which are commercially fished (Lauchlan, Halokvik, Surrey and Ekalluk rivers, Fig. 1B). We placed 1 acoustic receiver (VR2W-69 kHz, VEMCO) at the mouth of each commercial Arctic char-bearing river in our study area (i.e. Wellington

Bay and rivers that flow into it, Fig. 1B). We classify these stations as 'estuarine' receivers, based on their proximity (< 1 km to the mouth of the river), and their oceanographic setting (see Section 3.2). This classification is also consistent with that of Moore et al. (2016). A series of gates ($n = 6$), i.e. 2 receivers placed perpendicular from shore approximately 1 and 2 km out, were established between each of these rivers, and from 2013–2015, we established a 'curtain' of receivers across Wellington Bay (Fig. 1B). Additional gates were established at the areas locally known as Starvation Cove and Gravel Pit, which have subsistence and recreational importance to Cambridge Bay residents. Receivers that were included in gates or in the Wellington Bay curtain were considered 'marine' stations (see Moore et al. 2016). In the initial year (2013) the array consisted of 42 receivers, but the array changed slightly among years (see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m634p175_supp.pdf). Overall, 8 estuary and 39 marine stations were used in this study across all years, and the details for each station are described in Table S1. Detection ranges in our study area are generally above 50 % within 500 m of the receivers (Moore et al. 2016).

2.3. Oceanographic and environmental data collection

To describe the physical habitat and environmental conditions of the marine environment within our study area, we compiled data from both field observations and data available from online government sources. We measured profiles of salinity, temperature and chlorophyll *a* concentration using a conductivity-temperature-depth (CTD) instrument (Sea-Bird SBE 19plus V2 or RBR Concerto). The measurements were taken in 5 consecutive years (2013–2017) at some (but not all) the hydrographic stations noted in Fig. 1B. In particular, the stations across the Wellington Bay curtain were visited each year (see Fig. 1B). Although the stations were visited within a narrow window of dates (22 July to 8 August), sea ice conditions varied extensively among those 5 years, allowing for an assessment of ocean temperature/salinity structure as a function of the number of weeks elapsed since break-up.

Additionally, in 2016, we conducted a CTD survey near the Lauchlan River (Fig. S2), to characterize the oceanography of our estuarine receivers. Although each estuary in this study is unique, they do have similar sized rivers, similar coastal geomorphology and essentially the same tidal forcings. The estuaries should therefore experience similar circulation, and the Lauchlan River estuary can serve as a model for understanding the physical oceanography of these regions.

Daily and mean monthly SST data were obtained from the NOAA OI SST V2 high resolution dataset (free and available at: www.esrl.noaa.gov/psd/data/gridded/data.noaa.oisst.v2.highres.html). The SST dataset has a spatial grid resolution of 0.25° and a temporal resolution of 1 d. Additional details pertaining to this high-resolution dataset can be found in Reynolds et al. (2007). As our study area is spatially covered by 3 pixels of SST data, we calculated the daily average throughout the entire study area. Daily and mean monthly air temperatures for the marine feeding season in each year of study were determined from historical data compiled by Environment Canada taken from the Cambridge Bay weather station (http://climate.weather.gc.ca/historical_data/search_historic_data_e.html). Weekly sea ice charts from the Canadian Ice Service (<https://iceweb1.cis.ec.gc.ca/IceGraph/page1.xhtml?lang=en>) were used to determine the timing of sea ice break up (defined as 50% ice-free conditions in Wellington Bay). Sea ice data were also used to confirm that the timing of CTD measurements varied from immediately at break-up to 5 wk after break-up, thus covering a significant portion of the

time period in which Arctic char are expected to be in the marine environment (Moore et al. 2016). Date of peak run-off for each year of the study was estimated from daily average flow (discharge) values reported at the Environment Canada Water Office Freshwater Creek gauging station (10TF001) near the community of Cambridge Bay. Finally, we explored diel patterns of depth use with sunrise and sunset times determined from the National Research Council Canada (see www.nrc-cnrc.gc.ca/eng/services/sunrise/advanced.html). We classified each detection as either day (sunrise to sunset) or night (sunset to sunrise) based on these times. Note that at the latitude of the study area, the sun does not set for a large portion of the summer (i.e. 21 May to 23 July), and detections during this time would be classified as day.

2.4. Acoustic telemetry data analysis

To determine the spatial depth-use patterns of tagged fish, false detections (i.e. those produced as a result of environmental sounds or tag collisions) were first identified and removed from our acoustic data set (Heupel et al. 2006), as were detections not associated with any of the tags used in the study, and detections before tagging dates. Mean depth and temperature values were calculated for each individual. Because the depth of the water at the location where a fish was detected sets a maximal swimming depth that can bias assessments of depth preference, we also calculated a relative depth index (RDI). The RDI is a dimensionless index and was calculated as the depth at which the individual was recorded divided by the total depth of the water where the receiver that recorded the detection was located. Values close to 0 indicate that the individual is near the top of the water column (pelagic – surface), and values ~1 suggest the individual is near the bottom (benthic – sea floor). Linear models were fit (using the 'lm' function in R ver. 3.5.1, R Core Team 2018) to test the relationship between mean depth and mean temperature with calendar date for each year of the study to resolve potential depth and temperature patterns as the marine feeding season progresses. Linear models were fit to test if inter-annual variation in depth use was influenced by inter-annual variation in climatic and environmental variables (e.g. mean July and August air temperature, mean July and August SST, marine ice break-up conditions as defined above and peak flow during the spring freshet). Within years, we also compared mean daily depth with summer SSTs for the region to further test the hypothesis that depth use

should increase as the surface temperatures of the marine environment warm throughout the summer feeding season. We also classified putative ‘dives’ as any detection greater than 5 m, which corresponds roughly to the mean depth across all detections plus the 95 % CI. This is also consistent with the definition of a dive used in other north-temperate salmonids (Reddin et al. 2011, Kristensen et al. 2018). We then tested whether the frequency of putative dives differed between marine and estuarine habitats using chi-squared tests in R. We also used chi-squared tests to assess whether the frequency of dives differed between summer feeding months (i.e. July vs. August).

Finally, a linear mixed model (LMM) with a Gaussian error structure was used to test for variability in depth for Arctic char relative to biological and environmental parameters using the R package ‘nlme’ v3.1-128 (Pinheiro et al. 2019). Depth was square root-transformed for normality prior to analysis. Temperature data were normally distributed and no transformation was required. Fixed effects incorporated into the model included year, sex, inferred maturity (described in Section 2.1), fork length, Fulton’s condition factor (calculated as $K = [W \times 10^5] / L^3$, where K is the condition factor, and W and L are weight [g] and fork length [mm], respectively), presence of sea ice extent by week as a continuous variable and diel period (day or night, based on sunset times) as categorical variables. Arctic char ID was included as a random effect to account for repeated measures in the data. Continuous predictor variables were screened for collinearity prior to analysis using a Pearson’s correlation coefficient (≤ 0.6) and afterwards using variance inflation factors (< 3.0). We followed the model selection approach detailed by Zuur et al. (2009) using a backwards-step selection, beginning with the full model and eliminating the most non-significant covariate. Model selection was guided by Akaike’s information criterion for small sample sizes (AICc), where the lowest relative AICc ($\Delta AICc$) was used to select the most parsimonious model using the R package ‘MuMIn’ v1.15.1 (Bartón 2019). To assess model fit, we calculated marginal R^2 (proportion of variance explained by fixed effects) and conditional R^2 (proportion of variance explained by fixed and random effects) using the R package ‘MuMIn.’

3. RESULTS

3.1. Biological summary of tagged individuals

A total of 28 Arctic char were surgically implanted with acoustic transmitters from 2013–2015 (Table 1).

All individuals showed no adverse effects of the tagging procedure and immediately swam off upon release. Twelve of the individuals were males and 15 were females (Table 1). Overall, fork length ranged from 581–804 mm (701.0 ± 63.9 ; mean \pm SD) while round weight ranged from 2150–5850 g (3812.0 ± 985.7). Fulton’s condition factor ranged from 0.84–1.32 (1.13 ± 0.32). Given the available data on sizes at maturity for Arctic char in the region (i.e. 100 % maturity is attained by a length of 700 mm), we assume that 13 of the Arctic char tagged in the present study were mature. Of the 28 acoustically tagged Arctic char, 26 were detected at least once (Table 2).

