

Residency and movement patterns of Arctic charr *Salvelinus alpinus* relative to major estuaries

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Estuarine residency and marine movements of 43 anadromous Arctic charr *Salvelinus alpinus* (mean \pm s.d. fork length = 523 \pm 97 mm) were examined using acoustic tracking in inner Frobisher Bay (IFB; 63° N; 68° W), Canada, from July to September 2008 and 2009. A mean \pm s.d. migration duration of 63 \pm 7 days occurred from late June to early September. Detected *S. alpinus* were either continuously (maximum 34 days) or intermittently present in estuarine zones, on average residing approximately one third of time tracked and returning once every 9 days. Significantly higher estuarine residency during the final 15 migration days suggested that a transition phase may occur prior to freshwater re-entry. Low travel rates during flood tide suggested individuals staged before accessing intertidal and estuarine zones. Although the two main estuaries were c. 22 km apart, 19% of tagged individuals used both. Individuals remained relatively close to freshwater overwintering systems, although late-migration inter-estuarine movements may have indicated natal homing. Approximately half of the individuals exhibited extra-estuarine travel, mostly during mid-migration, but remained within 3 km of shore ranging < 30 km straight line distance (SLD) of either estuary. It was concluded that IFB *S. alpinus* (1) spent a significant portion of their migration within or adjacent to the estuaries and (2) had a restricted marine distribution within 30 km SLD of the river mouths.

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Key words: acoustic tracking; estuarine fidelity; marine distribution; tidal phase; travel rate.

INTRODUCTION

Anadromous Arctic charr *Salvelinus alpinus* (L. 1758) undertake a short, seasonally determined, summer sea residency of 1–4 months (Sprules, 1952; Dempson & Kristoferson, 1987; Bégout Anras *et al.*, 1999; Gulseth *et al.*, 2000; Klemetsen *et al.*, 2003; Morris & Green, 2012). Migration to the sea occurs in early spring as soon as rivers are ice-free (Moore, 1975; Gulseth & Nilssen, 2000; Klemetsen *et al.*, 2003) and individuals remain in warm, estuarine waters up to 10 days during a marine transition phase (Bégout Anras *et al.*, 1999). Marine migrations significantly increase or restore *S. alpinus* somatic growth, fecundity and lipid reserves (Dutil, 1986; Dempson & Kristoferson, 1987; Jobling *et al.*, 1998). Most anadromous populations overwinter in fresh

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water leaving the sea before water temperatures drop to 0° C (Moore, 1975; Dempson & Kristofferson, 1987); however, some Norwegian populations have been shown to overwinter in salt water (Jensen & Rikardsen, 2012).

Summer marine migrants travel along shorelines (Moore, 1975; Spares *et al.*, 2012), although some, mainly males (Dempson & Kristofferson, 1987), have been caught up to 5 km offshore (Rikardsen & Amundsen, 2005). Large, non-ripening fish travel the greatest distances (Dempson & Kristofferson, 1987), whereas smaller fish (fork length, $L_F < 200$ mm) remain close to natal river mouths. Marked fish have been recaptured 25–940 km away from the river mouth of origin within one season (Dempson & Kristofferson, 1987; Bégout Anras *et al.*, 1999; Klemetsen *et al.*, 2003), moving at rates up to 0.6 km h⁻¹ (13.8 km day⁻¹; Bégout Anras *et al.*, 1999). Considerable mixing of individuals occurs for populations within 80 km of each other (Moore, 1975; Dempson & Kristofferson, 1987). Marine migrants have been observed moving into intertidal zones and up rivers with flooding tides (Moore, 1975; Spares *et al.*, 2012).

Marine migration duration, stock mixing and movements of *S. alpinus* are influenced by local environmental conditions, availability of food resources, fish size, sex and state of maturation and proximity to other river systems (Dempson & Kristofferson, 1987). Relatively few details of marine distribution and movements, however, have been documented due to difficulties of tracking fishes underwater (Dadswell, 2009). Rikardsen *et al.* (2007) described the summer temperature and depth preferences of *S. alpinus* using archival tags, and suggested the need for concurrent spatial information. Acoustic tracking has illuminated aspects of marine entry transition, summer migration and overwintering phases (Bégout Anras *et al.*, 1999; Jensen & Rikardsen, 2008; Jensen *et al.*, 2014), but as of yet, no study has described spatial and temporal summer marine movements relative to freshwater inputs and tidal phase.

Environmental niche studies are important for predicting species-specific responses to climate change (Rikardsen *et al.*, 2007). Due to extreme variation in anadromous *S. alpinus* life histories, regional knowledge of marine migration timing and behaviours is needed to enhance fisheries management and conservation efforts (Brenkman *et al.*, 2007; Swanson & Kidd, 2009; Jensen *et al.*, 2014), especially in populations potentially isolated from outside recruitment (*i.e.* straying) and subjected to increasing human demands. This study describes the summer marine movements and residency of *S. alpinus* relative to freshwater inputs and tide phase. The aims were to (1) determine the degree of site fidelity adult *S. alpinus* have to river mouths and immediate estuaries and (2) characterize the marine movements (spatial patterns, migration range and travel rates) of individuals relative to two main estuaries, Bay of Two Rivers (BR) and Sylvia Grinnell (SG); migration period (early, mid and late) and tidal phase (high, ebb, low and flood). It was hypothesized that individuals will be limited to <40 km maximum straight line distance (SLD) from river mouths due to availability of freshwater input, and that movement patterns and travel rates will be influenced by daily tide phase (Moore, 1975).

MATERIALS AND METHODS

STUDY AREA

Frobisher Bay is a semi-enclosed, macrotidal bay located in southeast Baffin Island, Nunavut, Canada. Its length is divided by islands into a larger outer and a smaller inner bay. Inner Frobisher

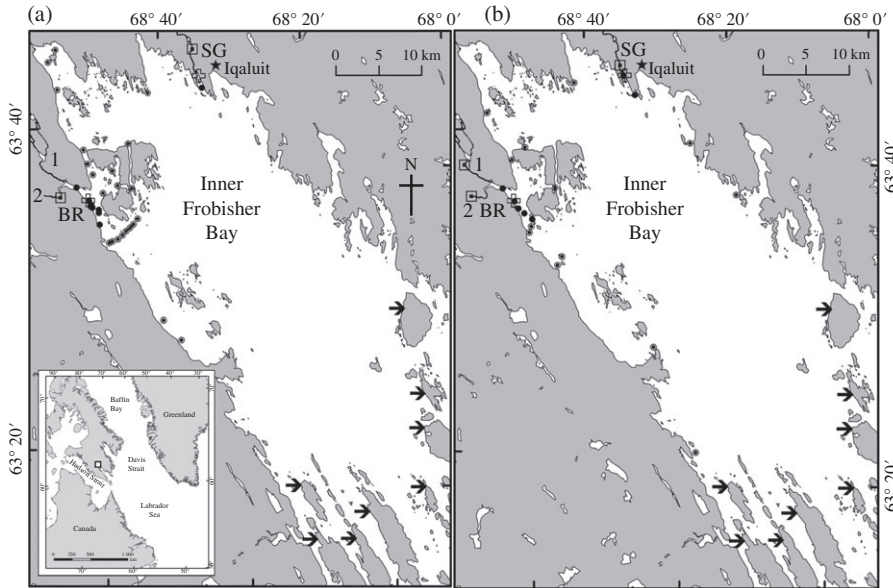


FIG. 1. Location of inner Frobisher Bay, Nunavut, Canada, showing the tag sites (+) at Bay of Two Rivers (BR) and Sylvia Grinnell (SG) estuaries, north-west (1) and south-west (2) branches of the Armshow River, city of Iqaluit (★), and Channel Islands (➔). Estuarine (●), extra-estuarine (⊙) and freshwater (◻) zone acoustic receivers (VR2/VR2W) are shown for (a) 2008 and (b) 2009.

Bay (IFB; 63° N; 68° W) is c. 25 km × 70 km [Fig. 1(a)] with depths <250 m. Maximum tidal amplitudes of 11 m move c. 17 km³ of water at a mean velocity of 1 m s⁻¹ (3.6 km h⁻¹) through the bay during a tidal cycle. Sea-ice cover occurs from November to June, with break-up around mid-June, leaving the bay relatively ice-free from July to October (Spares *et al.*, 2012).

Two major river systems within IFB, the Sylvia Grinnell River (SGR; 63° 44' N; 68° 34' W) and Armshow River [AR; 63° 36' N; 68° 50' W; Fig. 1(a)], contain anadromous populations of *S. alpinus*. Riverine temperatures from August to September range from 6.6 to 15.9° C. At its mouth, the SGR forms three branches, each with its own waterfall. Two of these waterfalls are adjacent to each other and their plunge pools form the innermost extent of the estuary. High tide rises to all three falls, reducing flow to rapids during spring tides. At low tide, c. 2 km of intertidal zone is exposed, yet shallow runoff still continues to the low tide mark. The AR consists of the north-west and south-west branches, with both emptying into the same cove c. 450 m apart at the head of BR estuary. The cove floods at high tide and offers a lagoon with a surface freshwater lens over top of a saline bottom layer at low tide. The lagoon empties over the intertidal flats, yet runoff is too shallow for passage of large fish. Runoff funnels into a 2 m deep tidal channel which begins at the BR tag site and runs c. 2 km, tide dependent, to the low tide mark. Approximately 12 km² of intertidal flats are exposed at low tide (Spares *et al.*, 2012).

The two estuaries offer significantly warmer (mean 6.4° C) and brackish (mean salinity 15.5) water in the top 3 m. This upper layer decreases in thickness with increasing distance from river mouths, often occurring over 4 km from freshwater inputs depending on river discharge. Outside the estuarine zone, water below the surface layer becomes significantly colder (<3° C) and increasingly saline (>30; Spares *et al.*, 2012).

ACOUSTIC TRACKING

Marine migrating *S. alpinus* to be tagged and released were captured intertidally with a 4.5'' (11.5 cm) gillnet or by spin casting at BR during 21–25 July and 9–11 August 2008 ($n = 41$),

and 17–21 July plus 14 August 2009 ($n = 16$). In 2009, *S. alpinus* ($n = 4$) were also captured by rod, tagged and released at the SG estuary during 7–9 July (Table I). Individuals were surgically implanted with one of the four models of acoustic transmitters [V6 (180 kHz frequency), V7, V9TP, V13TP (69.9 kHz frequency); length 18, 23, 39, 36 mm; diameter 6, 7, 9, 13 mm; mass in water 0.6, 1.0, 2.2, 6.0 g; battery life 113, 140, 205–510, 1030 days; Vemco; <http://vemco.com/>], according to procedures outlined by Spares *et al.* (2012). In 2009, 19 additional individuals captured at BR were Floy ID tagged only and released for recapture information. Fishers were requested to release tagged individuals if unharmed or, if dead, to be delivered to the Nunavut Research Institute. Upon receipt, a reward was offered.

