ARTICLE

Preference for nearshore and estuarine habitats in anadromous Arctic char (*Salvelinus alpinus*) from the Canadian high Arctic (Victoria Island, Nunavut) revealed by acoustic telemetry

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Abstract: We used an array of fixed acoustic receivers ($N = 42$) to track the summer marine movements of 121 anadromous Arctic char (*Salvelinus alpinus*) equipped with acoustic transmitters at three locations in the Cambridge Bay region, where commercial and subsistence fisheries target the species. The timing of transitions between salt and fresh water was influenced by the putative river of origin of tagged individuals, but not by their size or sex. Females, however, were more likely to remain proximate to rivers where they were tagged throughout the summer. A majority of fish migrated west from their rivers of origin, primarily moving between estuarine environments. Individuals occupied estuaries for several days between bouts of marine movement, and these periods of residency coincided with spring tides in some estuaries. We also recorded increased numbers of detections on receivers located less than 1.5 km from the coast, indicating a preference for nearshore habitats. Finally, we report evidence of extensive stock mixing throughout the summer, including at known fishing locations and periods, a finding with implications for fisheries management.

Résumé : Les mouvements estivaux en milieu marin de 121 ombles chevaliers (*Salvelinus alpinus*) anadromes équipées de transmetteur metteur acoustique issus de trois sites de marquages ont été suivis grâce à un réseau de récepteurs acoustiques ($N = 42$) ancrés dans la région de Cambridge Bay. Les périodes de transition entre les eaux douces et salées étaient influencées par la rivière d'origine des individus, mais pas par leur taille ou leur sexe. Cependant une proportion plus grande de femelles restait près de leur rivière de capture pour tout l'été. Une majorité d'individus ont migré vers l'ouest se déplaçant d'estuaire en estuaire. Ces périodes de résidence en estuaires duraient souvent plusieurs jours, et coïncidaient avec les marées de vives-eaux dans certains estuaires. Dans toute la zone d'étude, les récepteurs situés à moins de 1,5 km de la côte ont enregistré un plus grand nombre de détections, indiquant une préférence pour les habitats côtiers. Finalement, nos données révèlent un mélange des stocks durant la période estivale, notamment dans des zones et périodes de pêches, un résultat ayant d'importantes répercussions pour la gestion des pêches. [Traduit par la Rédaction]

Introduction

Arctic fish species are facing multiple threats associated with climate change, increased harvests, and growing pressures from the shipping industry and from nonrenewable resource exploration or extraction (Reist et al. 2006; Arctic Council 2009; Christiansen and Reist 2013). Managing these threats to ensure that conservation goals are met and that subsistence and commercial fisheries remain sustainable will require the identification of critical habitats, a key knowledge gap for many Arctic species (Christiansen and Reist 2013). Indeed, the spatial ecology of many Arctic fishes remains poorly understood, especially in Canadian waters, and characterizing habitat use in both space and time during relevant life stages is essential for effective management and conservation (Rosenfeld and Hatfield 2006; Costello et al. 2010; Walther et al. 2015). Passive acoustic telemetry offers a powerful tool for the study of habitat use and for the long-term monitoring of fish movement (Heupel and Webber 2011; Hussey et al. 2015). Studies tracking the marine migrations of adult salmonids,

however, remain rare (e.g., Drenner et al. 2012; Klimley et al. 2013), and this is particularly true in the Arctic.

The Arctic char (*Salvelinus alpinus*) is a facultatively anadromous salmonid with a circumpolar distribution (Johnson 1980; Nordeng 1983; Reist et al. 2013). Migratory individuals leave the fresh water at ice-breakup and spend the summer in the marine environment where they feed until they migrate back to fresh water before rivers freeze (Johnson 1980; Bégout Anras et al. 1999). While many other anadromous salmonids return to fresh water only to spawn (Fleming 1998, Quinn 2005; but see exceptions documented from Dolly Varden (*Salvelinus malma*; Armstrong 1974), brown trout (*Salmo trutta*; Jonsson 1985), and cutthroat trout (*Oncorhynchus clarkii clarkii*; Wenburg and Bentzen 2001)), anadromous Arctic char must return to fresh water every winter even as juveniles or nonspawning adults, presumably to avoid high salinity and subzero water temperature (Johnson 1980; Klemetsen et al. 2003; but see Jensen and Rikardsen 2012). Arctic char are iteroparous, and repeat spawning is common with up to 50% of adults spawning at least twice in some

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Fig. 1. Map of the study area showing the location of the moored acoustic receivers used in the study (grey circles for receivers that remained moored throughout the study period and grey diamonds for receivers that were only in place during summer in both 2013 and 2014). The tagging locations are shown with stars (filled black stars for 2013 tagging locations and open stars for 2014 tagging locations). The location of a receiver array operated by Oceans Network Canada is shown with a grey triangle near Cambridge Bay. The major features of the array design are highlighted: a receiver is placed at the mouth of each river (names identified) with known Arctic char runs in the Wellington Bay area; a curtain of 17 receivers was deployed across Wellington Bay; and six gates (i.e., pairs of receivers deployed perpendicular to the coast) were deployed along the coast. Three and two receivers were deployed in the Halokvik River and Ekalluk River estuaries, respectively, to increase likelihood of detection during saltwater–freshwater transitions.
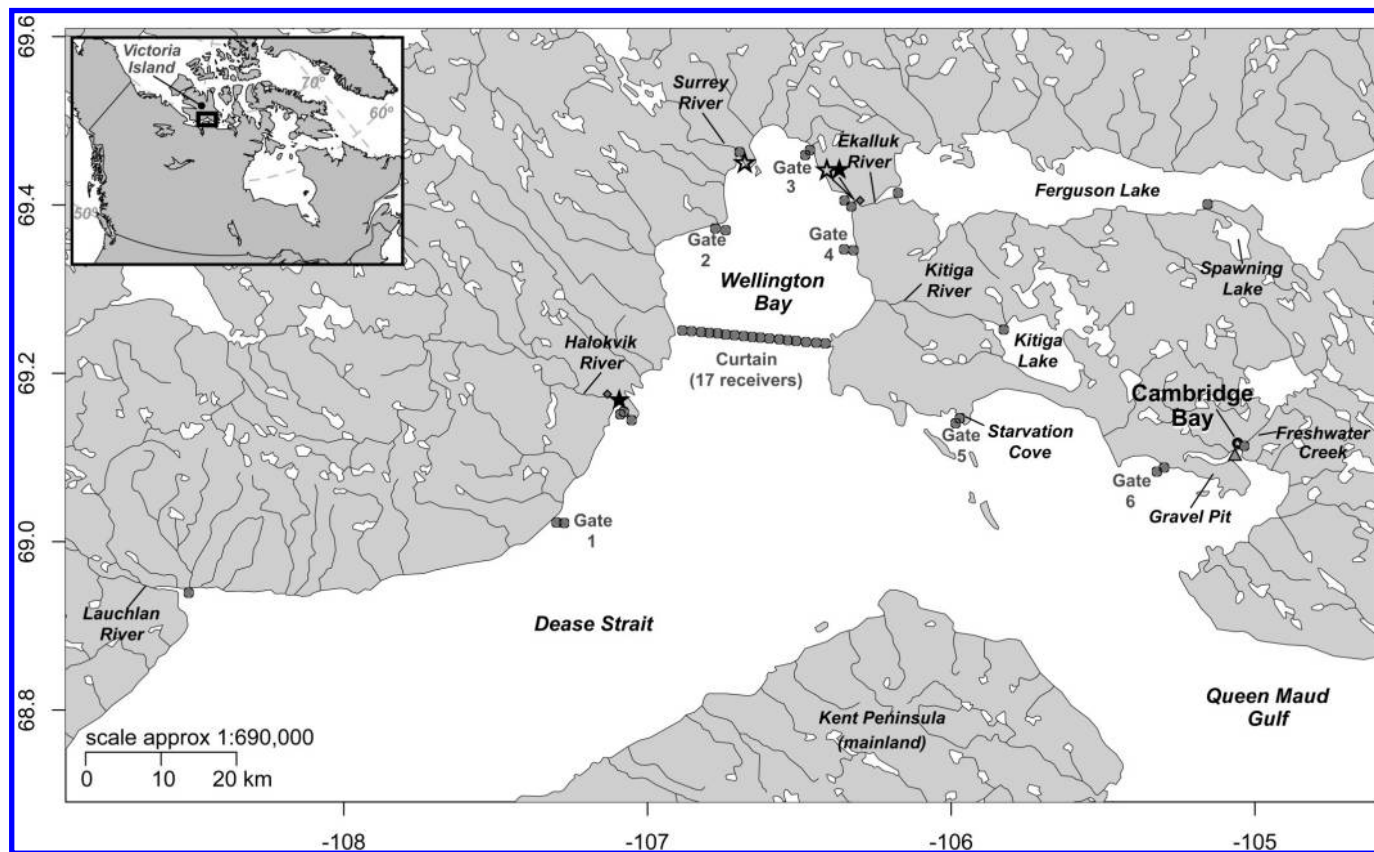
populations (Fleming 1998). Arctic char, however, do not usually spawn in consecutive years because the short ice-free period limits feeding opportunities in the marine environment, thus delaying gonadal development (Dutil 1986). In some populations, Arctic char forego marine migrations in the year before spawning (Gyselman 1994). Arctic char generally home to their natal system to spawn, but straying and stock mixing can be common (e.g., Dempson and Kristofferson 1987; Jensen et al. 2015), especially in years when individuals do not spawn (Moore et al. 2013, 2014). In some systems, spawning and overwintering sites are located in different areas, requiring a postspawning migration within fresh water (Johnson 1980; Beddow et al. 1998).