3.2. Oceanographic and environmental data

Temperature and salinity data compiled for all marine stations sampled between 2013 and 2016 show that in Wellington Bay, mean summer temperatures in the upper 5 m of the water column were typically within 4–7°C, and rarely exceeded 8°C (Fig. 2A,B). While the maximum temperatures within this analysis rarely exceeded 8°C, it is apparent from the maximum temperatures encountered by individual fish (Table 2) that they often had access to warmer water, likely in estuarine or shallow areas in the region (see estuarine habitat description below; Fig. 2C,D). Below 5 m depth, water cools rapidly, usually reaching 2°C by 8 m depth, and 0°C by 15 m. In the upper 5 m, salinity usually ranges from 14–24 PSU, and then increases rapidly to 27 PSU by 8 m depth.

Temperature and salinity showed strong seasonal patterns of variation along the Wellington Bay transect (Fig. 2A), illustrating the strong influence of ice melt on ocean structure throughout the season. When we measured the stations immediately after ice break-up, salinity was < 22 PSU through most of the upper 5 m of the water column, presumably due to ice melt and river runoff. This freshwater layer thinned rapidly in the weeks following break-up, and was essentially absent by the time Wellington Bay had been ice-free for 5 wk (surface salinity ~ 27 PSU). Water temperatures were coldest at ice break-up ($\sim 4^\circ\text{C}$ at the surface, and falling to less than 2°C at 5 m), followed by a deepening layer of warm water as the ocean was heated by solar radiation (reaching $\sim 5^\circ\text{C}$ at the surface and 4°C at 9 m after 5 wk of open water). Generally, the freshest water was observed on the western side of Wellington Bay (Fig. 2A), which is also where the warmest water was observed, a pattern explained by a counterclockwise estuarine circulation pattern in

Table 2. Detection summary for individual Arctic char acoustically tagged with temperature-pressure (i.e. depth) tags in the Cambridge Bay region of Nunavut, Canada. Shown is each tag ID and the associated number of detections (N) overall and by estuary (est) or marine (mar) stations for both depth and pressure detections. The associated mean (\pm SD), minimum and maximum recording for each fish are shown

Tag ID	N			Swimming depth (m)			N			Body temperature (°C)		
	(all)	(est)	(mar)	Mean \pm SD	Min	Max	(all)	(est)	(mar)	Mean \pm SD	Min	Max
13372	14	7	7	1.69 \pm 1.08	0.00	7.85	15	7	8	3.90 \pm 3.55	0.14	8.23
13374	606	476	130	2.77 \pm 2.71	0.00	8.91	617	484	133	5.56 \pm 1.83	1.36	11.06
13376	88	43	45	3.74 \pm 3.89	0.00	7.85	89	39	50	3.94 \pm 2.21	0.00	7.20
13386	239	231	8	2.18 \pm 3.62	0.15	2.26	235	227	8	3.29 \pm 1.79	-0.33	7.01
13388	246	246	0	0.85 \pm 0.31	0.00	1.82	258	258	0	2.99 \pm 0.14	2.78	3.06
13390	512	81	431	1.01 \pm 0.15	0.00	19.02	517	65	452	1.32 \pm 0.05	1.27	1.36
13378	234	60	174	1.53 \pm 2.64	0.00	8.91	240	60	180	6.33 \pm 1.86	0.80	8.89
13382	10	7	3	1.60 \pm 0.61	0.00	9.81	4	4	0	7.15 \pm 1.17	5.32	12.28
13384	12	12	0	5.03 \pm 3.41	0.61	31.53	14	14	0	4.71 \pm 2.20	1.46	10.02
12862	290	80	210	2.82 \pm 3.14	1.52	34.57	292	92	200	4.37 \pm 1.57	1.65	7.86
12864	1,562	994	568	4.52 \pm 4.83	1.52	3.94	1,553	990	563	5.99 \pm 2.36	1.18	12.75
12866	20	12	8	2.71 \pm 0.71	0.61	15.46	19	10	9	4.37 \pm 2.22	1.55	6.92
12868	1,368	1,072	296	1.96 \pm 1.45	2.43	36.08	1,401	1,091	310	4.59 \pm 1.60	0.42	9.74
12870	250	145	105	6.89 \pm 6.02	1.21	28.50	262	160	102	4.38 \pm 1.58	1.93	7.95
12872	1,248	1,106	142	2.87 \pm 1.72	2.12	23.04	1,276	1,146	130	6.27 \pm 2.17	0.52	10.49
12874	975	952	23	4.44 \pm 1.70	1.52	20.92	964	940	24	7.25 \pm 2.70	2.59	13.03
12878	642	527	115	3.78 \pm 1.76	0.61	3.64	652	534	118	3.45 \pm 2.50	0.05	10.30
12880	312	289	23	1.31 \pm 0.65	0.61	4.24	323	302	21	5.84 \pm 2.76	0.99	10.77
12223	52	19	33	1.21 \pm 1.82	0.00	14.55	53	15	38	3.61 \pm 1.59	1.18	5.79
12225	685	630	55	0.51 \pm 1.36	0.91	25.17	680	621	59	7.59 \pm 3.09	0.99	13.22
12227	606	408	198	0.07 \pm 0.49	0.00	23.65	590	396	194	8.34 \pm 2.33	1.65	12.75
12229	67	54	13	1.06 \pm 0.56	0.30	1.21	62	53	9	4.13 \pm 0.70	3.53	6.26
12231	282	264	18	0.04 \pm 0.16	0.91	1.21	293	275	18	9.15 \pm 1.53	6.26	11.90
12235	308	125	183	1.11 \pm 2.47	0.00	19.40	307	115	192	8.29 \pm 2.20	3.15	12.56
12237	522	491	31	0.57 \pm 1.23	0.30	4.85	525	497	28	8.23 \pm 2.21	2.49	11.43
12241	91	84	7	3.34 \pm 3.23	2.43	23.35	88	80	8	4.49 \pm 3.24	0.71	9.93
Average	432	324	109	2.71 \pm 3.12	0.68	14.68	436	326	110	6.02 \pm 2.70	1.68	9.34

Wellington Bay that concentrates river runoff along the western shore.

During the CTD estuary survey at the Lauchlan River, we observed a thin (<1 m) layer of river water extending at least 2 km offshore (Fig. 2C,D). This thin layer of river water (salinity = 0, temperature = 12°C, Fig. 2C) was overlying water with very similar characteristics to the west side of the Wellington Bay receiver curtain (salinity = 25, temperature = 5°C, Fig. 2A). The vertical structure and spatial extent of this freshwater layer confirms our classification of 'estuarine' receivers, and may have implications for the interpretation of char movements in these habitats.

Mean July and August air temperatures ranged from 8.0°C (2013) to 10.3°C (2016) and 6.1°C (2014) to 8.7°C (2015), respectively (Table 3). SSTs for July ranged from 0.13°C (2014) to 1.49°C (2016) while SSTs for August ranged from 4.8°C (2014) to 7.9°C (2013, Table 3). Date of 50% ice-off for Wellington Bay was as early as day of the year (DOY) 191 (2013) and as late as DOY 205 (2015, Table 3). Finally, dates

of peak flow ranged from DOY 171 (2013) to 180 (2014, Table 3).

Deep chlorophyll maxima were observed at various locations throughout the study area, although not along the Wellington Bay curtain transect. A clear example of this is illustrated in Fig. 3, which shows a deep chlorophyll maximum in Queen Maud Gulf. These maxima migrate deeper throughout the season, following the nutricline and the transmission of light (Martin et al. 2010). Our best measurements of the temporal evolution of these maxima come from Cambridge Bay itself (P.J. Duke unpublished data), where we have observed a phytoplankton bloom that initiates directly under the sea ice during the melt season, and then migrates to ~50 m depth by mid-August.