A passive acoustic receiver array (VR2W, Amirix/Vemco Ltd) was used to track tagged *S. alpinus* from 2 August to 30 September 2008 [Fig. 1(a)], and 24 June to 26 September 2009 [Fig. 1(b)]. Thirty receivers were deployed from 2 to 8 August 2008, covering BR, its adjacent coastlines extending *c.* 15 km north-west and south-east, and 1 km upstream the south-west AR. Three receivers were subsequently relocated to the SG on 21 and 22 August. Receiver recovery occurred from 20 to 30 September. Twenty-eight receivers (VR2/VR2W) were deployed from 24 June to 23 July and recovered 9 to 26 September 2009. The 2009 array again monitored the two estuaries and their respective rivers, but extended to include the coastline between them and along IFB's north and south coastlines ending near the Channel Islands [Fig. 1(b)]. Five receivers were lost during the two tracking periods.

Receivers were deployed according to the procedures outlined by Spares *et al.* (2012). Detection range was tested from 13 August to 29 September 2008 at the BR tag site in a 2 m deep tidal channel with a V13TP transmitter tied 0.5 m off the bottom to a vertical riser with a clear line of sight to a VR2W receiver anchored just off the bottom 47 m away. Detection efficiencies were calculated for the V13TP transmitter during *S. alpinus* tracking (13–29 August) and range test period. To determine any effects of tide phase on detection efficiency, detection efficiencies were calculated for each tide phase (high, ebb, low and flood) from 13 to 29 August. In 2009, a V7 was moored <10 m below a surface float for a minimum of one tidal cycle at stations 200–800 m from an intertidal VR2W receiver located at the mouth of the BR tidal channel corresponding to the low tide mark.

MARINE MIGRATION

Duration

The beginning of the marine migration 2009 occurred during ice-out in the SGR and was confirmed by the first catches of *S. alpinus* in the estuary below the falls at the river mouth. Duration was calculated as the period between saltwater entry and freshwater re-entry. Freshwater re-entry was considered the last saltwater detection by receivers closest to head of tide. If no marine detection was recorded near the head of tide, the first detection by a freshwater receiver in either the AR or the SGR was considered the re-entry date. Freshwater entry sites were considered to be natal rivers, and fidelity was assessed during the two seasons of tracking.

Estuarine residency

Two estuarine zones were delineated within IFB: BR (6.6 km²) and SG (1.5 km²). BR included all inter and sub-tidal receivers within the AR outflow to the low tide mark and included receivers 1 km alongshore from the tidal channel mouth. SG included two receivers within 3.5 km of the base of SG Falls. All other receivers in IFB were considered extra-estuarine (Fig. 1). During the 2009 marine migration, the total number of individuals detected in both BR and SG estuaries were displayed as percentages of all tracked individuals and of those tracked individuals that survived the marine phase (*i.e.* re-entered fresh water).

Estuarine residence for individual *S. alpinus* was determined by calculating the total and consecutive (continuous presence) amount of time present at BR or SG estuarine zones. Any estuarine continuous presence <2 min (two detections) was omitted (Collins *et al.*, 2007). The ratio between an individual's total time present at either estuarine zone to total time monitored was calculated to provide a residency index. Residency values range from 0 to 1,

TABLE I. Summary of *Salvelinus alpinus* tagged at Bay of Two Rivers estuary and detected ($n = 43$) from July to September 2008 and 2009 within inner Frobisher Bay, Nunavut, Canada

ID #	L_F (cm)	M (kg)	Tag type	$M_T \cdot M$ (%)	Tagging date	Estuary detected in	FW entry (2008–2009)
T2*	57.6	2.5	V9TP	0.25	22 July 2008	BR	10 August
T4	54.0	2.1	V13TP	0.57	22 July 2008	BR	30 August ^{¶¶}
T5	52.1	1.9	V9TP	0.34	22 July 2008	BR	29/23 August
T6†	61.2	3.0	V13TP	0.40	22 July 2008	SG	–
T7†	64.0	3.4	V13TP	0.35	22 July 2008	SG	–
T11	59.6	2.8	V13TP	0.43	23 July 2008	–	9 August
T12*	54.0	2.1	V13TP	0.57	23 July 2008	BR	24 August ^{¶¶}
T13	58.6	2.7	V13TP	0.45	23 July 2008	BR	4 September ^{¶¶}
T14*	56.1	2.3	V9TP	0.27	23 July 2008	BR	16 August/2 September
T18	51.9	1.9	V6	0.06	24 July 2008	BR	–
T20	58.5	2.6	V6	0.05	24 July 2008	BR	–
T25*†	56.6	2.4	V13TP	0.5	25 July 2008	SG	–
T27*	54.6	2.2	V13TP	0.55	25 July 2008	BR	23 August ^{¶¶}
T28	48.6	1.5	V9TP	0.41	9 August 2008	BR	21/29 August
T29	45.0	1.2	V9TP	0.52	9 August 2008	BR	14/28 August
T30	36.2	0.7	V6	0.18	9 August 2008	BR	–
T31	53.0	2.0	V13TP	0.60	9 August 2008	BR	10/18 August
T32	56.6	2.4	V13TP	0.50	10 August 2008	BR	19 August
T33	52.8	2.0	V13TP	0.61	10 August 2008	BR	12 August
T34	32.8	0.5	V6	0.24	10 August 2008	BR	16 August
T35	30.6	0.4	V6	0.30	10 August 2008	BR	12 August
T37	31.2	0.4	V6	0.28	10 August 2008	BR	27 August
T39	61.6	3.1	V13TP	0.39	11 August 2008	BR	20 August
T40	53.8	2.1	V13TP	0.58	11 August 2008	BR	22/23 August
T41*	54.4	2.1	V9TP	0.30	11 August 2008	BR	12/8 August

TABLE I. Continued

ID #	L_F (cm)	M (kg)	Tag type	$M_T:M$ (%)	Tagging date	Estuary detected in	FW entry (2008–2009)
T44‡§	49.2	1.0	V9TP	0.64	8 July 2009	SG	20 August
T45‡	32.9	0.3	V7	0.58	9 July 2009	BR, SG	28 August
T46	71.4	3.8	V9TP	0.17	17 July 2009	BR	3 August
T47*	60.0	2.2	V9TP	0.29	17 July 2009	BR	20 August
T48	56.7	1.8	V9TP	0.35	17 July 2009	BR	14 August
T49*	61.9	2.4	V9TP	0.26	17 July 2009	BR, SG	–
T50*	53.4	1.5	V9TP	0.42	17 July 2009	BR	24 August
T51	61.6	2.4	V9TP	0.27	17 July 2009	BR	18 August
T52	61.8	2.4	V9TP	0.26	17 July 2009	BR, SG	–
T53	56.6	1.8	V9TP	0.35	17 July 2009	BR	–
T54§	50.7	1.3	V7	0.14	18 July 2009	BR, SG	21 August
T55*	57.9	2.0	V7	0.09	18 July 2009	BR	22 August
T56	52.5	1.4	V7	0.12	20 July 2009	BR	16 August
T57	32.0	0.3	V7	0.60	20 July 2009	BR	25 August
T58	50.9	1.3	V7	0.14	21 July 2009	BR	20 August
T59	37.0	0.5	V7	0.38	21 July 2009	BR	25 August
T60*	54.5	1.6	V7	0.11	21 July 2009	BR, SG	2 September
T61*	53.3	1.3	V7	0.14	14 August 2009	BR	20 August
Mean \pm s.d.	52.3 \pm 9.7	1.9 \pm 0.9		0.35 \pm 0.17			
Minimum	30.6	0.3		0.05			
Maximum	71.4	3.8		0.64			

AR, Arnsow River; BR, Bay of Two Rivers estuary; FB, inner Frobisher Bay; SG, Sylvia Grinnell River and estuary; T##, acoustically and ID tagged fish; TP, temperature and pressure (depth) sensor tag; L_F , fork length; M , fish mass; M_T , tag mass; FW, fresh water.

*Fish recaptured.

†Fish tagged at BR 2008, but only detected at SG 2009.

‡Fish tagged at SG ($n = 2$).

§Fish entered SGR at end of marine migration, all others entered the AR.

¶FW entry in 2009.

with values close to 0 indicating low residence and values close to 1 indicating high residence (Knip *et al.*, 2012). Absence from either estuarine zone was considered any period ≥ 24.8 h (*i.e.* one lunar day). The number of times an individual char returned to BR or SG after an absence was tallied (Knip *et al.*, 2012) and standardized to number of returns per days monitored.

Estuarine continuous presence, residency, number of returns and return rates were calculated for each individual during 15 day intervals using freshwater entry as the endpoint to determine if *S. alpinus* were present in either estuarine zone for different lengths of continuous presence periods, residency and returned more often during a specific interval. If an individual did not survive the marine migration or no freshwater entry date was determined, the mean freshwater entry date of 20 August was used. The final date of an individual's marine migration included time until 1159 hours. Presence indices during migration intervals were tested for normality using Shapiro–Wilks tests. Normal and non-normal distributed data sets were compared using ANOVA or Kruskal–Wallis ANOVA, respectively (Baran & Warry, 2003).

Movement patterns

Tidally influenced: Detection distribution data were mapped relative to tide phase: high, ebb, low and flood (Curry *et al.*, 2006). High and low tides were defined as predicted tide time ± 1 h. Ebb was falling water levels between high and low tides, whereas flood was rising water levels between low and high tides (Materna *et al.*, 2000). The dependent variable of individual SLD from the AR or SGR mouth and independent variable of tide phase were examined with descriptive statistics, tested for normality using a Shapiro–Wilks test and compared using ANOVA or Kruskal–Wallis ANOVA depending on normal or non-normal data distribution, respectively (Baran & Warry, 2003).

Travel rates: Travel rate, expressed as km h^{-1} and km day^{-1} , was estimated by dividing the distance between two receivers (expressed in km and excluding two times the receiver detection range for transmitters used) by the time (h) it took for that fish to swim between the two receivers. Body lengths per second ($L_B \text{ s}^{-1}$) was calculated by dividing the distance travelled between receivers (m) by individual L_F (m) and the time (s) it took for that fish to swim between the receivers (Hubley *et al.*, 2008). Receiver detection range for the four transmitters used was assumed to be 100 (V6), 200 (V7), 350 (V9TP) and 500 m (V13TP, Vemco; Lacroix & Voegeli, 2000; Hubley *et al.*, 2008; D. Webber, pers. comm.). Movements between receivers spaced less than four times the assumed detection range (0.4–2.0 km) were excluded to avoid potential detection range overlap between successive receivers and to address potential issues that could arise due to variable receiver spacing (Halfyard *et al.*, 2012). Tide phase was assigned based on the mean time between the two detections used in travel rate calculations. Travel rate estimates with travel times >2 h were excluded as they may have spanned more than one tidal phase.