Relatively few studies have examined the spatial ecology of anadromous Arctic char during the marine phase of its life cycle (Moore et al. 2014). Existing data suggest that the migration from fresh water to the marine environment occurs after the river ice breaks, but before the sea ice is entirely melted (Bégout Anras et al. 1999). A period of estuarine residency follows marine entry and can last several days, at least until the sea ice is melted (Bégout Anras et al. 1999), and others have found that Arctic char may reside close to estuaries for the entire duration of the summer marine phase (Spares et al. 2015). Catches of Arctic char in fisheries in nearshore habitats tend to exceed offshore catches (Dempson and Kristofferson 1987; Finstad and Heggberget 1993), and some telemetry data also suggest a preference for nearshore habitats (Spares et al. 2012; Jensen et al. 2014). Preference for warmer and

less saline waters has also been suggested (Bégout Anras et al. 1999; Spares et al. 2012). Mark–recapture studies suggest that distances travelled by Arctic char at sea are typically short, with the majority of recaptures occurring less than 100 km from the tagging location (Dempson and Kristofferson 1987; Berg and Jonsson 1989; Finstad and Heggberget 1993), although some occasional long-distance migration events of more than 300 km have been documented (Jensen and Berg 1977; Dempson and Kristofferson 1987).

We used acoustic telemetry to describe the marine migratory behaviour and habitat use of anadromous Arctic char from the Cambridge Bay region of Nunavut. To address this overall objective, we examined three different spatiotemporal aspects of anadromous Arctic char habitat preference. First, we examined the timing of freshwater–saltwater transitions in relation to different biological variables (mainly size and sex). Second, we examined whether individuals from rivers distributed around Wellington Bay (Fig. 1) predominantly resided in or migrated out of Wellington Bay, and if they left, the timing of their departure and the direction they took once leaving the area. Third, we tested the hypothesis that tagged Arctic char preferred nearshore and estuarine habitats as opposed to offshore habitats, as suggested by previous studies (Dempson and Kristofferson 1987; Spares et al. 2012, 2015; Jensen et al. 2014). Furthermore, the largest commercial fishery for wild anadromous Arctic char in Canada operates in this region and targets several different stocks defined on a river-

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Table 1. Summary of tagging locations and biological characteristics of Arctic char tagged in 2013–2014.

Tagging location (year)	Lat. (°N)	Long. (°W)	Tagging dates	Capture method	N (M, F)	Fork length (mm)	Round mass (g)
Ekalluk River (2013)	69°24′	106°19′	10–12 July 2013	Gill net	30 (13, 16)	719 (57.0, 635–850)	4052 (1065.8, 2250–7100)
Halokvik River (2013)	69°10′	107°06′	15–21 August 2013	Weir	31 (12, 16)	706 (75.9, 520–869)	4257 (1284.4, 1600–7100)
Ekalluk River (2014)	69°24′	106°19′	11–13 July 2014	Gill net	30 (13, 17)	667 (84.8, 482–843)	3157 (1183.0, 1150–5950)
Surrey River (2014)	69°26′	106°40′	14–16 July 2014	Gill net	30 (15, 15)	691 (73.2, 569–833)	3548 (1066.1, 1850–5600)

Note: N is the number of individuals tagged at each location, and M and F represent the number of genetic males and females, respectively (note that the sum may not equal the total sample size because the genetic sex of some individuals could not be determined unambiguously). Fork length and round mass data show mean, with standard deviation (SD) and minimum–maximum range in parentheses.

by-river basis (the word "stock" is used throughout to refer to the management units that receive distinct quotas in the region, and we note that their biological validity remains to be tested). This fishery has been operating since 1960, with mean landings of 41 290 kg per year (Day and Harris 2013). Our last objective was therefore to test the hypothesis that currently recognized stocks mix at sea, with a particular emphasis on whether they mixed at the main fishing sites during the fishing periods.

Materials and methods

Area of study

The study centered on Dease Strait and Wellington Bay on the south shore of Victoria Island, Nunavut, Canada, close to the hamlet of Cambridge Bay (69°07′N, 105°03′W; Fig. 1). Arctic char are found in six watersheds in the focal region (from west to east): the Lauchlan River watershed (approximately 7935 km² area), the Halokvik River watershed (2450 km²), the Surrey River watershed (14 913 km²), the Ekalluk River watershed (5835 km²), the Kitiga River watershed (445 km²), and the Freshwater Creek watershed (1532 km²) (Kristofferson 2002; Fig. 1). Dease Strait and Wellington Bay (maximum depths of approximately 130 and 50 m, respectively) have relatively low salinity (~18 ppt above and ~27 ppt below the halocline, measured shortly after ice breakup; J.-S. Moore, unpublished data) and are covered by seasonal sea ice from approximately 22 October to 16 July (1981–2010 means from http://iceweb1.cis.ec.gc.ca; accessed 19 May 2015). Note that in 2014, the sea ice did not melt until the first week of August, which is unusual for the region. Tides in the region have a maximum tidal range of less than 1 m (www.tides.gc.ca).