3.3. Swim depth, temperature and estuarine use

Overall, a total of 11 241 pressure (depth) detections were recorded from 16 July 2013 to 2 September

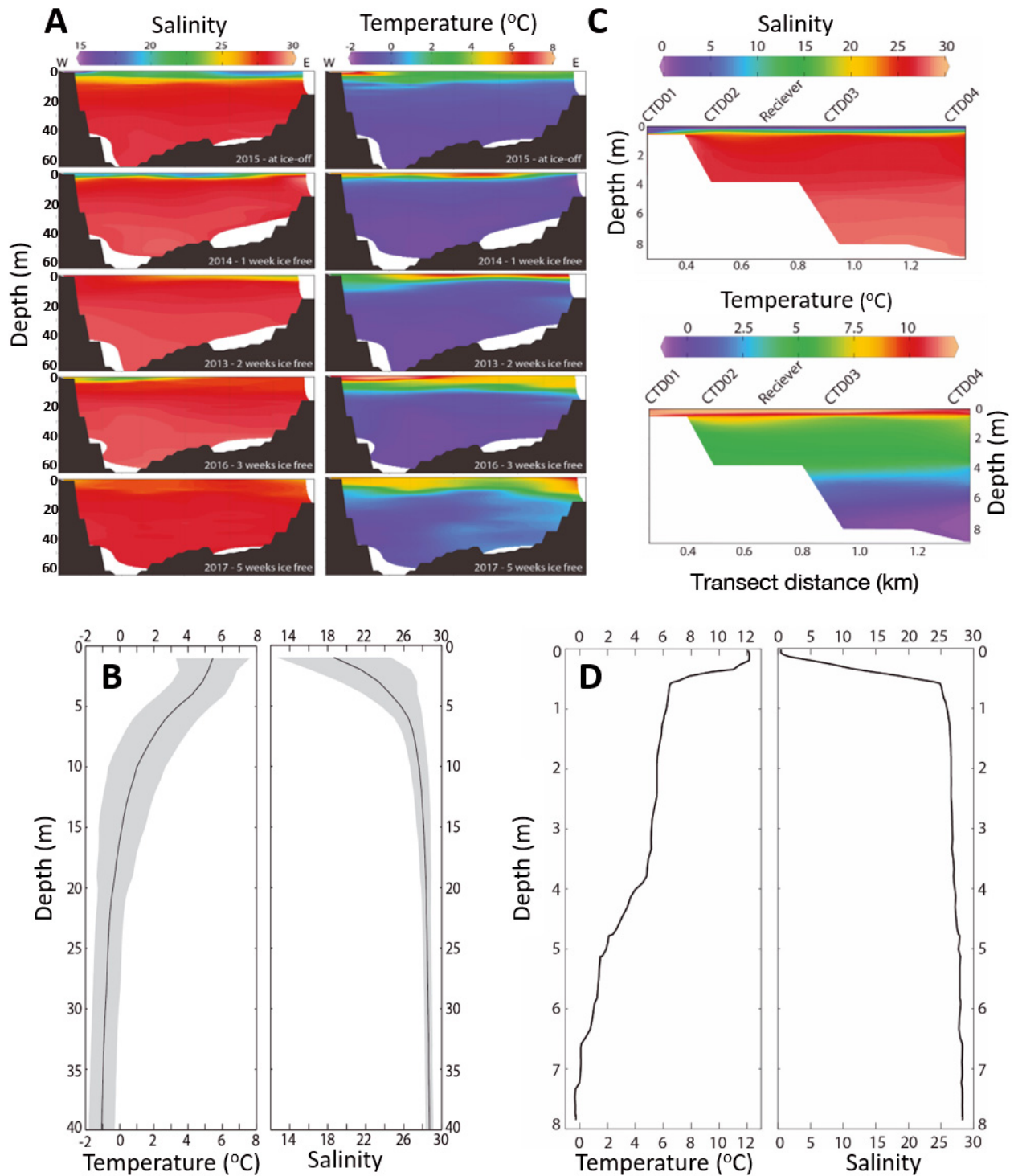


Fig. 2. (A) Cross-sections of salinity and temperature across the Wellington Bay curtain (see Fig. 1), by the timing of transects relative to ice-off dates. (B) Mean \pm SD temperature and salinity from CTD casts ($n = 53$) taken in the study region (Wellington Bay) during the research cruises. (C) Cross-section plots of salinity and temperature along the transect from CTD01 to CTD04 (see Fig. S2). The approximate off-shore location of the Lauchlan River receiver is noted on the top of the cross section, along with the CTD cast locations. (D) Temperature and salinity profiles at location CTD03 (Fig. S2), which is close to the depth and offshore distance of the Lauchlan River receiver

Table 3. Mean depth used by Arctic char in July and August for each year of the study, and variables that were included in linear models used to test if inter-annual variation in depth use was influenced by inter-annual variation in climatic and environmental variables. SST: sea surface temperature, DOY: day of the year

Year	Mean depth July (m)	Mean depth August (m)	Mean air temperature July (°C)	Mean air temperature August (°C)	Mean SST July (°C)	Mean SST August (°C)	DOY 50 % ice free	DOY peak flow
2013	1.97	3.92	8.0	7.3	1.22	7.90	191	171
2014	2.03	3.10	8.4	6.1	0.13	4.81	199	180
2015	2.12	4.31	9.5	8.7	0.58	6.02	205	177
2016	2.27	6.91	10.3	8.5	1.49	4.75	192	176

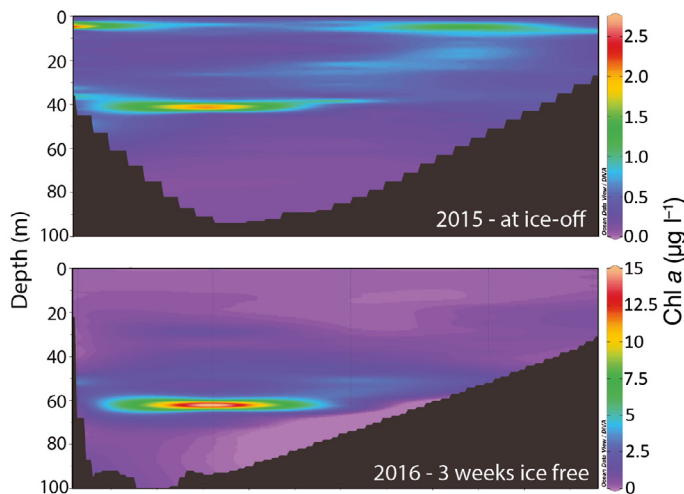


Fig. 3. Vertical distribution of deep chlorophyll maxima, observed ~50 km east of Cambridge Bay, in Queen Maud Gulf. The location where these measurements were taken is shown in Fig. 1A

ber 2016 (Table 2). The number of pressure detections per individual fish ranged from 10–1562 and averaged 432 ± 435 (mean \pm SD; Table 2). Mean swim depth calculated across all detections was 2.71 ± 3.12 m and was highly variable among individuals, ranging from 0.04–6.89 m (Fig. 4A, Table 2). Several fish were detected at least once at the surface of the water (i.e. 0 m), and the maximum swim depth detected in our study was 36.08 m (Table 2). The majority of detections were within the top 3 m of the water column (67.8%), and 27.1% of all detections were within the top 1 m of the water column. For most years (2013–2015), there was a significant relationship between daily mean depth occupied by Arctic char and calendar date such that Arctic char occupied deeper waters later in the summer (Fig. 5A–D). This trend of increasing depth use is also clearly shown when visualizing all detections for each summer marine feeding season (Fig. 5E–H) and when assessing daily mean depth for all years combined (Fig. S3A). The relationships between mean depths

occupied and any of the environmental variables tested were rarely significant (Fig. S4). Only the relationship between mean July depth and mean July air temperature was significant (Fig. S4A). Qualitatively, however, when we compared daily mean depth with satellite daily mean SST, depth use did appear to increase with SST of the marine environment (Fig. 5A–D). Finally, 72.7% of all detections were in estuaries (vs. marine habitats, Fig. 6A). However, when comparing the proportion of estuarine detections by date (for 2014 and 2015, years for which we had sufficient coverage of the marine feeding season), no clear patterns emerged (Fig. S5).

Eighteen of the 26 Arctic char that were detected at least once dove beyond 5 m in depth, with 13 individuals diving below 10 m and 9 individuals diving below 20 m at least once. These dives into deeper waters also appeared to be more common as the marine season feeding progressed, especially after ice-off in the marine environment (Fig. 5E–H). Chi-squared tests indicated that diving (i.e. detections >5 m) frequency was significantly more prevalent in marine vs. estuarine habitats (chi-squared = 286.36, $df = 1$, $p < 0.01$; Fig. 6B) and the frequency of dives increased later in the summer (i.e. July vs. August, chi-squared = 446.81, $df = 1$, $p < 0.01$; Fig. 6C,D). When diving events were mapped to our study area, however, it was clear that dives were still common in estuaries (Fig. S6). In the marine environment, there were disproportionately more dives at areas locally known as Gravel Pit and Starvation Cove and the east side of Wellington Bay (Fig. S6). Repetitive diving behavior, noted as periodic series of short, consecutive dives, was also recorded in several Arctic char (Fig. 7). Following each dive, the fish would quickly return to the surface for a short period of time before diving again (Fig. 7).