RESULTS

RANGE TESTING

In 2008, the V13TP transmitter located 47 m from a continuously submerged receiver yielded a detection efficiency of 79% from 13 to 29 August (16 days) when tagged *S. alpinus* were present. From 13 August to 29 September (47 days) 2008, detection efficiency remained relatively unchanged (83%). Median detection efficiencies during low (96%) and flood tides (92%) were significantly higher than those during high (33%) and ebb (85%) tides (Kruskal–Wallis, $H = 23.64$, d.f. = 3, $P < 0.05$; Table II). Range testing of a V7 transmitter and intertidal receiver yielded detections from 200 to 600 m away. Only one detection occurred at 600 m, with all other detections (98%) occurring at 200 m. Considering that the receiver was exposed at low tide, range testing detection periods were limited to high water and ranged from 2 h 22 min to 7 h

TABLE II. Mean \pm S.D., median, interquartile range (IQ), minimum, maximum and number (n) of acoustic tagged *Salvelinus alpinus* detection efficiencies (%) calculated during high, ebb, low and flood tide phases for a V13TP acoustic transmitter 47 m away from a continuously submerged VR2W receiver located in an intertidal zone tidal channel at Bay of Two Rivers, inner Frobisher Bay, Nunavut, Canada, from 13 to 29 August 2008

Tide phase	Mean \pm S.D.	Median, IQ	Minimum	Maximum	n
High	47 \pm 42	33, 86	0	100	32
Ebb	80 \pm 17	85, 27	46	100	31
Low	93 \pm 10	96, 9	53	100	32
Flood	92 \pm 5	92, 9	76	99	32

35 min. Detection efficiencies at the 200 m distance ranged from 38 to 63%. Simultaneous detection by adjacent receivers of *S. alpinus* tagged with a V13TP revealed that a detection range > 937 m may have been possible for this transmitter type within the study area.

TAGGING

Of the 61 individuals implanted with acoustic tags, 43 (mean \pm S.D. $L_F = 523 \pm 97$ mm; minimum–maximum $L_F = 306$ – 714 mm; Table I) were detected within two periods: 3–29 August 2008 and 1 July–4 September 2009. Mean \pm S.D. tag:body mass ratio was $0.4 \pm 0.2\%$, ranging from 0.1 to 0.6%.

MARK AND RECAPTURES

Of the 80 marine migrating individuals marked (acoustic and ID tags) during 2008–2009, 28.8% ($n = 23$) were recaptured from August 2008 to July 2012. Seventeen were caught within BR or SG estuaries from 22 July to 26 August, accounting for 73.9% of all recaptures and 21.3% of all marked fish. The remaining six recaptures, 26.1% of all recaptures and 7.5% of all marked fish, occurred in the AR from 6 October to 14 June. Estuarine recaptures were split 52.9 and 47.1% between BR and SG estuaries, respectively (Table III).

MARINE MIGRATION

Duration

River ice break-up in the SGR occurred on 18 June 2009 and *S. alpinus* were confirmed to be in the estuary on 27 June. Some stomachs sampled were full of marine prey which suggested that these fish had been in salt water for some time. A recapture (T19) on 14 June 2009, through lake ice in the north-west branch of the AR (Table III), suggested that seaward movement had not yet started. The first 2009 receiver was deployed within the SGR < 600 m upstream of the falls on 24 June and no tagged individuals were detected until 20 August when individuals were returning from the sea. Individuals tagged in 2008 ($n = 15$) and 2009 ($n = 18$) were detected in salt water from 1 July to 4 September 2009. Of the three individuals detected during early migration, all were tagged in 2008 at BR and first detected from

TABLE III. Recaptures of *Salvelinus alpinus*, ($n = 23$) tagged at Bay of Two Rivers estuary, inner Frobisher Bay, Nunavut, Canada, from July to August 2008 and 2009

ID	Tagging date	Recapture date	Recapture location
T1	21 July 2008	Late August 2009	BR
T2	22 July 2008	26 August 2009	BR
T8	22 July 2008	11 August 2008	SG
T12	23 July 2008	4 August 2010	BR
T14	23 July 2008	20 April 2010	AR
T15	24 July 2008	14 August 2008	SG
T19	24 July 2008	14 June 2009	AR
T21	25 July 2008	11 August 2008	SG
T25	25 July 2008	23 July 2009	SG
T27	25 July 2008	25 August 2009	BR
T41	11 August 2008	4 August 2010	BR
T47	17 July 2009	22 July 2012	BR
T49	17 July 2009	14 August 2009	SG
T50	17 July 2009	16 August 2011	BR
T54	18 July 2009	12 July 2012	SG
T55	18 July 2009	10 October 2010	AR
T60	21 July 2009	6 December 2009	AR
T61	14 August 2009	16 August 2010	SG
MR10	31 July 2009	6 October 2009	AR
MR13	31 July 2009	25 June 2010	SG
MR14	31 July 2009	11 October 2009	AR
MR16	31 July 2009	23 August 2010	BR
MR—	31 July 2009	25 August 2009	BR

AR, Armshow River; BR, Bay of Two Rivers estuary; MR##, Floy ID tagged fish only; SG, Sylvia Grinnell Estuary; T##, acoustically and ID tagged fish.

1 to 3 July 2009 in the SG estuary. The first detection occurred within a day of the first 2009 marine receiver being deployed. Final marine detections of 11 individuals occurred from 10 to 29 August 2008 in the cove connecting both AR branches. These individuals were not detected on the monitored south-west AR branch, thus were assumed to head up the north-west AR branch considering that it was not monitored by a receiver. Three others were detected migrating up the south-west AR branch: two large individuals ($L_F = 576$ and 596 mm) on 9 and 11 Aug 2008, and one smaller individual ($L_F = 312$ mm) on 27 August 2008. Analysis of L_F relative to all freshwater re-entry detections revealed only a slight trend of decreasing individual L_F with later freshwater re-entry date (t) ($L_F = -2.8484t + 119\,779$; $r^2 = 0.05$). All detected individuals re-entered fresh water from 9 to 29 August 2008, and 3 August to 4 September 2009. Mean \pm s.d. freshwater re-entry dates were 16 ± 7 days August 2008 ($n = 14$), 22 ± 6 days August 2009 ($n = 26$) and 20 ± 7 days August 2008 and 2009 combined (Table I). Assuming the same saltwater entry date (18 June) in both years, marine migration duration was 46–78 days for all tracked individuals which survived 2009. Mean \pm s.d. durations were 59 ± 6 in 2008, 65 ± 7 in 2009 and 63 ± 7 days for 2008 and 2009 combined.

Estuarine residency

Monitoring over two marine migration seasons recorded 38 982 detections, with 87% within 6.3 km SLD of the AR or SGR mouths. From 3 to 29 August 2008, and 1 July to 4 September 2009, mean \pm s.d. tracking periods of tagged *S. alpinus* were 9.0 ± 7.0 and 33.9 ± 9.3 days, respectively. Mean \pm s.d. total time present at either estuarine zone for all individuals detected in 2008 and 2009 was 4.2 ± 3.9 and 11.8 ± 7.1 days, respectively. Median continuous estuarine presences were compared for all monitored *S. alpinus* in 2008 and 2009 considering that both data sets failed normality tests (Shapiro–Wilk, $P < 0.05$). No significant difference was detected (Mann–Whitney U , $T = 3510$, $P > 0.05$), thus both years' data were pooled, resulting in a mean \pm s.d. continuous estuarine presence of 2.3 ± 3.7 days (1.1, 2.4; median, interquartile range) with a minimum continuous presence of 3.5 min. A maximum continuous estuarine presence of 33.9 days was recorded for an individual (T47) that never left BR (Table IV and Fig. 2).

Mean \pm s.d. residency to BR and SG estuaries during 2008 (0.51 ± 0.29) was higher than 2009 (0.37 ± 0.23) for tracked individuals (t -test, $t = -1.72$, d.f. = 24, $P < 0.05$), with 2009 residencies ranging from 0.10 to 0.99 (Table IV). In 2008 and 2009, 43.7 and 21.2% of tracked individuals spent more than half their time within either estuarine zone. For all *S. alpinus* tracked, the number of returns to either estuarine zone were significantly lower in 2008 compared with 2009 (Table IV; t -test, $t = -4.10$, d.f. = 44, $P < 0.001$). There was no significant difference in return rates between 2008 and 2009 *S. alpinus* tracks (t -test, $t = -0.65$, d.f. = 47, $P > 0.05$), thus mean \pm s.d. return rates for individuals returning to either estuarine zone during both seasons was 0.11 ± 0.09 ($n = 49$), approximately one individual returning every 9.1 days (Table IV).

Transition phase–early migration: Of the three individuals detected early in the marine migration, T7 remained near the SG estuary for the entire 22 days tracked (residency index = 0.60). Another individual (T6) demonstrated some degree of estuarine fidelity (residency index = 0.33), returning four times over the 12 days it was tracked (Table IV). The individual (T25) detected on 1 July remained near the same SG receiver for 3 days, until departing and returning daily until 9 July, demonstrating a residency index of 0.44 over the first 7.6 days tracked.