Sampling and surgeries

All Arctic char for tagging were captured between July 2013 and August 2014 with continually monitored 139 mm mesh gill nets or at an enumeration weir erected at the Halokvik River. Captured fish were left to recover in a net pen for >2 h before the surgeries. Only individuals larger than 400 mm were selected and were anaesthetized with tricaine methanesulfonate (MS-222; 75 ppm solution). Individuals were photographed, weighed (round mass; g), measured (fork length; mm), and a ~1 cm² piece of pelvic fin tissue was preserved in 95% ethanol for genetic analysis. The transmitters (Vemco V16-4L (2013) and V16-4H (2014); length: 54 mm; mass in air: 19 g) were inserted through a ~3 cm incision on the ventral side of the fish off the midline by ~1 cm. The incision was closed by three to five simple interrupted stitches (2-0 curved needle, undyed braided). The total amount of time for surgery was less than 5 min, and gills were continuously bathed with a solution of 45 ppm MS-222. All instruments were sterilized in a 10% betadine solution between surgeries, and blades, needles, and surgical gloves were replaced. Nominal transmission delays were the same in both tagging years: 15 to 45 s from June to October and 600 s from November to May. Estimated nominal battery life, however, differed: 1275 days for tags used in 2013 and 1825 days for tags used in 2014. After the surgery, fish were placed

in a freshwater tub and observed (<15 min) and then transferred in a net pen for an additional 6–18 h before being released in the wild. All fish not behaving normally after the recovery period were sacrificed (4/126 tagged fish), and all others were released and swam off vigorously. All procedures have been approved by the Fisheries and Oceans Canada Animal Care Committee and conform to all animal care laws in Canada (permit No. FWI-ACC-2013-006). Over the course of the study, 121 Arctic char were tagged (mean fork length = 695 mm (standard deviation (SD) = 73 mm); mean mass = 3748 g (SD = 1194 g); Table 1). The smallest fish tagged was 482 mm in length and 1150 g in mass (tag to body mass ratio = 1.7%). Finally, we inferred the sex of tagged individuals using the genetic-sex determination protocol of Yano et al. (2013). In brief, DNA was extracted from the fin tissue, and the PCR assay described in table 2 of Yano et al. (2013) was used to infer the genetic sex (Table 1). Six individuals of known sex (three males and three females) were used as controls.

Acoustic array

Between 13 July and 8 September 2013, Vemco VR2W acoustic receivers were deployed at 42 stations in the Wellington Bay region, including in eight freshwater locations (Fig. 1; also refer to online supplementary material in Table S1[1]). At 40 of the stations, acoustic receivers were attached to acoustic releases (PORT-MFE, ORE Offshore, West Wareham, Massachusetts, USA) so that equipment could be retrieved the following year without the necessity of a surface buoy to avoid disturbance of our moorings by ice formation and breakup. The other two stations (CB13-03 and CB13-10 in Halokvik and Ekalluk rivers, respectively) were set in rivers only for the summer to ensure that no equipment was lost to ice scouring during the spring melt. Details of the deployment and recovery dates for each receiver can be found in the online supplementary materials[1].

The acoustic array was designed to match the study objectives while accounting for limitations of the environment and based on limited a priori knowledge of Arctic char migratory behaviour (Heupel et al. 2006). First, we placed one receiver at each of the six Arctic char-bearing rivers in the focal region to detect movements in and out of fresh water and to infer patterns of homing. Second, a curtain of 17 receivers was deployed across Wellington Bay at a mean distance of 1170 m between each receiver (distance to coast: 640 m on the west and 770 m on the east). While the distance between each receiver does not ensure maximal detection probability of fish passing through the curtain given our range (see Range testing section in supplementary material[1]), the equal distance between receivers allows a test of the hypothesis that char preferentially travel close to shore. Third, a series of six gates comprising pairs of receivers set roughly perpendicular to the coast were deployed. One such gate was deployed between each pair of char-bearing rivers in the study area, and a sixth gate was deployed at the area locally known as Gravel Pit after consultation with local resource users indicated the potential importance of this area for Arctic char. These gates were deployed based on

previous evidence that most movement is coastal, and the paired design allowed further testing of this hypothesis. Finally, receivers were set in the estuaries of the rivers where fish were tagged in 2013 to ensure that downstream migrants would be detected in 2014 even in the absence of river receivers to examine timing of marine migrations. The range of the equipment was tested extensively using several boat-based range tests and with fixed sentinel tags to detect temporal changes in detection probability (Kessel et al. 2014). Details of the range testing can be found in the online supplementary materials[1].

Data analysis

For the purpose of data analysis, all receivers in the curtain and in the gates are defined as "marine" receivers, the five receivers in the Halokvik and Ekalluk estuaries and the one in the Lauchlan River are defined as "estuarine" receivers, and receivers at the Halokvik, Surrey, and Ekalluk rivers and in Ferguson and Kitiga lakes are defined as "freshwater" receivers. We examined the timing of freshwater–saltwater transitions and tested whether individual traits explained variation in migration timing. For fish tagged in 2013 that returned to the marine environment in 2014, we recorded the date of first detection on a marine or estuarine receiver. The date of freshwater entry (i.e., when char return back to fresh water after having spent some time in the marine or estuarine environment) in 2014 was recorded for fish from all tagging locations, using the first freshwater detection subsequent to the last marine detection. If these detections were recorded on freshwater receivers that corresponded to the tagging location, individuals were considered to have "homed". Finally, for fish tagged in 2013 and detected both at the marine and freshwater entry, we calculated the total duration of the marine phase of the migration as the number of days between first marine detection and freshwater entry. We tested whether there was a relationship between the timing of these transitions and individual biological traits using linear mixed effects models (LMMs). We included genetic sex, fork length (mm), total mass (g), and Fulton condition factor ($K = 100(M/L^3)$), where K is the condition factor, M is the mass, and L is the fork length) as fixed effects and tagging location as a random effect factor. Because length and mass were highly correlated ($r = 0.93$), we only used length in these models to avoid problems with multicollinearity (no other continuous variables were correlated). Continuous variables were scaled (mean = 0; SD = 1) prior to analysis. The LMMs were fit using the function lmer in package lme4 (Bates et al. 2015), ranked based on AIC_c values calculated using the package AICmodavg (Mazerolle 2015), and the marginal and conditional R^2 were calculated for each model to estimate the amount of variance explained by the fixed effect only (marginal) and the fixed and random effect variables together (conditional) using the function r.squaredGLMM in package MuMIn (Bartoń 2016), all in R (R Development Core Team 2006). For the tagging locations inside Wellington Bay (i.e., Ekalluk and Surrey rivers), we also examined whether tagged individuals left Wellington Bay, and if so, when this event occurred. For this analysis, individuals that were only detected at receivers inside Wellington Bay or the curtain we defined as residents, whereas individuals that were detected at any receivers outside further east or west of the curtain we defined as nonresidents of Wellington Bay. Note that individuals detected on the curtain but nowhere else outside of Wellington Bay may have left without being detected on our array. We tested whether Wellington Bay residents and nonresidents differed in length, mass, condition factor, or genetic sex with t tests and χ^2 tests. For nonresidents, we recorded the last detection on the curtain before the first detection outside of Wellington Bay as the time of departure and the first detection on the curtain before the first redetection inside the bay as the time of re-entry. Because of the timing of deployment and retrieval of the array, which both occurred midsummer, we only included the 2013 data for re-entry and the 2014 data for

departure. Fish that were not detected on the curtain at departure or re-entry were not included here even if they were detected outside the curtain to avoid biasing timing estimates because of variable distance of receivers. We also excluded fish that were not detected in fresh water at the end of the summer to avoid biasing estimates if mortality was associated with any of the aforementioned traits. For fish that left Wellington Bay, we recorded the maximum distance travelled to gain insight into general patterns of movement outside Wellington Bay. To test the hypothesis that Arctic char preferred nearshore environments, we compared the total number of detections recorded on different receiving stations along the curtain deployed across Wellington Bay and at each of the six gates for the summers of 2013 and 2014 separately (24 July to 5 September for 2013 and 4 July to 8 August for 2014). For detections recorded at the gates, the hypothesis that increased number of detections were recorded on the receiver nearest to shore was tested using one-tailed Wilcoxon signed rank tests.