All of the observations presented above were also recorded if RDI was used instead of depth (Fig. 3C; Table S2 and Fig. S7), and our findings are therefore not simply biased by the maximum depths of habitats

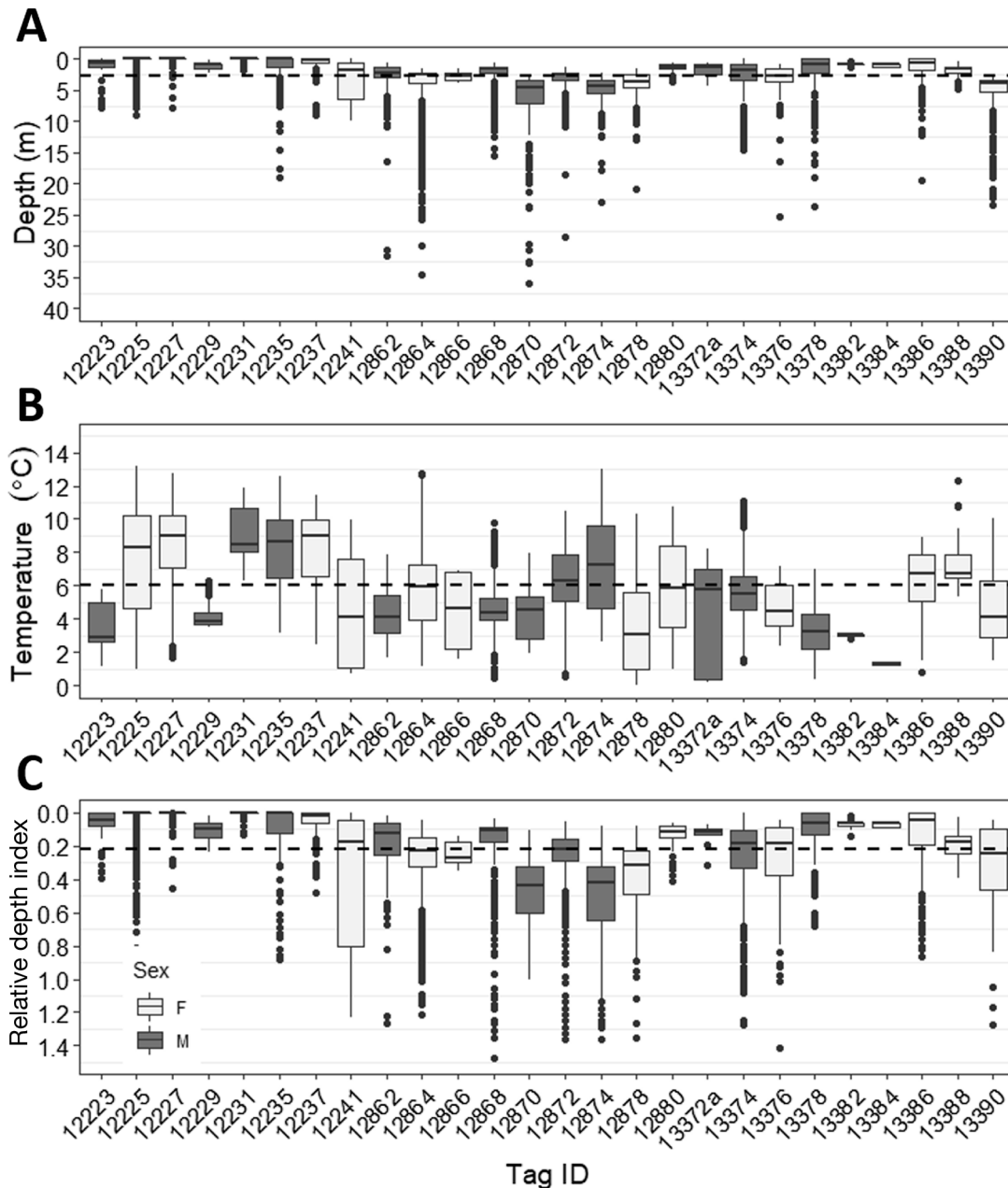


Fig. 4. (A) Depth, (B) temperature and (C) relative depth index (RDI) for individual Arctic char tagged at the Ekalluk River, NU, between 2013 and 2015 (see Table 1). Sexes are shown as different colors (females: white, males: grey), and the mean depth, temperature and RDI across all detections are shown as black dotted lines. Grey and white boxes show the 25th and 75th percentile or inter-quartile range (IQR), black lines within the boxes are the medians, whiskers are $1.5 \times$ the IQR, black dots are individual data points that fall outside this range

used by Arctic char. That is, when depth preference was evaluated based on RDI, it was still apparent that Arctic char preferred the top of the water column regardless of the overall depth of the habitat they occupied. Mean \pm SD RDI calculated across all detections was 0.19 ± 0.14 and ranged among individuals from 0.02–0.46 (Fig. 3C, Table S2). For all years, there was also a significant trend of increasing mean RDI throughout the marine feeding season (Fig. S7A–D).

A total of 11 329 temperature detections were recorded (Table 2). The number of temperature detections per individual fish ranged from 4–1553 (mean \pm SD: 436 ± 420 detections; Table 2). Mean body temperature over all detections was $5.37 \pm 1.97^\circ\text{C}$, and individual mean body temperature ranged from 1.32–9.15 $^\circ\text{C}$ (Table 2). The lowest internal body temperature recorded was -0.33°C , and the highest temperature recorded was 13.33°C (Table 2). Daily mean body

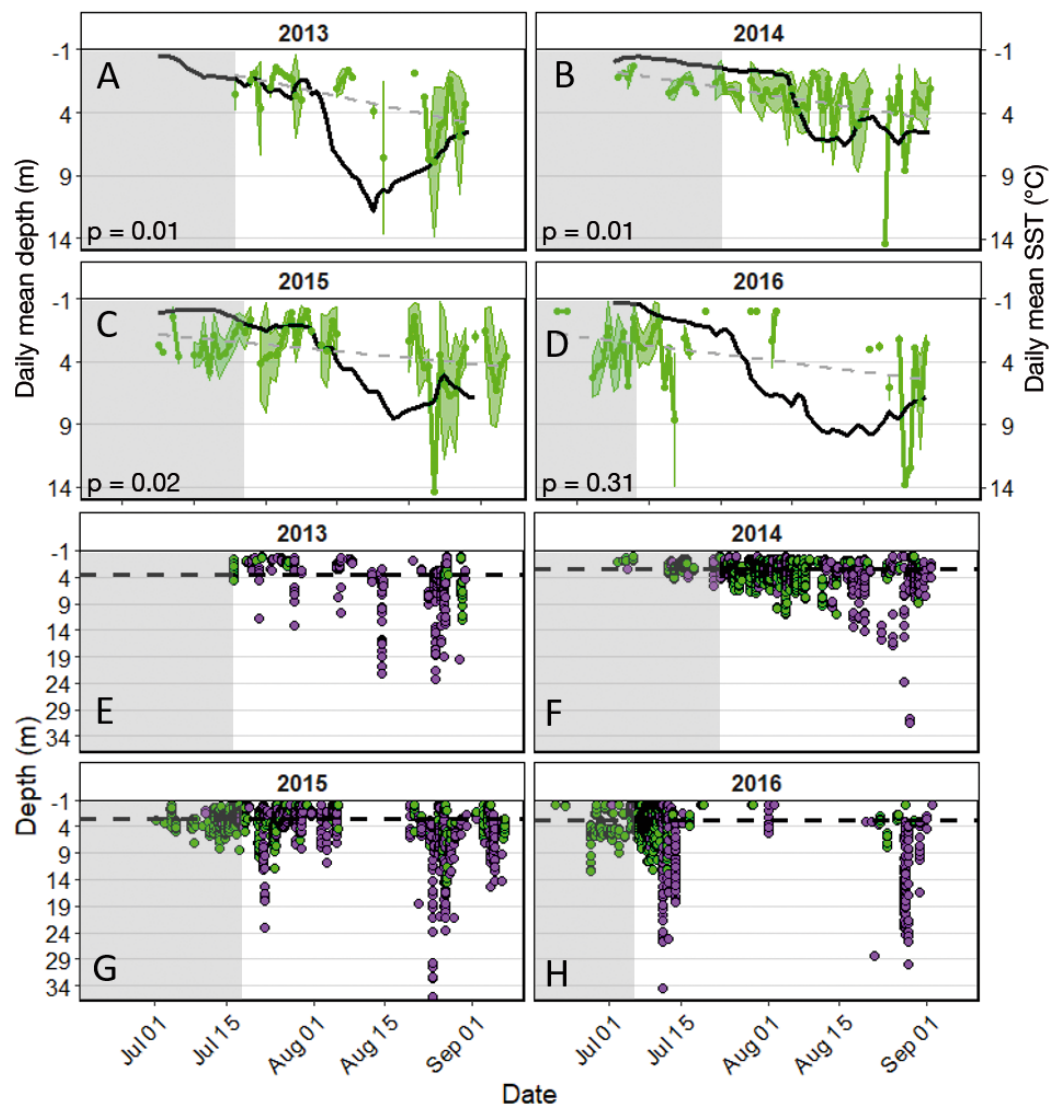


Fig. 5. Depth use (m) by Arctic char in the marine environment, Southern Victoria Island, NU. (A–D) Daily mean \pm SD depth (green shading) used by Arctic char for each summer marine feeding season. In 3 years (2013–2015) there was a significant relationship (grey dashed line, $p < 0.05$) between daily mean depth and calendar date. Mean daily sea surface temperature (SST) during the marine feeding season for each year is shown with a black line. (E–H) All detections for each year of the study by estuary (green circles) and marine (purple circles) acoustic receivers. Dates highlighted in grey represent ~50% ice cover for Wellington Bay

temperature did not change significantly throughout the marine feeding season (Fig. 8A–D), and this was also quite evident when visualizing the data for all detections (Fig. 8E–H) and when assessing daily mean temperature for all years combined (Fig. S3B).