Mid–late migration: All 15 day interval data sets failed Shapiro–Wilk normality tests ($P < 0.05$), thus statistical comparisons were performed using Kruskal–Wallis ANOVA *post-hoc* Dunn's method and described using median, interquartile range (minimum, maximum) values (Baran & Warry, 2008). The median number of days individuals were tracked within BR and SG estuaries were significantly higher (Kruskal–Wallis, $H = 23.76$, d.f. = 3, $P < 0.001$) during the last two (median 15.0; mean dates: 22 July to 5 August and 6 to 20 August) migration intervals (Dunn's method, $P < 0.05$) compared with the first two (medians 3.7 and 8.8; mean dates: 1 to 6 July and 7 to 21 July). Individuals spent significantly more time (Kruskal–Wallis, $H = 17.578$, d.f. = 3, $P < 0.001$) in the estuarine zone during the final 15 days of their marine migrations (median 5.0) compared with the first two intervals (medians 0.9 and 2.4; Dunn's method, $P < 0.05$; Table V and Fig. 2). Median continuous presence periods within the migration intervals revealed the final interval having a significantly higher median value compared with the first two intervals (Kruskal–Wallis, $H = 14.76$, d.f. = 3, $P < 0.01$; Dunn's method, $P < 0.05$; Table V). Considering the number of days tracked capped continuous presence periods, each continuous presence period was de-trended by dividing it by the total number of

TABLE IV. Tracking summary of individual *Salvelinus alpinus* from 3 to 29 August 2008 ($n = 16$), and 1 July to 4 September 2009 ($n = 33$), showing total number of days tracked and total and continuous presence residency, number of returns and return rates (number of returns day⁻¹) within Bay of Two Rivers and Sylvia Grinnell estuarine zones. Residency index values range from 0 to 1 (low to high residency), calculated as the ratio of an individual's total time present at either estuarine zone to total time monitored (Knip *et al.*, 2012)

ID	Number of days	Total presence (days)	Continuous presence [days; mean \pm S.D., (minimum and maximum)]	Residency	Number of returns	Return rate
2008						
T2	7	0.004	0.004	0.001	0	0.00
T5	26	12.48	2.08 \pm 2.40 (0.004, 6.56)	0.48	5	0.19
T14	11	9.88	4.94 \pm 1.24 (4.06, 5.81)	0.90	1	0.09
T18	18	5.48	1.10 \pm 0.94 (0.002, 2.44)	0.31	5	0.28
T28	12	9.96	3.32 \pm 0.99 (2.52, 4.43)	0.85	2	0.17
T29	5	3.88	3.88	0.80	0	0.00
T30	7	3.56	1.78 \pm 1.19 (0.94, 2.62)	0.54	1	0.15
T31	1	0.72	0.72	0.89	0	0.00
T32	9	3.12	1.55 \pm 2.01 (0.14, 2.98)	0.34	1	0.11
T33	2	1.80	1.80	0.91	0	0.00
T34	6	2.48	1.24 \pm 1.33 (0.30, 2.18)	0.42	1	0.17
T35	2	0.71	0.71	0.37	0	0.00
T37	17	1.45	1.45	0.09	1	0.06
T39	9	3.13	1.04 \pm 0.71 (0.35, 1.76)	0.35	2	0.22
T40	11	7.50	2.50 \pm 2.92 (0.009, 5.71)	0.69	2	0.18
T41	1	0.25	0.25	0.30	0	0.00
Mean \pm S.D.	9	4.2 \pm 3.9	1.90 \pm 1.77	0.51 \pm 0.29	1.3 \pm 1.7	0.10 \pm 0.10
Minimum	1	0.004	0.002	0.001	0	0
Maximum	26	12.50	6.56	0.91	5	0.28
2009						
T2	42	4.24	0.85 \pm 0.35 (0.36, 1.18)	0.11	4	0.10
T4	46	16.03	2.29 \pm 4.94 (0.006, 13.46)	0.35	6	0.13
T5	39	6.26	1.04 \pm 0.69 (0.15, 2.10)	0.16	5	0.13
T6	12	3.89	0.78 \pm 0.46 (0.01, 1.17)	0.33	4	0.33
T7	22	13.28	2.21 \pm 1.76 (0.53, 5.09)	0.60	5	0.23
T12	39	12.63	1.15 \pm 0.99 (0.003, 2.81)	0.32	10	0.26
T13	50	20.03	4.01 \pm 5.30 (0.07, 11.30)	0.40	4	0.08
T14	40	14.72	2.94 \pm 2.84 (0.11, 6.82)	0.37	4	0.10
T25	22	5.59	0.70 \pm 0.99 (0.03, 2.81)	0.26	7	0.32
T27	38	3.80	0.63 \pm 1.25 (0.03, 3.17)	0.10	5	0.13
T28	44	19.94	1.81 \pm 1.79 (0.03, 6.08)	0.46	10	0.23
T29	45	8.19	2.05 \pm 3.50 (0.07, 7.29)	0.19	3	0.07
T31	33	3.53	1.18 \pm 1.38 (0.005, 2.70)	0.11	2	0.06
T40	39	10.58	1.06 \pm 1.59 (0.04, 4.95)	0.27	9	0.23
T41	23	19.53	2.05 \pm 6.51 (0.03, 19.28)	0.86	2	0.09
T44	42	6.02	3.01 \pm 2.56 (1.19, 4.83)	0.14	1	0.02
T45	48	11.98	2.30 \pm 4.01 (0.20, 8.82)	0.25	3	0.06
T46	18	11.64	5.82 \pm 3.78 (3.14, 8.50)	0.67	1	0.06

TABLE IV. continued

ID	Number of days	Total presence (days)	Continuous presence [days; mean \pm s.d., (minimum and maximum)]	Residency	Number of returns	Return rate
T47	35	33.88	33.88	0.99	0	0.00
T48	28	12.20	6.10 \pm 4.01 (3.26, 8.94)	0.43	1	0.04
T49	27	5.14	1.71 \pm 1.89 (0.02, 3.75)	0.19	2	0.06
T50	39	13.00	4.33 \pm 5.10 (1.04, 10.21)	0.34	2	0.05
T51	32	6.48	1.30 \pm 1.09 (0.007, 2.65)	0.20	4	0.12
T52	21	9.50	3.17 \pm 3.14 (0.99, 6.77)	0.45	2	0.10
T53	36	7.34	1.83 \pm 0.95 (0.61, 2.92)	0.21	3	0.09
T54	34	8.55	2.85 \pm 2.22 (0.50, 4.90)	0.25	3	0.09
T55	35	12.85	1.84 \pm 1.98 (0.36, 5.93)	0.37	6	0.17
T56	27	24.30	12.15 \pm 5.32 (8.39, 15.91)	0.92	1	0.04
T57	36	25.16	3.59 \pm 3.60 (0.03, 8.69)	0.71	6	0.17
T58	30	6.00	3.00 \pm 2.25 (1.41, 4.59)	0.21	1	0.03
T59	34	17.56	1.95 \pm 1.92 (0.30, 6.61)	0.51	8	0.23
T60	43	10.19	3.40 \pm 3.73 (0.80, 7.67)	0.24	2	0.05
T61	21	5.76	1.92 \pm 2.00 (0.008, 4.00)	0.27	2	0.09
Mean \pm s.d.	34 \pm 9	11.8 \pm 7.1	2.44 \pm 3.98	0.37 \pm 0.23	3.9 \pm 2.7	0.12 \pm 0.09
Minimum	12	3.5	0.003	0.10	0	0
Maximum	50	33.9	33.88	0.99	10	0.33

days that individual was tracked within each interval. Median continuous presence residual comparisons between migration intervals revealed no significant differences (Kruskal–Wallis ANOVA, $H = 5.839$, d.f. = 3, $P > 0.05$). The final 15 day migration interval's residency (median 0.41) was only significantly higher than the previous 15 day interval (median 0.18; Kruskal–Wallis ANOVA *post-hoc* Dunn's method, $H = 10.45$, d.f. = 3, $P < 0.05$; Table V). Interval comparisons for number of returns and return rates revealed no significant differences (Kruskal–Wallis ANOVA, $H = 7.459$, d.f. = 3, $P > 0.05$ and $H = 2.953$, d.f. = 3, $P > 0.05$; Table V) with multiple returns occurring for most individuals throughout their monitored migration (Fig. 2).

Movement patterns

Tidally influenced: Detected *S. alpinus* moved in and out of the intertidal zone with the tide (Figs 3 and 4), often using deeper channels as staging areas to access flooding shallows (A. D. Spares, pers. obs.), demonstrated by T18 detected by VR2W-180 KHz receivers limited to a 100 m listening range [Fig. 3(a)]. Illustrated per cent detections during ebb and low tides revealed that individuals retreated from intertidal to sub-tidal zones [Fig. 4(b), (d)], with some individuals subsequently detected along coasts further away from river mouths (Figs 3(b), (d) and 4). A higher % of detections occurred nearer river mouths within the intertidal zone during flood tides [Fig. 4(c)]. Mean \pm s.d. SLD of *S. alpinus* from either AR or SGR mouths during high and low tidal phases were 2.6 ± 2.8 km ($n = 7849$) and 5.4 ± 4.8 km ($n = 5515$) (Fig. 4). Significant differences

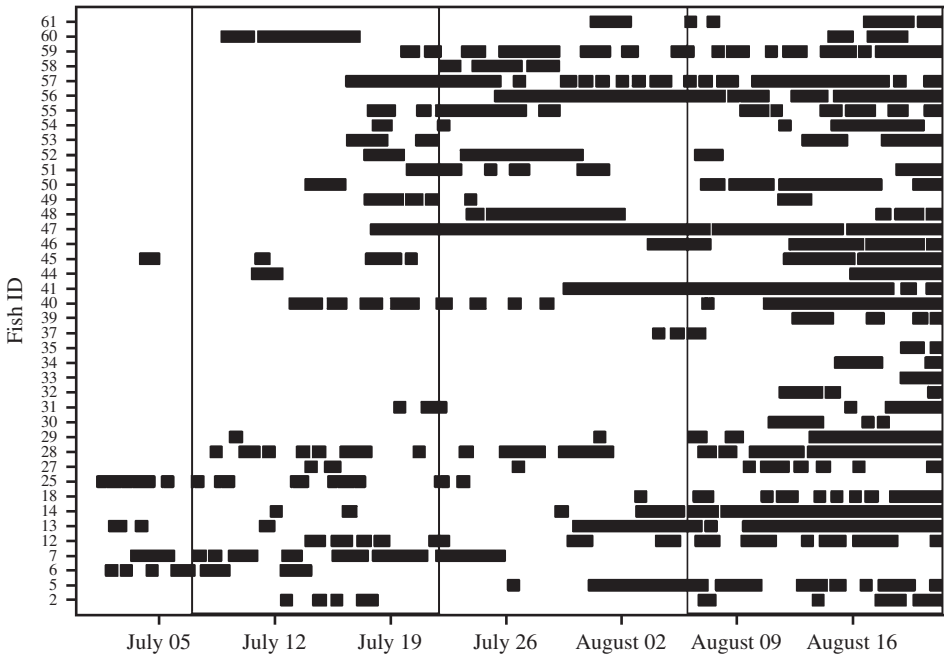


FIG. 2. Presence of individual *Salvelinus alpinus*, at Bay of Two Rivers and Sylvia Grinnell estuarine zones within inner Frobisher Bay, Nunavut, Canada, during 2008–2009. For all individuals that completed their marine migration or survived beyond a mean endpoint of 20 August, timestamp data were adjusted accordingly. Any individual removed from the migration before 20 August retained original timestamps. |, start and end dates of 15 day intervals used for residency analyses.