Results

Between July 2013 and September 2014, the array recorded a total of 376 236 acoustic detections (after quality filtering; see online supplementary materials and Fig. S3[1] for details). Details of the range tests results can be found in the online supplementary materials[1]. In brief, detection probability was generally above 50% within 500 m of the receivers (Fig. S1[1]). Depth had a strong influence on detection range, with lower detection probability at shallower depths (Fig. S1[1]). Close proximity detection interference (Kessel et al. 2015) was not a major issue at most receivers except the one in the mouth of Freshwater Creek (CB13-12; Fig. S1[1]).

Timing of saltwater–freshwater transitions

The median date of freshwater entry for Ekalluk River fish in 2013 was 10 September (range: 24 July – 11 October). In 2013, all fish unambiguously detected at freshwater entry homed, except for two fish tagged at the Halokvik River that were later detected ascending the Ekalluk River. The median date of first marine detection in 2014 for individuals tagged in 2013 was 7 July (range: 6 June – 3 August). These first marine detections were all recorded at the location of the individual's inferred freshwater entry in 2013. The median date of freshwater entry in 2014 was 25 August (range: 26 July – 5 September). Of the 62 unambiguous fresh water entries considered, five were recorded at the Halokvik River receiver, 47 at the Ekalluk River receiver, and 10 at the Ferguson Lake receiver (meaning they passed the Ekalluk receiver without being detected). Of those 62 fish, 35 were tagged in the Ekalluk River and all homed to the Ekalluk River, 17 were tagged at the Surrey River and all ascended the Ekalluk River, and nine were tagged at the Halokvik River and either homed (five) or ascended the Ekalluk River (four). The median marine duration in 2014 was 43 days (range: 7–61 days). Results of the general linear mixed model suggested that the biological traits measured did not strongly predict marine entry date, freshwater entry date, or marine duration (Table 2). Indeed, even if the full model had the lowest AIC_c value in all three cases, many models also had small ΔAIC_c values (indicating similar levels of support; Burnham and Anderson 2002), and the amount of variance explained was often less than 10% (Table 2; Fig. S4[1]). The only exception was for marine duration, where the model including only the Fulton condition factor explained 21.6% of the variance (lower condition factor was associated with longer marine duration). In addition, tagging location also explained over 20% of the variance in freshwater entry date and marine duration (Table 2), with fish tagged in Surrey and Halokvik rivers returning earlier to fresh water and having a shorter marine duration (see also Fig. S4[1]). Model-averaged parameter estimates for each model can be found in Table S2[1].

Table 2. Ranking of the linear mixed models (including the null model with only the random effect variable "Source" representing the tagging location) based on AIC_c values for the effects of biological traits (length, sex, Fulton condition index) on three timing of migration dependent variables: marine entry, freshwater entry, and marine duration.

	AIC_c	ΔAIC_c	AIC_c weight	mR^2	cR^2
Marine entry (N = 31)					
~ Length + Fulton + Sex + (1|Source)	219.23	0	0.5	0.063	0.063
~ Length + Sex + (1|Source)	220.25	1.02	0.3	0.030	0.030
~ Sex + (1|Source)	221.35	2.12	0.17	1.23×10^{-5}	1.23×10^{-5}
~ Length + Fulton + (1|Source)	227.31	8.08	0.01	0.053	0.053
~ Fulton + (1|Source)	227.95	8.72	0.01	0.037	0.037
~ Length + (1|Source)	228.22	8.99	0.01	0.029	0.029
~ (1|Source)	229.36	10.13	0	NA	0
Freshwater entry (N = 62)					
~ Length + Fulton + Sex + (1|Source)	449.51	0	0.23	0.016	0.317
~ Length + Sex + (1|Source)	450.1	0.59	0.17	0.007	0.327
~ Sex + (1|Source)	450.32	0.82	0.16	0.002	0.314
~ Length + Fulton + (1|Source)	450.63	1.12	0.13	0.015	0.322
~ Fulton + (1|Source)	450.71	1.2	0.13	0.014	0.312
~ Length + (1|Source)	451.27	1.76	0.1	0.006	0.332
~ (1|Source)	451.63	2.12	0.08	NA	0.317
Marine duration (N = 25)					
~ Length + Fulton + Sex + (1|Source)	194.03	0	0.57	0.258	0.258
~ Length + Fulton + (1|Source)	195.93	1.9	0.22	0.253	0.261
~ Fulton + (1|Source)	197.83	3.8	0.09	0.216	0.227
~ Length + Sex + (1|Source)	198.2	4.17	0.07	0.058	0.252
~ Length + (1|Source)	200.34	6.31	0.02	0.060	0.263
~ Sex + (1|Source)	200.64	6.61	0.02	0.007	0.233
~ (1|Source)	203.15	9.12	0.01	NA	0.239

Note: The marginal (mR^2) and conditional (cR^2) 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 models. N is the number of individuals included in the analyses.

Wellington Bay residency

A majority of tagged fish from the Surrey and Ekalluk rivers tagging locations left Wellington Bay in 2014 (44 of 69 individuals detected on marine and estuarine receivers outside of Wellington Bay; Fig. 2). Of the fish that remained in Wellington Bay, 15 were detected at least once on the curtain, suggesting that departure from the array is possible. Also note that six of the Surrey fish and one of the Ekalluk fish that stayed in Wellington Bay were captured a few days after being tagged in the commercial fishery operating at the Surrey River between 11 and 16 July and may have thus left the area if not captured. There were no differences in fork length, total mass, or condition factor between the fish that stayed and the fish that left Wellington Bay (Table 3), but there was a statistically significant increased frequency of females among the fish that remained residents of the bay ($\chi^2 = 4.39$; $p = 0.036$). The median date of curtain crossing for fish leaving the bay was 23 July (range: 4 July – 6 August). The median date of re-entry into the bay in 2013 was 26 August (range: 28 July – 5 September). Second, most of the fish that left Wellington Bay ventured west (39 of 44) and many (28) travelled as far as the Lauchlan River (Fig. 2). Third, few of the fish that left Wellington Bay went eastward (total five), and all of them were tagged at the Ekalluk River. Of those five fish, four travelled as far as Gravel Pit, an important subsistence harvest site for residents of Cambridge Bay. A local subsistence fisher also returned a tag from a fish captured east of Cambridge Bay more than 100 km (coastal distance) from the tagging location at Ekalluk River. Fourth, a number of fish either stayed in fresh water the entire summer or went directly back to fresh water after being tagged (total 11).

Preference for nearshore habitats

The patterns of detection on the curtain receivers and the gates suggested a preference for nearshore habitats. In both 2013 and 2014, the nearshore receivers along the curtain always recorded the greatest number of detections (Fig. 3a). Higher numbers of detections were also associated with higher numbers of individuals detected at those receivers, suggesting that the pattern was not the result of a few individuals residing near the shoreward receivers (Fig. 3a). Note, however, that the easternmost receiver consistently recorded most detections even if it detected a similar (in 2013) or lower (2014) number of unique IDs compared with the westernmost receiver. Detections at paired receivers on each of the six gates were also higher on the nearshore receiver; in 2013, the number of detections on the receiver closest to shore was higher for five of the six gates and in 2014 for all gates (Fig. 3b). In both years, the number of detections on the shoreward receiver significantly exceeded that on the receiver away from shore (2013: $p = 0.031$; 2014: $p = 0.016$; one-tailed Wilcoxon signed rank tests; df = 5).