3.4. Linear mixed effect modeling

The LMM for depth use with the lowest AICc values indicated that throughout the marine feeding season, Arctic char preferred deeper water during

the day and when there was less ice cover (Tables 4 & 5). Year also had a significant effect on depth use, such that Arctic char also appeared to occupy deeper depths throughout the study (2013–2016; Table 4). None of the biological variables (i.e. length, condition, sex or inferred maturity) was a significant predictor for depth use. The model with the lowest AICc values indicated that Arctic char used water temperatures coincident with seasonal temperature changes where they occupied warmer temperatures during times of darkness (suggesting they were more surface oriented at night where waters are warmer) and

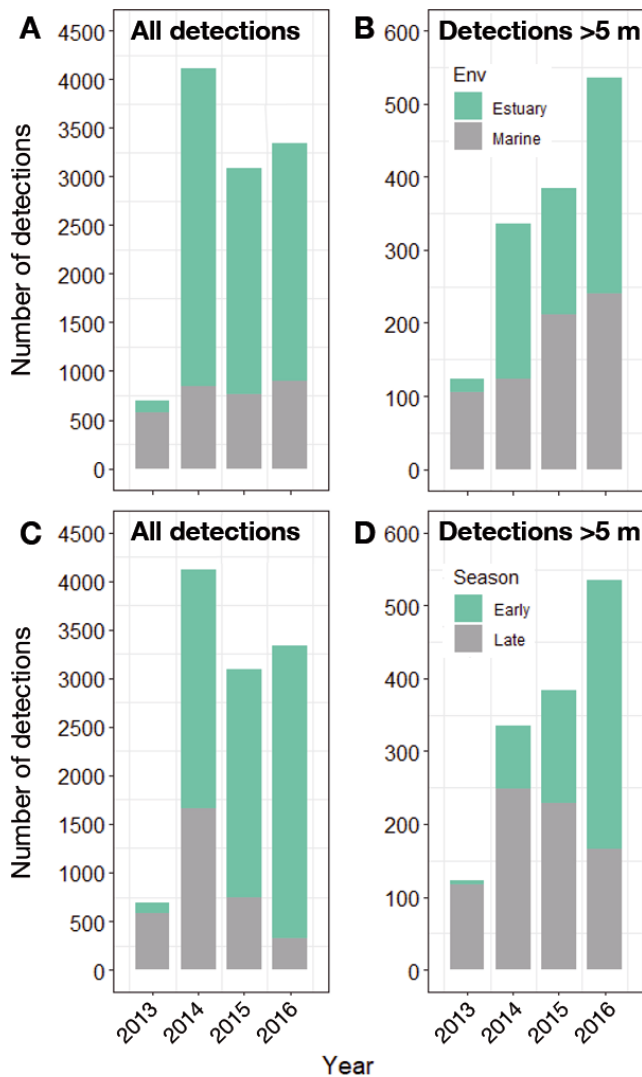


Fig. 6. (A) Overall number of detections by environment (estuary vs. marine) and (B) overall number of dives detected (classified as detections > 5 m) by environment for each year of the study; 72.6% of all detections were in estuaries, and dive events were statistically more common in marine vs. estuary habitats. (C) Overall number of detections by season during marine feeding (defined as early, before 30 July; and late, after 1 August) for each study year and (D) overall number of dives detected by season for each year. Dive events were statistically more common later in the season

when there was less ice (Table 4). We also found a significant positive relationship for year over the study period from 2013–2016 (Table 4). Both fixed and random effects accounted for a moderate amount of the variation explaining both Arctic char depth use (marginal r^2 of 0.05 and a conditional r^2 of 0.66; Table 5) and temperature preference (marginal r^2 of 0.09 and a conditional r^2 of 0.42; Table 5).

4. DISCUSSION

The climate of the Arctic is changing rapidly, impacting the marine and freshwater habitats that many aquatic species rely on for survival. Understanding how species will respond to potential changes such as increased temperature in both freshwater and marine biomes is critical and relies on an accurate understanding of the drivers of habitat choice. Thus, multi-year data on the habitats that species occupy and how these may change seasonally or annually with different environmental conditions will be extremely valuable for predicting the response of marine and freshwater taxa to warming Arctic conditions.

Here, we comprehensively describe depth use of 26 anadromous Arctic char during the marine feeding phase within the Kitikmeot Sea over 4 consecutive years and show that char were highly associated with surface waters (with 67.3% of all detections in the upper 3 m) and estuarine habitats (72.6% estuary vs. 27.4% marine detections). Arctic char also responded to seasonal warming of surface waters during the summer by moving to deeper waters, presumably to stay within a more optimal thermal range and/or potentially following preferred prey. Additionally, nearly half of the individuals dove past 15 m and several over 30 m, and these dives were always followed by a rapid return (within seconds to minutes) to surface waters. Deeper dives were often repetitive in nature, with multiple dives/returns to surface waters occurring over short periods of time in both marine and estuarine habitats. Arctic char preferred deeper water when there was less ice and during periods of sunlight. Finally, the overall mean internal body temperature across all detections was 6.02°C, although there was inter-individual (1.32–9.15°C) variation in mean temperatures. There were also multiple detections ($n = 341$) where body temperatures were below 1°C for several individuals, typically early during the marine feeding season (i.e. when sea-ice is still present) or during forays to deeper waters. Overall, the results of this study should prove valuable for predicting how high-latitude populations of anadromous salmonids that rely on marine habitats for summer foraging may alter their behavior and habitat use as waters continue to warm.

The only study to date that has focused on elucidating depth and temperature preferences during the marine feeding phase for Arctic char in the Canadian Central Arctic region involved acoustically tagging 9 char at the estuary of Freshwater Creek near the community of Cambridge Bay (Bégout Anras et al.

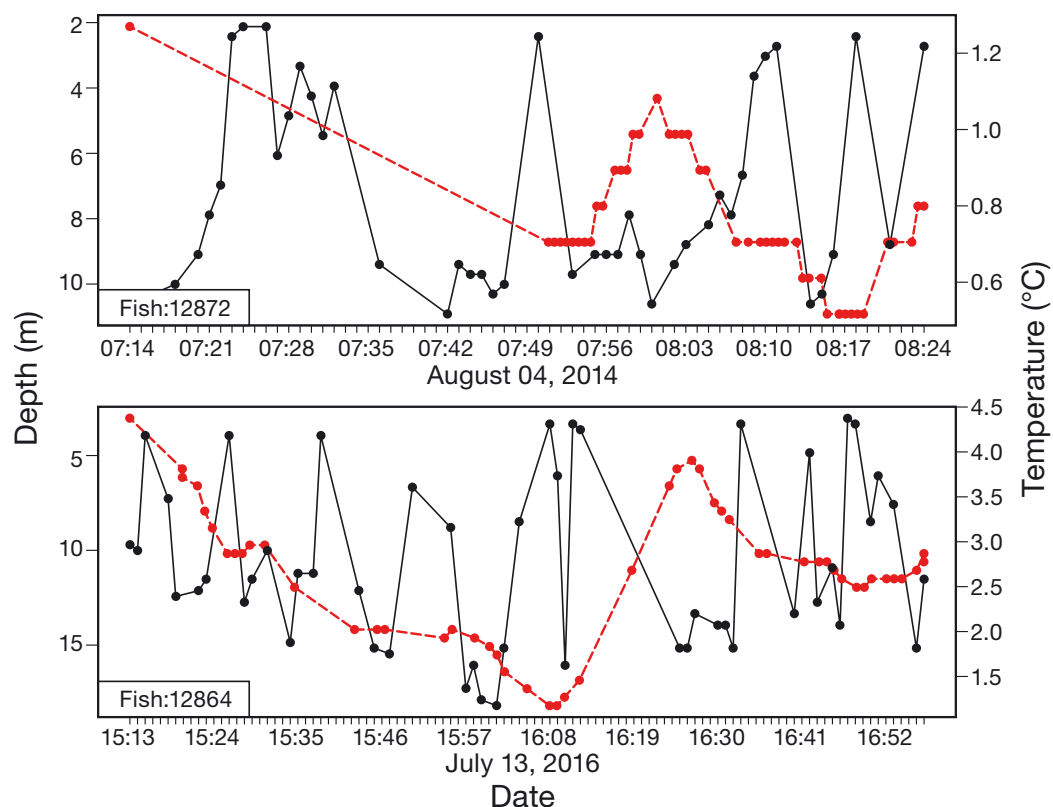


Fig. 7. Depth (m; black solid line) and body temperature (°C; red dashed line) shown for 2 Arctic char (IDs 12872 and 12864) from Southern Victoria Island, NU, highlighting repetitive diving behavior during the marine feeding phase and its impact on body temperature