(Kruskal–Wallis, $H = 3881$, d.f. = 3, $P < 0.001$) in SLD from either river mouth occurred during all tidal phases (Dunn’s method, $P < 0.05$). Percentage of detections revealed 72% occurred < 2 km SLD away during high tide. The highest percentage of detections during ebb, low and flood tides occurred < 2 km, 4–6 km and 2–4 km SLD from river mouths (Fig. 4). Travel rates (km h^{-1} , $L_B \text{ s}^{-1}$) during high and ebb tide phases were significantly higher than during flood (Kruskal–Wallis, $H = 23.84$, d.f. = 3, $P < 0.001$, *post-hoc* Dunn’s method, $P < 0.05$; Table VI). Tidally influenced movement pattern was recorded throughout the marine migration period, but occurred more frequently during estuarine residency periods (*i.e.* late migration; Figs 2, 5 and 6).

Inter-estuarine: Evidence of inter-estuarine movements was provided by three individuals tagged at BR in 2008 and recaptured by SG fishers that same season (Table III). Another three 2008 BR-tagged individuals were detected only in the SG early the following 2009 season (Table I). Based on these recaptures and detections, six (15%) of the 41 BR-tagged individuals made the journey to SG. Of the 33 individuals tracked in 2009, 15% visited both estuaries. Of those surviving the 2009 migration ($n = 26$; Table I), 19% were detected in both estuaries (Table IV). Four survivors tagged at BR made the trip to the SG (17%) and three returned [Fig. 3(c)]. One of the two survivors tagged at the SG in 2009 travelled to BR [Fig. 3(b)]. Of all *S. alpinus* marked with acoustic or ID tags during 2008–2009 ($n = 80$), 11 (14%) were either detected or recaptured in the opposite estuary between July 2008 and August 2011 (Tables III and IV).

TABLE V. Median, interquartile range (minimum and maximum) for number of days tracked, estuarine and extra-estuarine total and continuous presence (days), continuous presence residuals, residency, number of returns, return rates (returns day⁻¹) and travel rates (km h⁻¹, body lengths (L_B) s⁻¹) for *Sabvelinus alpinus*, tracked within inner Frobisher Bay, Nunavut, Canada, during 15 day intervals based on the mean migration endpoint of 20 August. Residency index values range from 0 to 1 (low to high residency), calculated as the ratio of an individual's total time present at either estuarine or extra-estuarine zone to total time monitored (Knip *et al.*, 2012)

Mean interval dates	1–6 July	n	7–21 July	n	22 July–5 August	n	6–20 August	n
Number of days tracked	3.7, 2.0 (0.5, 5.4)	6	8.8, 8.8 (2.3, 15.0)	27	15.0, 2.8 (1.5, 15.0)	35	15.0, 6.0 (0.8, 15.0)	46
Estuarine zones								
Total presence (days)	0.9, 1.5 (0.01, 2.8)	6	2.4, 2.5 (0.08, 7.8)	27	3.5, 6.0 (0.02, 15.0)	25	5.0, 6.9 (0.004, 14.5)	45
Continuous presence (days)	0.47, 0.88 (0.006, 2.8)	10	0.97, 1.30 (0.005, 7.7)	53	0.67, 2.60 (0.001, 15.0)	51	1.80, 3.00 (0.002, 14.5)	97
Continuous presence residuals	0.13, 0.22 (0, 0.58)	10	0.09, 0.19 (0, 1.0)	53	0.06, 0.25 (0, 1.0)	51	0.14, 0.28 (0, 0.97)	97
Residency	0.26, 0.43 (0, 0.58)	6	0.30, 0.40 (0, 1.0)	27	0.18, 0.45 (0, 1.0)	35	0.41, 0.48 (0, 0.97)	46
Number of returns	0.5, 1 (0, 2)	6	1.2 (0, 4)	27	1, 1 (0, 5)	35	1, 1 (0, 5)	46
Return rate (returns day ⁻¹)	0.09, 0.21 (0, 0.41)	6	0.12, 0.26 (0, 0.36)	27	0.07, 0.13 (0, 1.4)	35	0.13, 0.11 (0, 0.56)	46
Extra-estuarine zone								
Total presence (days)	2.6, 1.5 (0, 4.3)	5	4.7, 7.5 (0, 14.8)	24	10.1, 10.2 (0, 15.0)	33	5.7, 6.9 (0, 15.0)	46
Continuous presence (days)	1.5, 1.0 (0, 3.1)	8	2.0, 2.9 (0, 12.7)	46	2.6, 6.7 (0, 15.0)	60	2.0, 2.2 (0, 15.0)	86
Residency	0.63, 0.49 (0, 0.90)	5	0.66, 0.34 (0, 0.99)	24	0.81, 0.47 (0, 1.0)	33	0.54, 0.49 (0, 1.0)	46
Migration travel rates								
km h ⁻¹	0.30, 0.27 (0.1, 0.5)	5	0.70, 1.18 (0.02, 6.3)	205	0.50, 0.88 (0.007, 9.5)	442	0.70, 1.35 (0.02, 4.9)	461
km day ⁻¹	7.8, 6.4 (2.6, 12.4)	5	17.4, 28.2 (0.5, 151.9)	205	12.0, 21.0 (0.17, 227.5)	442	17.5, 32.3 (0.44, 118.1)	461
L_B s ⁻¹	0.15, 0.13 (0.05, 0.24)	5	0.39, 0.61 (0.01, 3.26)	205	0.26, 0.47 (0.004, 4.27)	442	0.37, 0.71 (0.01, 2.45)	461

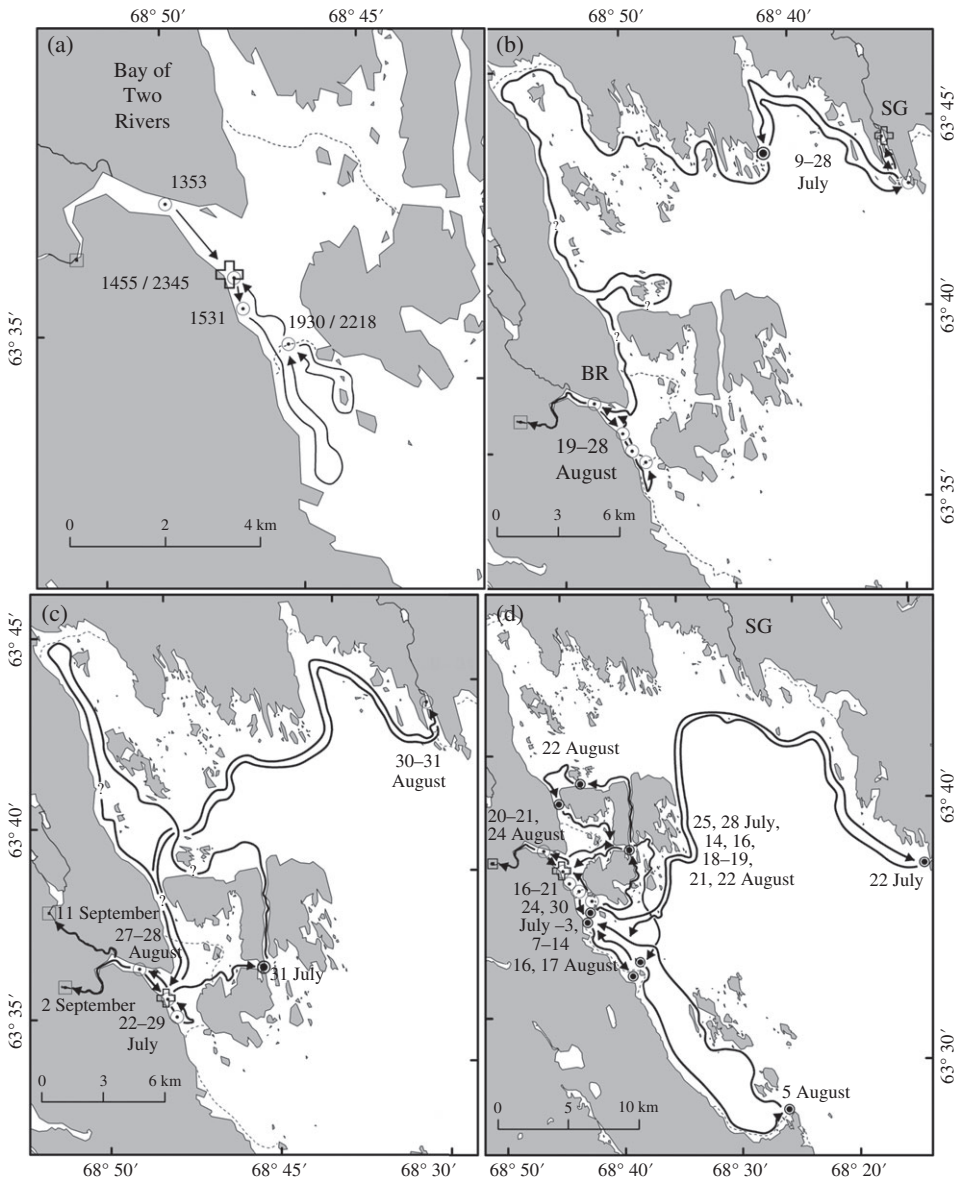


FIG. 3. Tidally influenced, inter-estuarine, possible homing and maximum range migration movements of *Salvelinus alpinus* tracked in inner Frobisher Bay, Nunavut, Canada, during 2008–2009. Detection times (hours) and locations (⊙, estuarine; ⊗, extra-estuarine) of individual (a) T18 relative to high (1425 hours) and low (2042 hours) tides at Bay of Two Rivers on 21 August 2008, (b) T45 showing movement between Sylvania Grinnell (SG) and Bay of Two Rivers estuaries, (c) T60 showing a return trip between Bay of Two Rivers and SG and (d) T12 showing maximum straight line distance travelled away from either estuary. →, known direction of travel with hypothetical tracks between receivers; approximate position of the low tide mark; ?, VR2 receivers which were unable to detect the V7 transmitter carried by T45 and T60; ⊕, tagging site for each tracked individual.