Stock mixing and freshwater and estuarine residency

The numbers of detections at estuaries and freshwater receivers were much greater than the number of marine detections during both years (Fig. 4; Table S1[1]; Fig. S3[1]). The Halokvik River estuary and receivers at the Lauchlan River recorded more detections and individual tag IDs than other estuarine or marine receivers (Fig. 4). Fish from all tagging locations were detected simultaneously at these two receivers, indicating extensive stock mixing at these sites. In both estuaries, there was also evidence of increased residency during spring tides (although this pattern was less strong in the Halokvik River estuary for number of unique IDs; Fig. 4). This pattern was unlikely to be the result of increased detection probability during spring tides, since detection probability of the sentinel tag in the Halokvik River estuary did not change substantially during this period (Fig. S2[1]). There was no evidence of increased estuarine or freshwater residency during spring tides at any other location on the array (Fig. 4). The Surrey River receiver also recorded several detections, but only a few days after fish were

Fig. 2. General patterns of movements of 93 Arctic char tagged at three tagging locations in 2013 and 2014 and detected in summer 2014. Black arrows indicate movement from tagging location for fish tagged in 2014 or from fresh water for returning migrants tagged in 2013. The thickness of the arrows is proportional to the number of individuals observed performing a specific movement pattern (also indicated by numbers). Note that these movements are not necessarily simultaneous and represent a synthesis for the entire summer largely based on detections at maximum distance from tagging locations. The arrows pointing in Wellington Bay represent fish that were not observed outside of the bay, either because they did not leave the bay or because they were not detected elsewhere on the array. Arrows pointing back to fresh water represent individuals that either never left or went directly back to fresh water after tagging. The grey arrow in the Halokvik 2013 panel represents individuals that migrated to the Lauchlan River and subsequently were detected on receivers inside Wellington Bay. Of those six, four migrated up the Ekalluk River in August 2014 and two returned to the Halokvik River.
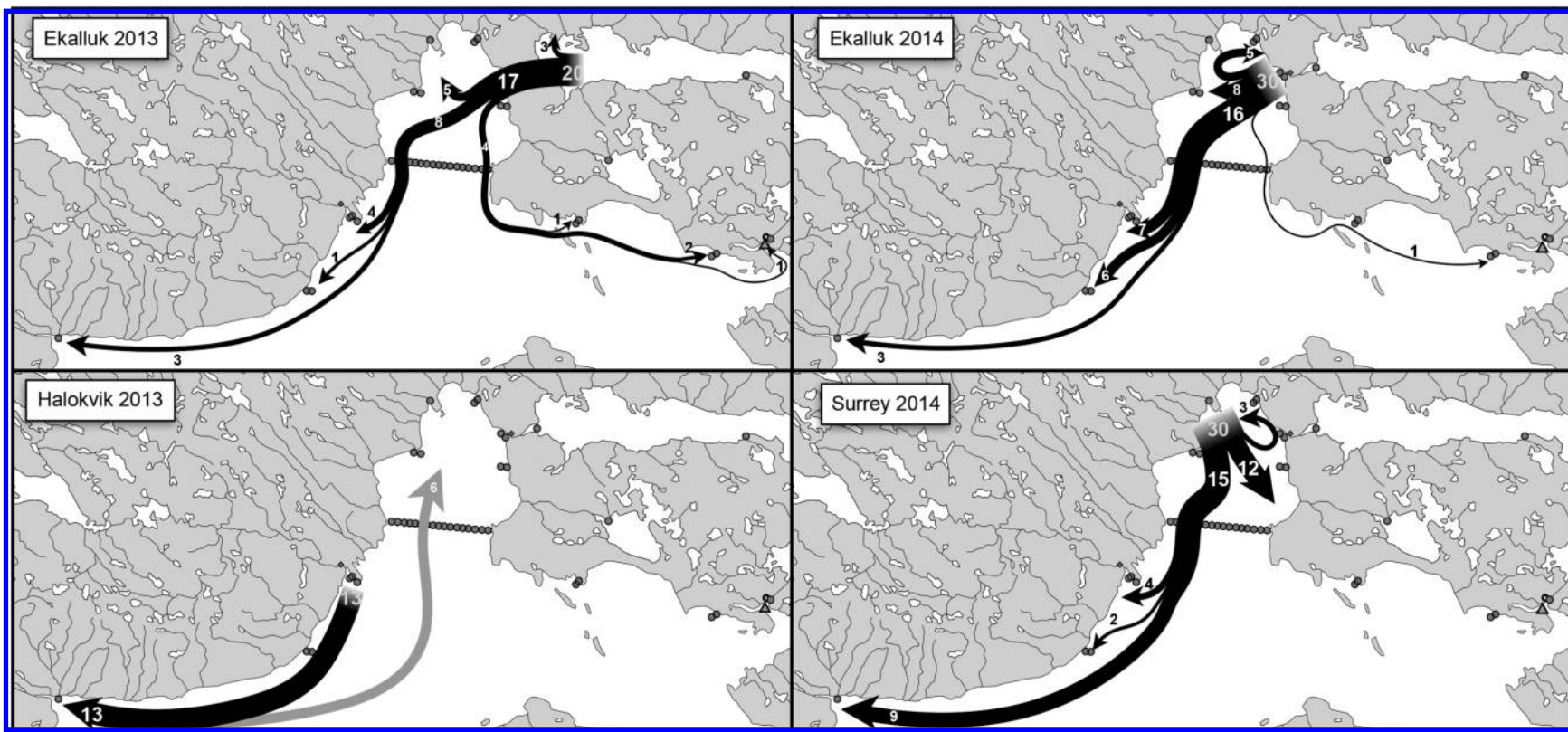
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Table 3. Biological differences between tagged Arctic char that left Wellington Bay (nonresidents) and those that resided (residents) in the bay for the entire duration of their marine phase in 2014.

	Sex				Fork length (mm)			Mass (g)			Fulton condition factor		
	Female	Male	χ^2	p	Mean (SD)	t	p	Mean (SD)	t	p	Mean (SD)	t	p
Residents	14	5	4.39	0.036	705 (63.2)	1.589	0.118	3608 (869.6)	0.759	0.451	1.02 (0.14)	−0.900	0.377
Nonresidents	13	20			672 (86.3)			3368 (1390.9)			1.06 (0.08)		

Note: Nonresidents were individuals that were detected at least once outside of Wellington Bay (boundaries defined by the "curtain") and were subsequently detected entering fresh water (to avoid trait-related mortality to bias estimates).

tagged at that location, suggesting that tagged fish left the area shortly after recovering. No other detections were recorded at that receiver for the remainder of the summer.

Discussion

In this study, we tracked 121 acoustically tagged anadromous Arctic char with a fixed array of 42 moored acoustic receivers deployed throughout the Wellington Bay and Dease Strait area, Nunavut, over an entire year. The marine phase of the migration typically lasted from early July to late August, but interindividual variation in the timing of saltwater–freshwater transitions was important. We found weak associations between biological characteristics (size and sex) and the timing of these transitions. We also showed that a majority of tagged individuals left Wellington Bay and that they utilized estuarine habitats throughout the summer. When travelling outside of estuaries, we found evidence of a preference for nearshore habitats, with most detections occurring <1.5 km from shore. Finally, our study demonstrated stock mixing in the marine environment throughout the summer, including at known commercial fishing locations, which has implications for fisheries management in the region.