1999). The authors intended to document depth and temperature preference as char migrated from freshwater overwintering habitats to estuarine habitats for summer feeding. Similar to our study, they found that Arctic char remained in the warmer brackish surface layer, which was typically <2 m deep, and that they rarely moved into the colder underlying marine waters. Unfortunately, sample sizes were small ($n=9$), the spatial scale was restricted (~10 km²), and the duration of tracking time was limited (~5–14 d). Moore et al. (2016) provided a more detailed assessment of the horizontal space use patterns for char in the region and showed that char movement was primarily coastal and that they used estuaries extensively, but the authors did not assess temperature and depth preferences. More comprehensive acoustic telemetry studies in Frobisher Bay on Baffin Island (Spares et al. 2012, 2015) were largely concordant with our results and with those of Bégout Anras et al. (1999). Arctic char in that area were also detected most often in the top 3 m of the water column, and many deeper detections (>50 m) were also sporadically recorded (Spares et al. 2012). There was also a

clear preference for estuarine habitats (Spares et al. 2015). Finally, several Norwegian telemetry studies have also revealed similar aspects of Arctic char biology, including extensive pelagic and estuary habitat use and that diving to access deeper water habitat is common (Rikardsen et al. 2007, Jensen & Rikardsen 2012, Jensen et al. 2016). It is therefore quite clear from the results of our study and others that Arctic char have a high affinity to surface waters, a preference that has also been documented in a variety of other anadromous salmonids (e.g. Strøm et al. 2017, Courtney et al. 2018, Kristensen et al. 2018). The primary drivers of depth use, however, remain unclear and likely include a combination of factors such as more favorable temperatures, salinities and prey availability or predator avoidance in these pelagic habitats (Rikardsen & Amundsen 2005, Spares et al. 2012, Jensen et al. 2014). Overall, the present study adds to the collective understanding of the behavior and movement ecology of Arctic char while at sea and provides the first account of depth and temperature for this species in the Kitikmeot Sea region of Canada's Central Arctic.

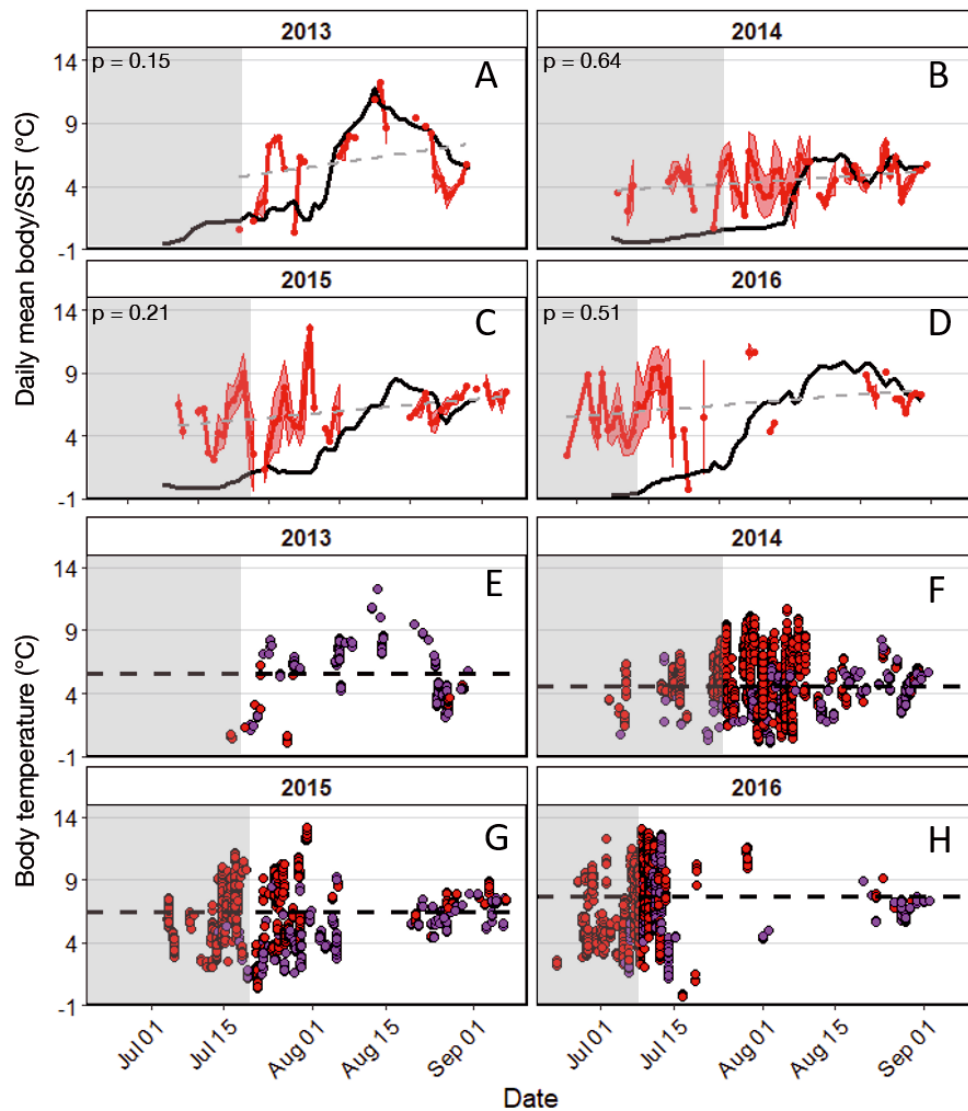


Fig. 8. Internal body temperature ($^{\circ}\text{C}$) of Arctic char in the marine environment, Southern Victoria Island, NU. (A–D) Daily mean \pm SD body temperature (red shading) of Arctic char for each summer marine feeding season. There were no significant relationships (grey dashed line, $p > 0.05$) between daily mean body temperature and calendar date. Black line is the mean daily sea surface temperature (SST) during the marine feeding season for each year. (E–H) All temperature detections for each year of the study by estuary (red circles) and marine (purple circles) acoustic receivers. The dashed line is the mean for each year while at sea. Dates highlighted in grey represent $\sim 50\%$ ice cover for Wellington Bay

The multi-year data set presented here is unique for the Canadian Arctic and has allowed for an assessment of inter-annual differences in marine depth use and to infer environmental drivers (e.g. air surface temperatures, ice cover and flow regimes) of marine habitat use in a high-latitude population of anadromous Arctic char. We found a positive association between mean depth occupied by Arctic char in July with mean July air temperature, but no other environmental variables were significantly associated with depth use. Although lack of significance for

the majority of tests could be the result of low sample size ($N = 4$ years) or of important inter-individual differences in depth use, they could also be indicating a lack of plasticity in depth-use behavior of anadromous Arctic char. Indeed, the years during which the observations were collected were quite variable in terms of climate and ice conditions. For example, the date of 50% ice-off during the earliest ice-year (2013) was 2 wk earlier than the latest ice year (2015). This constitutes a major change in the environment, considering that the length of the ocean phase for char in

Table 4. Parameter estimates from the linear mixed model with the lowest ΔAICc value predicting Arctic char depth and temperature use relative to biological (sex, length and Fulton's condition index) and environmental factors (day vs. night [photoperiod], sea ice concentration). Significant p-values (<0.05) are highlighted in **bold**

Predictor variables	Value	SE	<i>t</i>	<i>p</i>
Depth				
Intercept	-128.82	5.66	-22.78	<0.001
Day/night	-0.05	0.01	-9.57	<0.001
Sea ice concentration	-0.22	0.01	-26.50	<0.001
Year	0.06	0.00	22.87	<0.001
Temperature				
Predictor variables				
Intercept	-1670.00	66.04	25.29	<0.001
Day/night	0.63	0.08	7.60	<0.001
Sea ice concentration	-1.37	0.17	-8.20	<0.001
Year	0.83	0.03	25.35	<0.001
Fulton's condition factor	0.55	0.91	0.58	0.56

the Cambridge Bay area averages ~40 d (Moore et al. 2016). This lack of response in the depth use by char despite extreme inter-annual variability in ocean conditions could therefore suggest that this behavior is relatively fixed. Such an interpretation, if correct, would have important implications for forecasting the effects of climate change on this species because it would suggest a lack of capacity to respond advantageously to changes in, for example, the availability or depth distribution of prey to maximize feeding. A test of this hypothesis would require observations showing that prey depth distributions respond to

variability in ocean conditions, and future studies of these biotic variables would be important for understanding the drivers of depth-use in Arctic char.