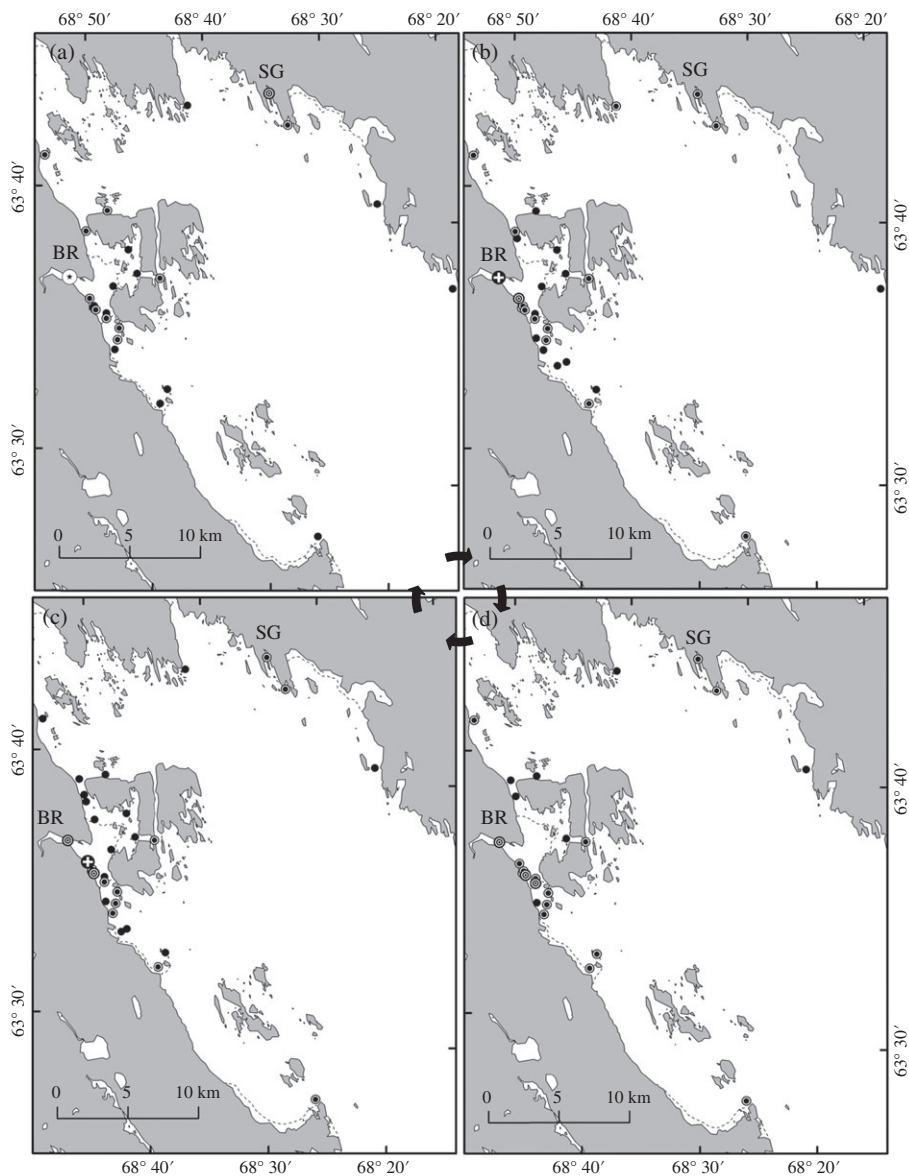


FIG. 4. Percentage of detections recorded at each receiver relative to total number of detections (\oplus , <60%; \otimes , <40%; \odot , <20%; \circ , <10%; \bullet , <1%) recorded for tracked anadromous *Salvelinus alpinus* during (a) high, (b) ebb, (c) flood and (d) low tide phases in inner Frobisher Bay, Nunavut, Canada, from July to September 2008/2009.

Extra-estuarine: Movement beyond monitored estuaries occurred mid-migration [mid-late July to mid-August; Figs 3(b)–(d), 5 and 6], although many individuals still returned to either estuary throughout this period [Fig. 3(d)]. One individual (T51) demonstrated estuarine fidelity during its initial and final two monitored migration days and extra-estuarine movements from 29 July to 16 August (Fig. 5). Individuals

TABLE VI. Median, interquartile range, minimum and maximum travel rates [km h^{-1} , body length (L_B) s^{-1}] of *Salvelinus alpinus*, relative to tide phases (high, ebb, low and flood) within inner Frobisher Bay, Nunavut, Canada, from 1 July to 4 September 2008 and 2009

Tide phase	km h^{-1}	Minimum	Maximum	$L_B \text{ s}^{-1}$	Minimum	Maximum	<i>n</i>
High	1.8, 0.9	0.5	6.3	0.93, 0.48	0.28	3.26	69
Ebb	2.0, 1.3	0.2	4.6	0.99, 0.65	0.11	2.45	109
Low	1.4, 1.6	0.4	8.5	0.76, 0.82	0.22	3.81	36
Flood	1.2, 0.9	0.3	9.5	0.60, 0.49	0.17	4.27	143

n, sample size.

spent more overall time and longer periods outside either BR or SG estuaries during 2009 compared with 2008 (Table VII).

Total time in the extra-estuarine zone was significantly higher in the second last 15 day migration interval compared with both adjacent intervals (Wallis–Kruskal *post-hoc* Dunn’s method, $H = 10.7$, d.f. = 2, $P < 0.01$). There were no significant differences in the duration of extra-estuarine excursions during all three intervals ($H = 5.81$, d.f. = 2, $P > 0.05$; Table V). Extra-estuarine residency during the final 15 day migration interval revealed similar values in 2008 and 2009 (0.52 and 0.60; Mann–Whitney *U*, $T = 319.5$, $P > 0.05$), thus both years were pooled for residency interval comparisons. A significantly higher median extra-estuarine residency (Kruskal–Wallis, $H = 12.01$, d.f. = 3, $P < 0.01$) occurred during the second last migration interval compared with the final 15 days of the migration (Dunn’s method, $P < 0.05$; Table V).

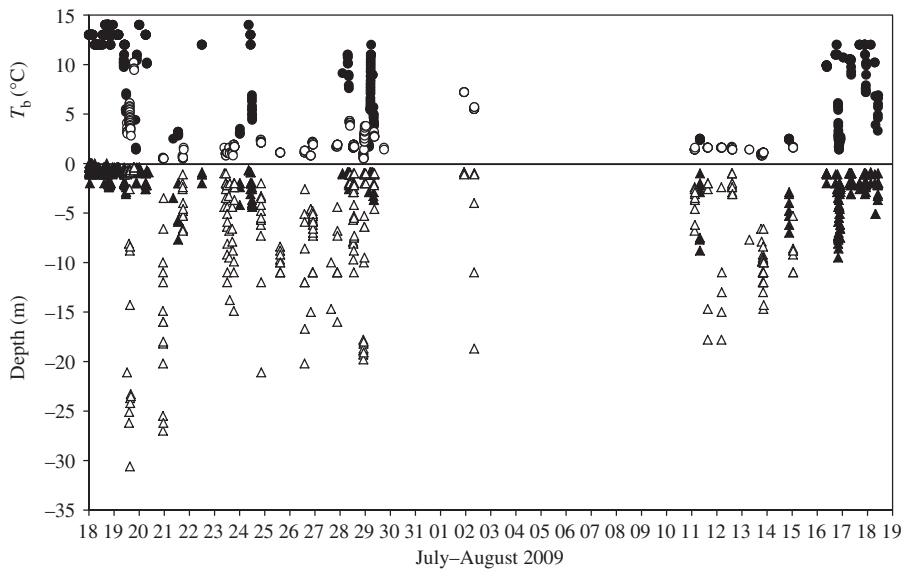


FIG. 5. Depth (Δ , \blacktriangle) and body temperature (\circ , \bullet) of *Salvelinus alpinus* T51 relative to intertidal (Δ) and sub-tidal (\circ) zones during marine migration in inner Frobisher Bay, Nunavut, Canada, from 18 July to 18 August 2009.

TABLE VII. Mean \pm S.D. and median, interquartile range (IQ) of extra-estuarine total and continuous presence (days) and residency indices for *Salvelinus alpinus*, tracked from 3 to 29 August 2008, and 1 July to 4 September 2009, in inner Frobisher Bay, Nunavut, Canada. Residency index values range from 0 to 1 (low to high residency), calculated as the ratio of an individual's total time present in the extra-estuarine zone to total time monitored (Knip *et al.*, 2012)

Extra-estuarine	Mean \pm S.D.	Median, IQ	Minimum	Maximum	<i>n</i>
2008					
Total presence	6.1 \pm 4.5	5.2, 4.8	1.1	15.3	11
Continuous presence	2.9 \pm 3.0	1.7, 2.1	1.0	14.2	23
Residency	0.39 \pm 0.33	0.48, 0.57	0	1.0	16
2009					
Total presence	22.5 \pm 10.2	25.0, 14.2	2.0	35.9	32
Continuous presence	5.1 \pm 6.8	2.1, 3.1	1.0	35.0	140
Residency	0.62 \pm 0.23	0.67, 0.26	0	0.92	33

n, sample size.

Of the 33 *S. alpinus* tracked in 2009, 14 (42%) ventured over 11 km SLD away from either estuary. Assuming the same migration endpoint of 20 August, individuals ventured over 10 km SLD from either the AR or SGR mouths from 7 July to 16 August and reached 27 km SLD away from 19 July to 13 August. During the final four migration days, all detected individuals were within 10 km SLD of either river mouth (Fig. 6). Original tracking timestamps revealed that four individuals ($L_F = 521\text{--}540$ mm) were 27 km SLD away from the AR mouth from 21 July to 13 August, 2009. These individuals remained at or near this receiver for periods of 3 h up to 22 days before returning to BR [Fig. 3(d)]. A receiver placed *c.*13 km further along the same coastline recorded no detections [Fig. 1(b)].

Travel rates: Mean \pm S.D. and median, interquartile travel rates for all tracked individual's consecutive marine detections during 2008 and 2009 ($n = 994$), excluding calculations with inter-receiver distance less than four times the respective detection

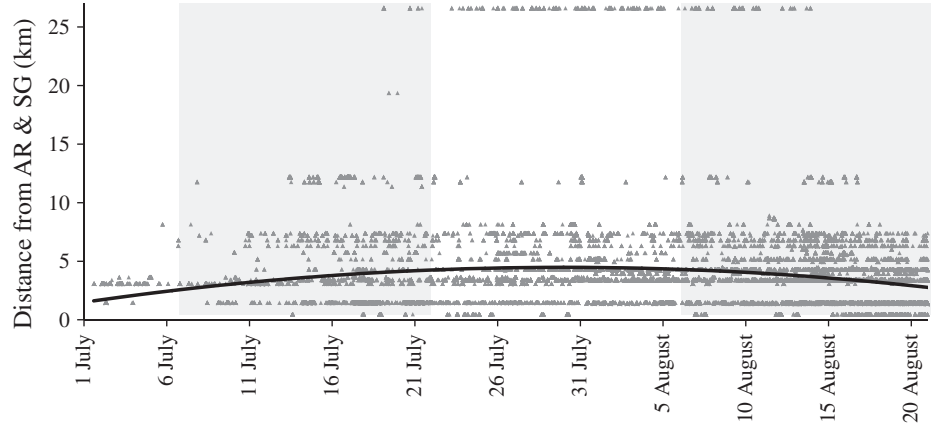


FIG. 6. Distance of *Salvelinus alpinus* detections (\blacktriangle) from Armshow (AR) and Sylvia Grinnell (SG) river mouths relative to detection date adjusted to mean freshwater entry of 20 August.