Timing of saltwater–freshwater transitions and Wellington Bay residency

Arctic char migrate to marine environments to exploit their increased productivity (Gross et al. 1988) and generally attain faster growth than nonmigratory individuals (Rikardsen et al. 2000). In fact, summer feeding is crucial for Arctic char to build the energy reserves required for the winter months, where much energy is expanded for spawning and survival with little opportunity for replenishment until the next summer (Dutil 1986). At such northern latitudes, however, productive marine waters are only accessible during the very short period when rivers are free of ice. Given this constraint, the dates of saltwater–freshwater transitions and extent of marine durations reported here are similar with other estimates from the region (Bégout Anras et al. 1999; McGowan 1990) or other comparable populations (Berg and Berg 1993; Klemetsen et al. 2003). A striking result was that interindividual differences in run timing were important, with extreme values often differing by more than 2 weeks from the median. This represents a large proportion of the observed median marine duration of 43 days. Understanding why some individuals do not use the entire ice-free period to maximize summer marine feeding will be important to predict growth pattern in these stocks, especially in the face of climate change. Tagging location seemed to be the strongest predictor of both freshwater entry date and marine duration, with fish tagged at the Surrey River and Halokvik River returning earlier. The earlier return of these fish might be linked to the much longer migrations needed to reach the headwater lakes in these systems (see Fig. 1). Note, however, that all but five of these fish returned to Ekalluk River in 2014, suggesting that timing of return might be genetically determined and not linked to the specific river where the upstream migration occurs in that year. Interindividual differences in size or sex, however, did not strongly predict timing of freshwater–saltwater transitions in this system. The only exception was the observation that the negative relationship between condition fac-

tor and marine duration explained 21.6% of the variation in marine duration. This could be explained by the earlier return of the Halokvik fish, which were tagged in the fall after the marine feeding period and therefore had higher condition factor than Ekalluk River fish, which were tagged in the spring as they entered the salt water after overwintering in fresh water. Data on condition factor at the time of upstream migration would therefore be needed to validate this finding.

In other anadromous salmonids, older and larger individuals tend to migrate upriver before younger and smaller ones (Atlantic salmon (*Salmo salar*): Shearer 1990; Klemetsen et al. 2003; Pacific salmon (*Oncorhynchus* spp.): Quinn 2005). Previous studies have also indicated that older and larger Arctic char tend to enter salt water earlier in the spring (Dempson and Kristofferson 1987; Berg and Berg 1989; Berg and Jonsson 1989). We did not observe either of these patterns in the present study. One likely explanation for the absence of run structuring is that we selected large individuals to minimize potential negative impacts of tagging. For instance, Berg and Jonsson (1989) found that veteran migrants returned earlier than first-time migrants, but all tagged fish in the present study were probably veteran migrants. Previous studies also suggested that female Arctic char returned to fresh water before males (Moore 1975; Berg and Berg 1993), but this pattern was not observed in the present study. Females preceding males during the upstream migration is not necessarily a widespread phenomenon in other salmonids. For example, there is no difference between sexes in run timing in Atlantic salmon (Fleming 1996; but see Jonsson et al. 1990), and males tend to return before females in Alaskan chum salmon (*Oncorhynchus keta*; Molyneaux and Dubois 1998).

Unlike Atlantic and Pacific salmon, who migrate over hundreds of kilometres offshore (Hansen and Quinn 1998; Quinn 2005), anadromous salmonids of the genus *Salvelinus* tend to remain closer to their natal stream during marine migrations (e.g., Spares et al. 2015; Curry et al. 2006). Our results showed not only that a substantial proportion of tagged fish left Wellington Bay, but also suggested that the predominant pattern of migration was towards the west. These results further our understanding of critical marine habitats for the species in the region and suggest that feeding opportunities are increased in these areas. Such information will be useful to frame questions in future studies of relative productivity and prey abundance in the region. We also documented that there were three times more females than males among the tagged fish that were never detected outside of Wellington Bay (i.e., that were presumed to have resided in Wellington Bay the entire summer). Dempson and Kristofferson (1987) also observed a greater proportion of females than male in the inshore areas off the coast of Labrador. These observations suggest that the costs and benefits of long migrations might differ between sexes in anadromous Arctic char, but more data would be required to ensure this pattern is repeatable.

Coastal movement and preference for estuarine and freshwater habitats

Documenting habitat use provides crucial information for mitigating impacts of human activities and environmental change and is the first step in identifying what factors make these habitats favorable. The present study reinforced previous findings that