When food availability is not limited, the preferred temperature of a fish species often reflects its optimal temperature for growth (Jobling 1981). Laboratory studies of juvenile Arctic char fed in excess suggest that their preferred temperatures (11–12°C; Larsson 2005, Mortensen et al. 2007) and optimal temperatures for growth (13–18°C; Larsson & Berglund 1998, Larsson et al. 2005) are markedly higher than those available in our marine study area. Despite this fact, our results along with previous studies show that, in their marine environment, anadromous Arctic char do not simply use the warmest available water but rather actively select more moderate temperatures (5–9°C; Rikardsen et al. 2007, Spares et al. 2012, Jensen et al. 2016). Furthermore, to our knowledge, the only study to date to estimate a physiological thermal optimum in large, wild, sea-run Arctic char suggests that their optimal cardiorespiratory performance would occur at ~7°C when acclimated to SSTs of ~7°C (Hansen et al. 2017). This estimate is well below the optimal temperature for growth found previously in laboratory studies of captive-reared Arctic char in fresh water.

Many factors may have given rise to these discrepancies in preferred and optimal temperatures between laboratory and field studies. First, the growth efficiency of Arctic char declines linearly with increasing temperature (Larsson & Berglund 2005), which suggests that in the wild where food is often limited and fish have to expend energy to secure food,

Table 5. Ranking of linear mixed models based on AICc and ΔAICc values for biological (sex, length and Fulton's condition index) and environmental effects (photoperiod [day/night] and sea ice concentration) on Arctic char depth and temperature use with individual as a random effect. The marginal R^2 and conditional R^2 giving the proportion of variation explained by the fixed effects only, and the fixed and random effects together, respectively, are also given for each model

Model	<i>k</i>	AICc	ΔAICc	Akaike weight	Marginal R^2	Conditional R^2
Depth						
Photoperiod + Year + Sea ice concentration	6	-6286.9	0.00	0.99	0.05	0.66
Photoperiod + Year + Sea ice concentration + Length	7	-6275.3	11.64	0.01	0.09	0.66
Photoperiod + Year + Sea ice concentration + Length + Fulton	8	-6275.2	11.73	0.00	0.22	0.65
Photoperiod + Year + Sea ice concentration + Length + Fulton + Sex	9	-6271.0	15.94	0.00	0.21	0.34
Null	3	-5230.0	1057.00	0.00	0.00	0.55
Temperature						
Photoperiod + Year + Sea ice concentration + Fulton	7	49707.1	0.00	0.41	0.09	0.42
Photoperiod + Year + Sea ice concentration	6	49707.7	0.54	0.31	0.09	0.41
Photoperiod + Year + Sea ice concentration + Fulton + Sex	8	49708.0	0.85	0.27	0.09	0.40
Photoperiod + Year + Sea ice concentration + Fulton + Sex + Length	9	49718.6	11.45	0.00	0.07	0.39
Null	3	50382.3	765.43	0.00	0.00	0.43

cooler temperatures may be preferable as they may optimize the tradeoff between energy expenditure on foraging and digestion relative to energy intake. Second, juvenile char (fry and parr) were used in the laboratory studies and are therefore considerably smaller than those in the present study (see Table 1 and also Larsson & Berglund 1998, Larsson et al. 2005, Mortensen et al. 2007). In other anadromous salmonids, optimal growth and preferred temperatures tend to decrease with increasing body size, with larger individuals found in waters $\sim 5^{\circ}\text{C}$ cooler than those preferred by individuals in their first year at sea (Morita et al. 2010a,b). Finally, during early rearing and overwintering, wild Arctic char spend much of their time at cold temperatures ($0\text{--}2^{\circ}\text{C}$; Mulder et al. 2018), while in previous laboratory studies, Arctic char were reared at much warmer temperatures ($\sim 11^{\circ}\text{C}$; Larsson & Berglund 1998, Larsson et al. 2005), which suggests that thermal history and physiological plasticity may underlie differences in thermal preference between studies and may also play an important role in shaping responses to ongoing climate warming. These discrepancies highlight the need for further investigation of the thermal physiology of wild Arctic char and emphasize the importance of validating laboratory results in a field setting (Speers-Roesch & Norin 2016). Given that the preferred temperatures recorded in the field overlap with the only thermal optimum estimated in sea-run Arctic char (Hansen et al. 2017), we suggest that their preferences do reflect a physiological thermal optimum in this context.

In our marine study area, temperatures in the preferred range of sea-run Arctic char ($5\text{--}9^{\circ}\text{C}$) are only found near the surface ($<5\text{ m}$), which could explain the general affinity for these depths. In each year of the study, Arctic char increased their depth in this surface region as temperatures increased throughout the feeding season. This increase in depth resulted in relatively stable temperature use, which suggests that fish were regulating their temperatures, perhaps avoiding cold temperatures which may limit metabolism, activity or growth. Similar behavioral thermoregulation has been inferred in sea trout *Salmo trutta* (Rikardsen et al. 2007, Jensen et al. 2014), which also progressively reside in deeper waters as SST increases throughout the marine feeding season (Eldøy et al. 2017). Other anadromous species such as Chinook salmon *Oncorhynchus tshawytscha* exhibit patterns of vertical movement as SSTs warm, which allow them to maintain a relatively consistent temperature (Hinke et al. 2005). Cumulatively, this information demonstrates that anadromous salmonids tend to occupy a narrow range of thermal habitats

while at sea and will adjust their position in the water column accordingly to persist within that optimal range (e.g. Hinke et al. 2005).

In depths over 5 m , temperatures drop below 4°C and are close to 1°C by 10 m . Around 24 m in depth, temperatures are near the freezing point of Arctic char (-1°C ; Fletcher et al. 1988, Fig. 2B). These colder temperatures likely constrain important physiological performances (e.g. activity, metabolic rate, digestion; Fry 1947, Donaldson et al. 2008, Farrell 2009) and reduce growth rate (Mortensen et al. 2007) enough to deter char from spending considerable amounts of time below 5 m . Indeed, in the present study, depths below 5 m were only accessed for relatively brief periods during diving. During the rapid changes in external temperature experienced during diving, body temperature lags behind external temperature, especially in large-bodied fish. As such, some physiological functions may be temporarily protected by this lag if excursions through waters of sub-optimal temperature are sufficiently brief (Pépin et al. 2015). However, the gills are highly effective heat exchangers ($80\text{--}90\%$ heat transfer; Stevens & Sutterlin 1976), and so the vital organs perfused immediately after blood leaves the gills (e.g. brain and heart) would experience ambient temperatures. This means that the severity of cold exposure during diving and the subsequent rewarming of vital tissues during brief recovery periods in surface waters are likely not fully apparent in core body temperature measurements (Fig. 7). This temperature difference may explain why dives and resurfacing events may be shorter than would be expected based on changes in body temperature alone.

Prey availability and distribution is also an important driver of vertical habitat use in the marine environment (Spares et al. 2012) and may be influencing the transition to deeper waters observed in late summer. Our study clearly revealed that Arctic char were surface-oriented during the beginning of the marine feeding season compared to later in the summer and that photo-period likely has some role in driving vertical habitat use. Our data also showed that the frequency of dives (those $>5\text{ m}$) increased later in the summer. Others have also documented preference for pelagic marine feeding and the occurrence of repetitive foraging dives in this species (Rikardsen & Amundsen 2005, Spares et al. 2012, Jensen et al. 2016). Unfortunately, very little is known regarding the diet and feeding behavior of Arctic char in the Kitikmeot Sea, although it is clear that Arctic char are opportunistic feeders that consume a wide variety of prey items (Dempson et al. 2002, Spares et al. 2012).