TABLE VIII. Mean \pm S.D. and median, interquartile range (IQ) of calculated travel rates [km h^{-1} , km day^{-1} , body length (L_B) s^{-1}] of *Salvelinus alpinus*, tracked within inner Frobisher Bay, Nunavut, Canada, from 1 July to 4 September 2008 and 2009

Travel rate	Mean \pm S.D.	Median, IQ	Minimum	Maximum	<i>n</i>
km h^{-1}	0.9 ± 1.0	0.6, 1.1	0.01	9.50	994
km day^{-1}	22.7 ± 24.1	14.6, 26.9	0.17	227.50	994
$L_B \text{ s}^{-1}$	0.50 ± 0.52	0.33, 0.60	0.004	4.27	994

n, sample size.

range ($n = 326$), were $0.9 \pm 1.0 \text{ km h}^{-1}$ ($22.7 \pm 24.1 \text{ km day}^{-1}$) and $0.6 \pm 1.1 \text{ km h}^{-1}$ ($14.6 \pm 26.9 \text{ km day}^{-1}$); with a maximum rate of 9.5 km h^{-1} (227 km day^{-1}). Travel rates expressed as $L_B \text{ s}^{-1}$ were 0.50 ± 0.52 and 0.33 ± 0.60 ; with a maximum of 4.27 (Table VIII). Median travel rates differed significantly (Kruskal–Wallis, $H = 16.92$, d.f. = 2, $P < 0.001$) with the second last 15 day interval being significantly lower than the intervals before and after it (Fig. 7). First interval travel rates were excluded from statistical analysis due to a low sample size ($n = 5$).

Freshwater re-entry

Of the 41 migrations monitored until freshwater re-entry, 39 (95.1%) ended with individuals choosing the river closest to their tagging site, while two individuals used

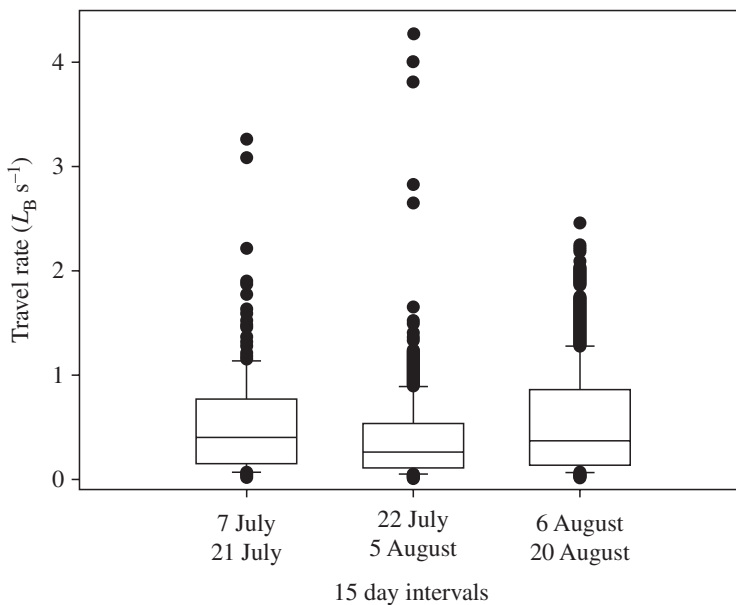


FIG. 7. Box-and-whisker plot showing median travel rate (body length, $L_B \text{ s}^{-1}$) during 15 day intervals with freshwater entry as marine migration endpoint for *Salvelinus alpinus* tracked within inner Frobisher Bay, Nunavut, Canada. \square ends and \square represent interquartile range and minimum and maximum values, respectively. Outliers shown by \bullet . Interval dates labelled using mean freshwater entry of 20 August.

the opposite estuary's river. Of the two individuals tagged at SG, one entered the SGR and the other entered the AR. Six individuals were detected using the AR in both 2008 and 2009 (Table I). One individual (T60) travelled from its tagging site at BR to the SG and returned to enter the south-west branch of the AR within the final 6 days of its marine migration [Fig. 3(c)]. Surprisingly, after 5 days in the south-west AR, T60 briefly returned to the cove connecting the two river branches on 7 September to enter the north-west AR, where it overwintered, further confirmed by its recapture under lake ice by gillnet on 6 December (Table III).

DISCUSSION

RANGE TESTING

Detection range varied considerably considering use of four different transmitters, and highly variable environmental factors such as study site bathymetry, water column stratification, density, current speed, levels and temperature and wind speed and direction. Range tests conducted were limited due to inaccessibility of open water or inadequate equipment. Poor detection efficiency during high tide may have resulted in underestimates of estuarine residencies for tracked *S. alpinus*, however, considering multiple receivers were deployed within the estuarine zones, individual presence was most likely detected during ebb and flood tides, even during periods of poor detection efficiency. One possible reason for lower detection efficiencies during high and ebb tide may be due to the receiver's location in a tidal channel which was protected from winds until water level rose well above the surrounding intertidal flats. Another possibility marine water surrounded the test site during high and ebb tides (Spares *et al.*, 2012). On the Ocean Tracking Network's New Minas Passage listening line within the Bay of Fundy (13 m tidal range), Nova Scotia, poor detection efficiency occurred when current velocities were $>2\text{ m s}^{-1}$ due to excessive noise interference (Reddin *et al.*, 2014). Current velocities were not concurrently recorded at range test sites within this study, yet the macrotidal nature of IFB (11 m tidal range; Spares *et al.*, 2012) suggests that similar interference occurred. According to criteria used for a standardized assessment of how well detection range was accounted for, this study scored 25 from 45, which may be described as passable compared with a maximum score of 39 from 378 passive acoustic telemetry studies scored (Kessel *et al.*, 2014).

MARINE MIGRATION

The migration of anadromous *S. alpinus* has been proposed to have three phases: (1) freshwater overwintering site to the sea, (2) estuarine transition residency and (3) marine migration and feeding (Bégout Anras *et al.*, 1999). Marine migration aspects were examined in this study (see Spares *et al.*, 2012 for marine diving behaviour, feeding and temperature preference), as receiver deployment and fish tracking were difficult during estuarine transition due to sea-ice break-up and high potential for recaptures in the SG fishery. Although few individuals were tracked during the first 2 weeks at sea, of those detected, all remained within 5 km of the SGR mouth, suggesting that estuarine transition occurred.

Duration

The marine migrations of IFB *S. alpinus* lasted 46–78 days; however, if an estuarine transition phase of *c.* 10 days is recognized (Bégout Anras *et al.*, 1999), the actual marine migration phase may be as short as 36 days. Migration duration varies depending on seasonal ice break-up and latitude, with IFB (63° N) falling between the recorded minimum of 28 days in the central Arctic (68° N; Johnson, 1989) and maximum of 109 days in northern Labrador (58° N; Dempson & Kristofferson, 1987).

Estuarine residency

Estuarine residency of anadromous salmonids aids osmoregulation stresses associated with movement between fresh and salt water, and provides a rich foraging environment resulting in faster growth and often higher marine survival (Miller & Sadro, 2003). Juvenile salmonids, coho *Oncorhynchus kisutch* (Walbaum 1792) and Chinook *Oncorhynchus tshawytscha* (Walbaum 1792), spend days to months in the estuarine zone before entering and remaining in the open sea until migration end (Miller & Sadro, 2003; Bottom *et al.*, 2005). As first-time individuals, small *S. alpinus* (mean $L_F < 150$ mm) resided in estuaries due to poor osmoregulation while larger individuals successfully entered full-strength salt water (Gulseth *et al.*, 2000). Anadromous IFB *S. alpinus* were large enough to endure cold marine waters beyond intertidal zones and surface waters (Spares *et al.*, 2012), thus estuarine fidelity should not be taken as evidence of poor osmoregulation (Gulseth *et al.*, 2000). Other *S. alpinus* populations have been documented migrating year-round in salinities ≥ 32 and temperatures ranging from -1.5 to 1.0° C (Bystriansky *et al.*, 2007; Jensen & Rikardsen, 2008, 2012).

Estuarine use by *S. alpinus* does occur year-round, as demonstrated by a Norwegian fjord population remaining within the estuarine zone during winter (Jensen, 2013). Within IFB, *S. alpinus* spent on average 37% of their total time tracked during summer 2009 in the estuaries. Estuarine residency was significantly higher in 2008, yet this was believed to be due to tracking covering the final 3–4 weeks of the marine migration when individuals were returning to fresh water. Individual estuarine residence indices in 2009 ranged from 0.10 to 0.99, suggesting that some individuals roamed while others stayed home (Knip *et al.*, 2012). In one case, high estuarine fidelity was demonstrated by an individual that remained within BR virtually the entire time monitored (34 days continuous presence), suggesting a low degree of anadromy (Dempson & Kristofferson, 1987). Yet, most individuals (78.8%) revealed $>50\%$ of their time tracked was spent beyond either estuary monitored, suggesting that alternative warm water refuges or feeding grounds were used (Spares *et al.*, 2012). Interestingly, 81.8% returned to either estuary multiple times throughout their migration, averaging once every 9 days. Similar behaviours of continuous (*c.* 2 months) and intermittent (cumulative 1 month) presence were recorded for anadromous bull trout *Salvelinus confluentus* (Suckley 1859), with estuarine returns averaging once per week (F. Goetz, pers. comm.). Estuaries with large intertidal zones may serve as rich foraging grounds and aid in osmoregulation, and may also act as heat recovery arenas, encouraging estuarine residency of individuals which forage in significantly colder extra-estuarine waters. The optimum temperature for efficient digestion in *S. alpinus* occurred within IFB's intertidal–estuarine zones, further reinforcing estuarine residency as a behavioural thermoregulation adaptation (Spares *et al.*, 2012).