Fig. 3. Evidence of preference for nearshore habitats in Cambridge Bay area Arctic char. (*a*) Area plots showing the total number of detections recorded in summer 2013 (top) and 2014 (bottom) on each of the 17 acoustic receiving stations deployed across Wellington Bay (i.e., the curtain identified in Fig. 1; where "1" is the westernmost station and "17" is the easternmost). The colours identify the tagging location of recorded individuals: EK13 for Ekalluk River 2013, EK14 for Ekalluk River 2014, HA13 for Halokvik River 2013, and SU14 for Surrey River 2014. The numbers on the graph show the number of unique tag IDs (i.e., individual Arctic char) recorded at each receiving station. The receivers were deployed on 25 July 2013 and were recovered on 8 August 2014. The last detection recorded on the curtain in 2013 was on 5 September and the first detection in 2014 was on 4 July. (*b*) Strip charts showing the total number of detections in summer 2013 (top) and summer 2014 (bottom) for each pair of receivers in the six gates deployed along the shore of the study area (the gates were all deployed and retrieved at different times, but each pair of receiver in a gate were deployed and retrieved simultaneously). Lines connect the number of detections at the receiver closest to shore (shore) to that of the receiver in the same gate but deployed away from the shore (away). The thick black lines show the median number of detections for each class of receivers, and the *p* values are for one-tailed Wilcoxon signed rank tests. The gate number (see Fig. 1) is provided for each pair of receivers. [Colour online.]
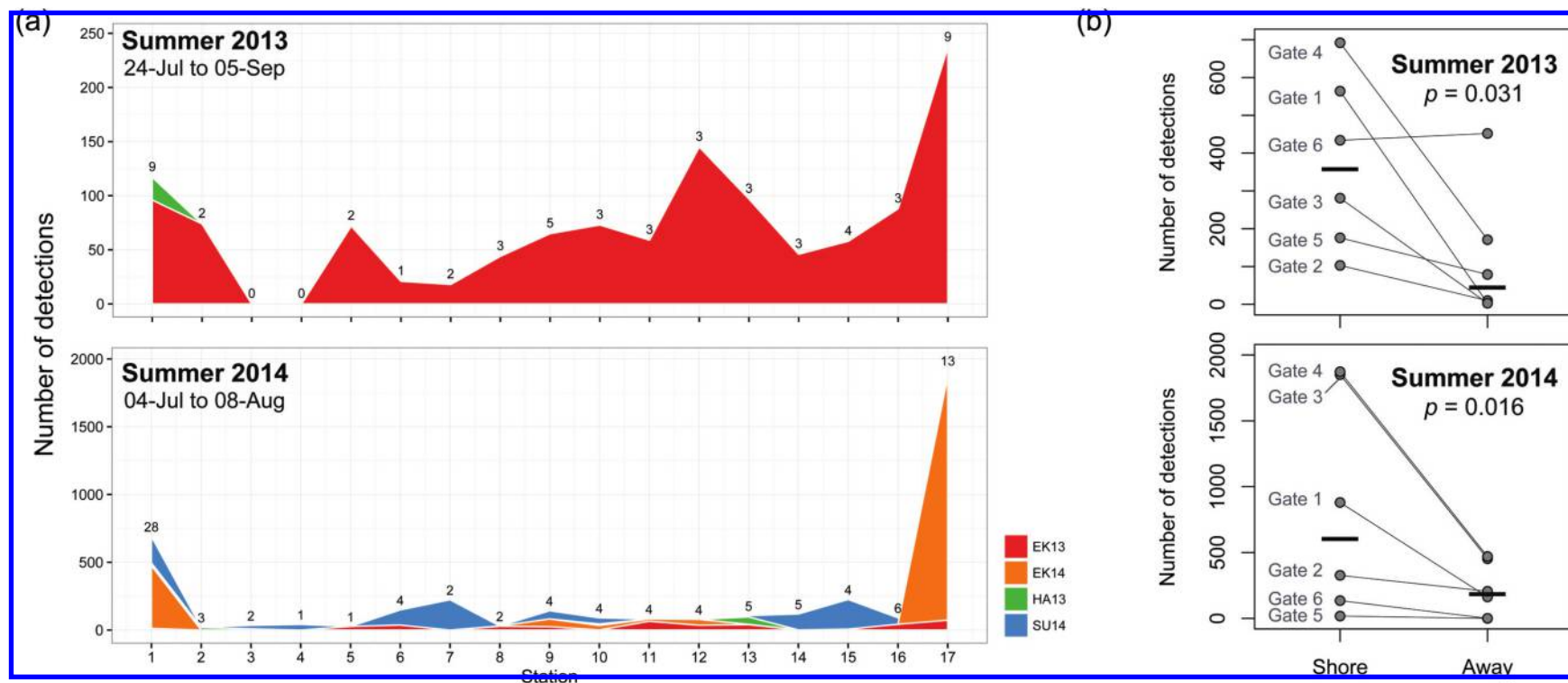
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Fig. 4. Total number of detections (*a*) and number of unique tags IDs (i.e., individual char) (*b*) of tagged Arctic char recorded daily during summer 2014 at six receiving stations located in estuarine or freshwater environments in the Cambridge Bay region. For both estuaries, only one receiver is shown to avoid simultaneous detections of single transmissions on multiple receivers (other receivers showed comparable number of detections). The total number of daily detections on all 17 receivers on the curtain (summed; not corrected for multiple detections) is also shown for comparison in the bottom panel. The colours identify the tagging location of recorded individuals: EK13 for Ekalluk River 2013, EK14 for Ekalluk River 2014, HA13 for Halokvik River 2013, and SU14 for Surrey River 2014. The vertical lines indicate phases of the lunar cycle associated with spring tides (solid lines for full moon and dashed lines for new moon). Shaded areas indicate periods during which individual receivers were not recording data. [Colour online.]
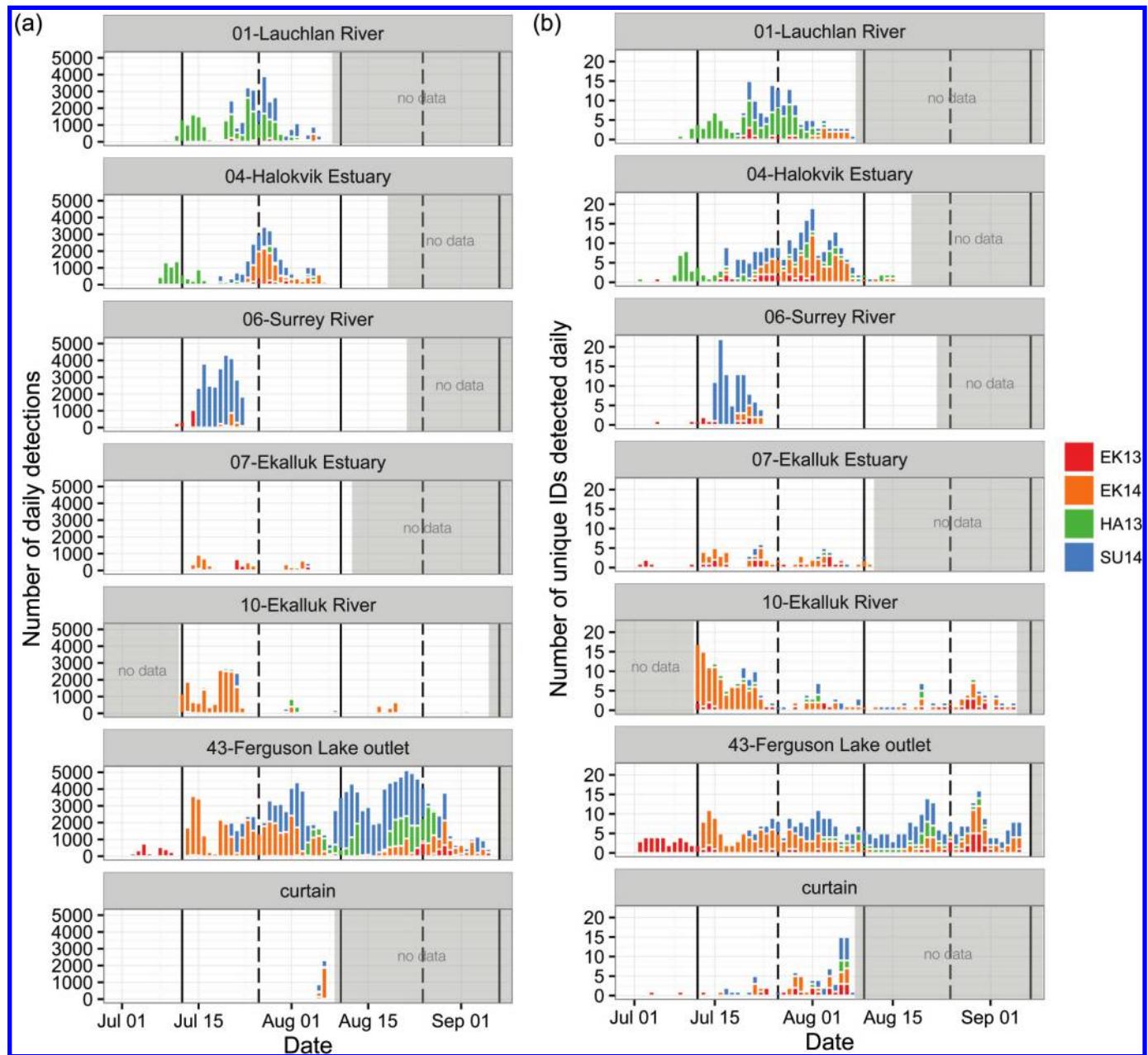
nearshore and estuarine habitats are preferred by Arctic char during their marine migrations (e.g., Dempson and Kristofferson 1987; Spares et al. 2015). Indeed, we observed that Arctic char rarely ventured more than 1.5 km from shore and that they spent a large proportion of the marine phase of their migration in or close to estuarine and freshwater habitats. Previous studies have also provided evidence that Arctic char at sea tend to remain close to shore (Johnson 1980; Dempson and Kristofferson 1987; Klemetsen et al. 2003; Jensen et al. 2014; Spares et al. 2015), although movement further offshore is also possible (Gyselman 1984; Rikardsen