Preliminary analyses for char in the Kitikmeot Sea suggest that capelin *Mallotus mallotus* (H. Swanson unpublished data) and amphipods (L. Harris unpublished data) are important prey items in the region (Gyselman 1994). Both capelin and amphipods are key forage species in Arctic marine food webs (Hop & Gjørseter 2013) and have been identified as important prey sources for Arctic char in other regions of the Canadian Arctic (Spares et al. 2012, Ulrich 2013). Pelagic habitat use by Arctic char early on during the marine migration may be explained by foraging on ice-associated and pelagic fish species (e.g. Crawford & Jorgenson 1993) and amphipods (Poltermann 2001). Arctic populations of capelin spawn in late June and early July in shallow-water beach habitat (McNicholl et al. 2016). This is in synchrony with the first marine entry of Arctic char in our study and therefore it is plausible that early-season shallow water depth use is associated with foraging on the patchy distribution of beach-spawning capelin. The transition to deeper waters as the marine feeding season progresses may reflect a transition in foraging tactics once capelin spawning has finished and subsequent to the end of the spring bloom once the sea ice has melted. Indeed, others have also suggested the importance of ice in influencing habitat selection early in the marine feeding season (Bégout-Anras et al. 1999). The vertical shift of chlorophyll maxima towards deeper waters as the season progresses (Fig. 3) may represent a migration of the entire marine ecosystem that char are presumed to be following. Our LMM also suggested use of deeper waters during periods without ice, and during times of daylight. Seasonal shifts in diet should not be surprising given seasonal variability in abundance and distribution of Arctic marine fish species and invertebrates (Zhou et al. 2005, Majewski et al. 2013). Furthermore, both capelin and amphipods occupy deeper habitats after ice melt and both are known to exhibit DVM where they also move deeper during periods of sunlight (Benoit et al. 2010, Regular et al. 2010, Berge et al. 2014). Our results are in accordance with these observations and thus increased depth use and increased frequency of diving in char as the marine feeding season progresses could also relate to the tracking and spatial distribution of their primary prey items. Our results also suggest that Arctic char display some degree of DVM related to foraging opportunities on prey species that also undergo DVM as the light/dark cycle returns to the region. Finally, it should be noted that predator avoidance cannot be discounted as a driver of vertical habitat use and repetitive diving behavior. Whales are extremely

uncommon in our immediate study area and therefore the most likely predators of Arctic char in the region are ringed seals *Pusa hispida* and bearded seals *Erignathus barbatus*. There are no published accounts of seal predation on Arctic char in our study area, but seals have been observed actively chasing char within our acoustic array (L. N. Harris pers. obs.). There have also been accounts of ringed seal predation on Arctic char in other areas where these species occur in sympatry (Gjerttz & Lydersen 1986). Future studies on preferred prey items and the habitats they use at different times of the marine feeding season and the predators that Arctic char must avoid for survival would be beneficial for furthering our understanding of depth use and repetitive diving behavior in this species.

Finally, salinity is also likely an important driver of depth preference and marine habitat use by Arctic char (Spares et al. 2012). Arctic char are a relatively saline-intolerant species compared to other anadromous salmonids (Bœuf & Payan 2001, Bystriansky et al. 2006, 2007) and can exhibit disturbances in blood osmolality, and impaired growth and feed intake at high salinities (35 ppt, Arnesen et al. 1993). In anadromous salmonids, salinity also influences growth hormone signaling, and the cost of osmoregulation can account for a substantial portion of the total energy budget (Bœuf & Payan 2001). As such, the lower salinity conditions (<22 PSU) that persist in the surface waters during ice-melt early in the marine feeding season may be physiologically favorable and help explain the strong preference for shallow depths found in the present study. Additionally, Arctic char are thought to have lower salinity tolerance at colder temperatures (Finstad et al. 1989, Berg & Berg 1993), making the less saline and warmer surface layer even more appealing when marine conditions are colder earlier on during the marine feeding phase. The warmer, less saline upper layer may also act as an important transition habitat for Arctic char as they enter and acclimatize to the marine environment in early summer after having spent the winter in fresh water (Bégout Anras et al. 1999). However, the relatively fresh surface layer of the water does not persist for the duration of the summer marine habitat use (Fig. 2A). We therefore conclude that salinity may not be as important as a driver of depth use later in the season compared to temperature and prey availability.

The preference of Arctic char for estuarine habitat after migrating to the marine environment in the spring has previously been documented (Harwood & Babaluk 2014, Spares et al. 2015, Moore et al. 2016), and our study further supports these observa-

tions. Indeed, over the marine feeding season, more than 70% of all detections were recorded in estuaries, and previous work in the region suggests that multiple estuaries are used throughout the feeding season and not just those of natal origin (Moore et al. 2016). Thorpe (1994) suggested for salmonids that estuaries provide transition zones for acclimation between fresh- and saltwater environments, productive foraging areas and refuge from predators. We showed that the estuaries in the region, at least that of the Lauchlan River, are accompanied by a thin freshwater surface layer. This freshwater surface layer may act as a refuge from more saline conditions that char can use as they transition and acclimate to marine habitats. This layer may also be important in the foraging of Arctic char in estuaries, in that it allows them to undertake feeding forays or dives into higher salinity habitats as they search for marine prey while providing a proximate, freshwater habitat that is less stressful for osmoregulation. Given that char in the region appear to move synchronously among estuaries throughout the summer (Moore et al. 2016), it is reasonable to assume that these habitats are likely key for foraging areas and not just important areas for acclimation between fresh- and saltwater environments. Our results also revealed that dives >5 m were common in estuaries, suggesting that prey availability in these habitats might drive estuarine use. In the future, it would be interesting to quantify relative prey availability in estuaries vs. full marine environments to better test this hypothesis.

5. CONCLUSIONS

The movement decisions made by aquatic biota and their interactions with the surrounding environment provide insights into many aspects of animal biology, including foraging behavior, habitat preference, home ranges, trophic interactions, stock structure and the timing of key life cycle events (Cooke et al. 2004, Donaldson et al. 2014). The horizontal and vertical space use patterns of animals in the 3-dimensional aquatic environment are influenced by a variety of environmental and biological factors (Spares et al. 2012, Hussey et al. 2015) that dictate optimal or preferred habitats used by animals during specific times of the year (Guzzo et al. 2017) or specific stages of their life histories (e.g. overwintering vs. feeding seasons; Rikardsen et al. 2007, Mulder et al. 2018). Predicted temperature increases across marine, estuarine and freshwater environments, however, will

undoubtedly impact the aquatic biota that rely on these habitats in terms of their physiological tolerance, distribution, habitat use, survival and life cycle (Reist et al. 2006a, Poesch et al. 2016, Guzzo et al. 2017). This is especially true for the Arctic, where climate-driven changes to marine and freshwater habitats are predicted to be the most severe and rapid (Serreze & Barry 2011) and for Arctic char in particular that are thought to be especially vulnerable to the impacts of climate change (Reist et al. 2006a).

Here, a 4 yr (2013–2016) acoustic study documented depth and temperature preferences in Arctic char from the Kitikmeot Sea region of Canada's Central Arctic. We showed that (1) Arctic char prefer surface waters that are typically around 5–8°C, (2) they move deeper as surface waters warm throughout the marine feeding season, possibly to access habitat that was previously cold enough to constrain physiological performance, (3) they have a strong preference for estuarine habitats as has previously been documented (Moore et al. 2016), and (4) foraging dives were frequent in both estuarine and marine habitats. Temperature has clearly been shown to impact vertical and horizontal space use patterns for Arctic char and other salmonids (Hinke et al. 2005, Spares et al. 2012, Jensen et al. 2014). Therefore, habitat use in the marine environment could be significantly impacted by climate change in the region, and the results from this study could be important for predicting how char will respond to changing marine conditions. For example, anticipated warming SSTs could result in a preference for deeper, cooler water habitats as surface layers warm and could impact estuarine use if these habitats primarily function as a refuge from colder marine waters. These baseline data on species such as Arctic char are especially valuable given their subsistence and cultural importance throughout their range. The Cambridge Bay region is also home to the largest commercial fishery for this species in Canada (Roux et al. 2011, Day & Harris 2013). Changes in environmental conditions could impact Arctic char recruitment, spawning biomass, abundance (Criddle et al. 1998, Power et al. 2000) and potentially fishing revenue for the residents who commercially fish for this species. Therefore, understanding the temperature and depth preferences of these fish in the region and the abiotic and biotic/biological drivers that influence their marine migratory ecology provides important information for assessing how Arctic char will continue to adjust in a warming Arctic marine environment, which will undoubtedly be integral for ensuring the long-term sustainability of this key resource.

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