and Amundsen 2005). In the present study, both the curtain and the gates showed clear evidence that Arctic char preferred the very nearshore habitats. Given the disposition of the receivers and the detection range of our equipment, it can be deduced that most detections were from fish swimming less than ~1.5 km from shore. Range tests conducted on the two easternmost receivers of the curtain indicated that detection probabilities were similar (Fig. S2[1]), suggesting that these patterns do not result from lower detection probability on receivers located further away from shore. Fish detected at the curtain and gates were typically only

detected for a few minutes before leaving the area. In contrast, continuous detection of individuals for hours to days was typical at estuarine and freshwater receivers. From these observations, we hypothesize that fish detected at the curtain and the gates were in transit and that potential increased feeding opportunities close to shore are an unlikely explanation. Nonetheless, opportunistic feeding while in transit might be important, and studies of relative prey abundance in inshore versus offshore waters would seem valuable. Shallower waters might provide a refuge from predation, but the importance of predation by seal, the only potential predator in the area, is unknown (we rarely observe scar marks from seals, and no systematic assessment of predation exist from the region). Because fish seemed to be in transit, following the shore might make navigation easier. Indeed, following the shore provides the shortest route between most estuaries in the area, and increased detections near shore might simply reflect geography as opposed to an active preference for nearshore habitats. Preference for nearshore habitats seems widespread in Arctic char and other anadromous salmonid species (Curry et al. 2006; Quinn and Myers 2004), and the present system would appear well suited to investigate possible explanations for this behaviour.

The much larger number of detections recorded at estuarine and freshwater receivers compared with marine receivers throughout the summer also suggested an active preference for these habitats. Recently, Spares et al. (2015) observed that acoustically tagged Arctic char resided in estuaries a third of the time during their marine phase and returned to estuaries on average every 9 days. Harwood and Babaluk (2014) also inferred a preference for estuarine habitats from tag return data in Hornaday River Arctic char. The closely related brook char (*Salvelinus fontinalis*) also displays a preference for estuarine habitats (Curry et al. 2006). In both these studies, however, tagged individuals preferred their natal estuaries, and Curry et al. (2006) suggested this may be explained by the physiological barrier posed by the cold, saline waters of the open ocean. Our results show that if such waters are indeed a barrier to Arctic char movement, it is not an absolute one. Previous studies have also shown that when in estuaries, individuals tended to move closer to the river during ebb and flood tides, but moved further at low tide (Spares et al. 2015; Curry et al. 2006). The design of our array did not allow observation of such fine-scale movements within estuaries, but we did observe a potential influence of the lunar tidal cycle on migrations, with greater numbers of detections in the Lauchlan and Halokvik estuaries at spring tides. Currents out of fresh water should be lower and salinity higher during spring tides, and the increased flooding of tidal areas may increase terrestrial nutrient inputs to the littoral zone, but it is not known whether any of these factors could explain increased estuarine residency during spring tides, especially since tides are small in the region (tidal range <1 m).

Three hypotheses have been proposed to explain why estuarine habitats might provide advantages to anadromous salmonids: productive foraging, refuge from predators, and intermediate salinities to facilitate transitions between saltwater and freshwater physiological control systems (Thorpe 1994). As indicated before, we have no evidence of important predation targeting adult Arctic char besides humans. Given the importance of summer feeding for the overall energy budget of Arctic char (Dutil 1986), increased feeding opportunities in estuaries should be seriously considered. Little is known, however, on Arctic char diet from the Cambridge Bay region, in part because they usually have empty stomachs prior to the upstream migration when sampling is usually conducted (Day and Harris 2013). Nonetheless, future studies could use stable isotopes and fatty acids to infer diet composition. Small fish, and to a lesser extent zooplankton, predominate in the diet of anadromous Arctic char in other regions (Dempson et al. 2002; Rikardsen et al. 2007; Harwood and Babaluk 2014). Future studies documenting the diet of Arctic char in the region, as well as rela-

tive abundance of prey items in estuaries versus other areas, would be necessary to understand the factors determining preference for estuarine environments. Estuaries could also have great importance for osmoregulation in Arctic char. While anadromous Arctic char would no longer be transitioning between freshwater and saltwater physiological states midsummer (Bystriansky et al. 2007), there may still be growth benefits to residing in brackish water. Indeed, salinity in estuaries might be closer to blood osmolarity, leading to lower energy expenditures to maintain ion homeostasis and could thus result in higher growth (Wootton 2011; Gunnarsson et al. 2014). In short, estuaries seem to provide critical habitats for Arctic char during their summer migrations, and future studies should focus on the factors that make these environments favorable.

Stock mixing: implications for fishery management

We observed substantial mixing of stocks at several locations, including commercial fishing areas, and throughout the entire summer. Stock mixing and (or) straying has been documented in Arctic char (e.g., Moore et al. 2013, 2014; Jensen et al. 2015), including in the Cambridge Bay region (Dempson and Kristofferson 1987). The telemetry approach used in the present study, however, showed with a greater level of detail that stock mixing is extensive and occurs throughout the summer. Indeed, the simultaneous detection of fish from all tagging locations at the receivers at the Lauchlan and Halokvik estuaries, and in the Ekalluk River receivers (Fig. 4), suggested that all fish from the Wellington Bay stock complex travel synchronously to, and reside together in, estuarine habitats. Furthermore, fish did not all return to the same river at which they were tagged to spawn and overwinter at the end of the summer, as documented by Dempson and Kristofferson (1987) and Kristofferson (2002).

An important result for fishery management is the observation that all individuals tagged at the Surrey River migrated upstream into the Ekalluk River – Ferguson Lake system at the end of the summer. Because tagging occurred simultaneously with commercial fishing at the same area (the Surrey River is the only stock in the region where fishing occurs in July shortly after the river-ice breaks), we are confident that our sampling targeted the same fish as the commercial fishery. This observation is also consistent with genetic evidence showing a lack of genetic differentiation between individuals caught in the Surrey River and Ekalluk River fisheries (L. Harris, J.-S. Moore, R. Bajno, and R. Tallman, unpublished data). There is currently a distinct quota of 9100 kg assigned to the Surrey River stock, and harvests between 1999 and 2009 averaged 7441 kg (Day and Harris 2013). Our results suggest that this stock does not represent a demographically independent unit and should be considered part of the Ekalluk River stock. The current practice of fishing at the Surrey River in the spring has remained unchanged over the past several decades, with no apparent negative effects on the Ekalluk River stock (see table 2 in Day and Harris 2013). Management should nonetheless recognize that both the Surrey River and Ekalluk River fisheries target fish from the same stock.

Anadromy is an important trait in many salmonid species, but it is expressed at different levels, with species varying in the amount of time spent at sea or in the spatial extent of their marine habitat use (Quinn and Myers 2004). Because of the extreme environments it inhabits, documenting patterns of migration at sea of anadromous Arctic char can provide insights into our understanding of marine migrations of other species displaying low levels of anadromy, such as cutthroat trout, brown trout, brook char, or Dolly Varden (Quinn and Myers 2004). A key finding was that estuaries were used by Arctic char throughout the summer. Interestingly, however, Arctic char did not remain in their natal estuaries for the entire summer as documented in other Arctic char and brook char populations (e.g., Curry et al. 2006; Spares et al. 2015), but rather moved synchronously from estuary to es-

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tuary. Understanding why char did not spend the entire summer in a single estuary could help better understand the importance of estuaries for salmonids in general (Thorpe 1994). Furthermore, the continued operation of the acoustic array described in the present study will also document interannual variation in migratory behaviour, thus helping to identify the environmental determinants of the patterns and timing of migrations. Such data would provide important insight regarding the impacts of a rapidly warming Arctic on the migrations of Arctic char and other northern species of anadromous salmonids.

Acknowledgements

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