Movement patterns

Tidally influenced: Movement that is influenced by the tide movement has been documented for *S. confluentus* which moved between shoreline and estuarine zones with changing tides, particularly during flooding tide. F. Goetz (pers. comm.) has hypothesized that individual *S. confluentus* exploit the intertidal zone at high tide and return to permanently submerged tidal channels during ebb and low tide, remaining until flooding resumes. Lower travel rates during flood tides suggested that IFB *S. alpinus* waited for the intertidal zone to flood, with significantly higher travel rates occurring during high and ebb tides possibly indicating active hunting and rapid exits, respectively. Individuals' use of tidal channels, confirmed by tracking and observations made during this study, and increased catchability during flooding tides further supported these results. A previous study revealed that these inter and sub-tidal movement patterns were possibly motivated by increased prey availability and behavioural thermoregulation (Spares *et al.*, 2012). Studies of other anadromous salmonid populations [cutthroat trout *Oncorhynchus clarkii* (Richardson 1836), *O. kisutch*, *S. alpinus* and *Salvelinus fontinalis* (Mitchill 1814)] have shown the same link to tidal periodicity (Moore, 1975; McCart, 1980; Power, 1980; Castonguay *et al.*, 1982; Trotter, 1989; Montgomery *et al.*, 1990; Miller & Sadro, 2003) with individuals remaining near shore during low tide to exploit the littoral zones during high tide (Curry *et al.*, 2006).

Inter-estuarine: Past-tagging has revealed that summer coastal movements are geographically localized (Dempson, 1995), with the majority of *S. alpinus* recaptures in northern Labrador occurring within 70 km of tagging sites (Dempson & Kristofferson, 1987). Individuals may use different rivers from year to year, with dispersal of migrating individuals ranging from 0 to 66% and absences from original tagging river lasting 1–2 years (Dempson & Kristofferson, 1987; Gyselman, 1994; Moore *et al.*, 2013). Distinct populations exist on a microgeographic scale (<10 km) considering that sufficient genetic divergence occurs. This implies that most straying involves overwintering of non-spawning individuals (Bernatchez *et al.*, 1998; Moore *et al.*, 2013).

Moore *et al.* (2013) found that dispersal of anadromous *S. alpinus* varied from 15.8 to 25.5% among rivers within Cumberland Sound, Nunavut, which agrees with this study's results (14–19%). In a study conducted during 2009–2011, VanGerwen-Toyne *et al.* (2013) marked *S. alpinus* at the SG with all recaptures occurring within SG or just east or west of the estuary, and no individuals recaptured at BR. Of the 72 individuals marked at BR, only two (3%) were recaptured at the SG or Iqaluit (VanGerwen-Toyne *et al.*, 2013), which is considerably lower compared with this study (15–17%). This study revealed that individuals tagged in either BR or SG moved between both estuaries, with one of the two SG tagged individuals detected within BR. Perhaps, lower recapture returns by fishers *v.* acoustic tracking detection rates accounted for the inter-estuarine dispersal difference estimated in these two studies.

One individual completed a 40 km SLD return trip between the estuaries within its final week of migration, suggesting site fidelity to BR (*i.e.* AR). It was possible that this individual was seeking its natal river, and its subsequent river branch switch soon after entering an overwintering site (A. D. Spares pers. obs.) may have been due to homing to a specific spawning site (Sprules, 1952; Johnson, 1980) and relative density of individuals present within the first site triggering a migratory response (Tsukamoto *et al.*, 2009). Genetic analyses revealed BR and SG stocks to be genetically distinct, but with some mixing (VanGerwen-Toyne *et al.*, 2013), which may lend support to this individual homing to a specific spawning site.

Extra-estuarine: Large *S. alpinus* ($L_F > 300$ mm) have averaged travel rates of 0.6 km h^{-1} (maximum 4.3 km h^{-1}) during their first 2 weeks at sea in the Canadian Arctic (Bégout Anras *et al.*, 1999). Travel rates for IFB *S. alpinus* during the second last 15 day interval were significantly lower than the intervals before and after. An explanation for this apparent behavioural difference may be longer periods between detections as many individuals were within the extra-estuarine zone where receiver coverage was lower. Other studies have estimated mean marine migration travel rates of 1.1 km h^{-1} (maximum 5.3 km h^{-1}) and 1.6 km h^{-1} (maximum 3.6 km h^{-1}) for dolly varden *Salvelinus malma* (Walbaum 1792) and *S. alpinus* (Armstrong & Morrow, 1980; Jensen, 2013). Travel rates of IFB *S. alpinus* were similar, averaging 0.9 km h^{-1} (maximum 9.5 km h^{-1}). Considering that sustained swimming speeds for salmonids average $2\text{--}3 L_B \text{ s}^{-1}$ with burst speeds up to $10 L_B \text{ s}^{-1}$ (Brett, 1965), this study's estimated rates (mean \pm s.d. = 0.5 ± 0.5 ; maximum $4.3 L_B \text{ s}^{-1}$) were well within the capability of *S. alpinus* and mirror marine migrating Atlantic salmon *Salmo salar* L. 1758 ($0.6 L_B \text{ s}^{-1}$; Jákupsstovu, 1988).

Maximum distances travelled by *S. alpinus* during one marine migration season varies considerably (Klemetsen *et al.*, 2003), with IFB *S. alpinus* matching the lower end of recorded maximums (<30 km). Many studies have shown that *S. alpinus* follow coastlines evidenced by recaptures and detections occurring near river mouths and along shorelines, even at distances up to 30 km SLD from origin of river mouths (Bégout Anras *et al.*, 1999; Jensen *et al.*, 2014). Marine distribution of *S. confluentus* was similar, with captures occurring in river delta and near shore marine habitats and acoustic tracking revealing paths following shorelines and island coasts (F. Goetz, pers. comm.). Tracking of IFB *S. alpinus* revealed an estuarine and near shore (<3 km) distribution during the final 2–3 weeks of the marine migration (Spares *et al.*, 2012). Maximum distance detections from the two monitored rivers still occurred <1 km from shore, suggesting a preference for near shore and littoral zones. Tracking of *S. confluentus* revealed that individuals remained in deeper water just offshore during the day to move into the shallow waters near shore at night (F. Goetz, pers. comm.). Although IFB *S. alpinus* used the littoral zone, this was synchronized by tidal rather than by diel cycles as migration occurred during the annual period of perpetual daylight. It was still possible that individuals ventured into pelagic zones of IFB, as *S. alpinus* has been caught up to 5 km offshore in other regions (Dempson & Kristofferson, 1987; Rikardsen & Amundsen, 2005); however, no long-term pelagic monitoring was conducted to verify this.

Freshwater re-entry

It has been suggested that *S. alpinus* undergo physiological modifications (*i.e.* reverse smoltification) before freshwater re-entry, often moving in and out of estuaries while slowly accumulating salts to be diluted once in fresh water (Bystriansky *et al.*, 2007). Chum salmon *Oncorhynchus keta* (Walbaum 1792) demonstrate this process where osmoregulatory processes are shut down and vertical parr-like marks develop prior to freshwater entry (Uchida *et al.*, 1997). Stomach content examination of *S. alpinus* re-entering fresh water revealed minimal occurrence of estuarine prey and undigested marine prey, suggesting little to no estuarine feeding and rapid transit from the marine environment (Bégout Anras *et al.*, 1999). Rapid freshwater re-entry was demonstrated by T60 travelling from the SG to the south-west AR during its final two marine migration days, yet this individual may have undergone reverse smoltification

during its final 6 days within both estuaries. Most individuals demonstrated a significantly higher estuarine residency during their final 15 day migration interval, with extra-estuarine movements restricted within 10 km of the river mouth (Spares *et al.*, 2012).

Individuals tagged at BR demonstrated preference (97%) for overwintering in the AR, with six individuals detected re-entering the AR in consecutive years, suggesting high site fidelity. Although *S. alpinus* have been documented overwintering in the nearest freshwater system towards the end of their marine migration (Dempson & Kristofferson, 1987), there appeared to be specific homing in the case of some monitored individuals. Considering that tagging of individuals occurred within the estuaries 2–4 weeks following saltwater entry, natal and previous overwintering of river origin could not be verified, except for the six individual consecutive re-entries. In 2008, detections of two large *S. alpinus* re-entering fresh water earlier than a smaller individual suggested that larger individuals returned first, agreeing with Moore (1975), yet overall analysis revealed only a slight trend which may have been due to size-selective tagging ($L_F > 300$ mm).

In conclusion, detected *S. alpinus* spent on average approximately one third of their time tracked within either monitored estuaries, with individuals displaying continuous or intermittent presence. IFB's macrotides directed *S. alpinus* intertidal–estuarine movements, with the lowest mean travel rates during flood tides suggesting staging of individuals before movement into intertidal zones. Although the estuaries were *c.* 22 km apart, a portion of tagged individuals used both (19%). Individuals remained relatively close to freshwater overwintering systems, although late-migration inter-estuarine movements may have indicated natal homing. Approximately half of the individuals exhibited extra-estuarine travel, mostly during mid-migration, but remained within 3 km of shore ranging < 30 km SLD of either estuary. Tracking evidence suggested that an estuarine transition phase may also occur towards the end of marine migration prior to freshwater re-entry, similar to saltwater entry at the migration's beginning (Bégout Anras *et al.*, 1999). It was concluded that IFB *S. alpinus* (1) spent a significant portion of their migration within or adjacent to the estuaries and (2) had a restricted marine distribution within 30 km SLD of the river mouths. An effective *S. alpinus* marine management plan should address anthropogenic pressures on adjacent as well as on the focal estuary due to inter-estuarine mixing of different populations (Moore *et al.*, 2013; VanGerwen-Toyne *et al.*, 2013).

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References

- Armstrong, R. H. & Morrow, J. E. (1980). The dolly varden charr, *Salvelinus malma*. In *Charrs: Salmonid Fishes of the Genus Salvelinus* (Balon, E. K., ed.), pp. 99–140. The Hague: Dr. W Junk bv Publishers.
- Baran, E. & Warry, F. (2008). *Simple Data Analysis for Biologists*. Phnom Penh: WorldFish Center and the Fisheries Administration.
- Bégout Anras, M. L., Gyselman, E. C., Jorgenson, J. K., Kristofferson, A. H. & Anras, L. (1999). Habitat preferences and residence time for the fresh water to ocean transition stage in Arctic charr. *Journal of the Marine Biological Association of the United Kingdom* **79**, 153–160.
- Bernatchez, L., Dempson, J. B. & Martin, S. (1998). Microsatellite gene diversity analysis in anadromous arctic char, *Salvelinus alpinus*, from Labrador, Canada. *Canadian Journal of Fisheries and Aquatic Sciences* **55**, 1264–1272.
- Bottom, D. L., Jones, K. K., Cornwell, T. J., Gray, A. & Simenstad, C. A. (2005). Patterns of Chinook salmon migration and residency in the Salmon River estuary (Oregon). *Estuarine, Coastal and Shelf Science* **64**, 79–93.
- Brenkman, S., Corbett, S. & Volk, E. (2007). Use of otolith chemistry and radiotelemetry to determine age-specific migratory patterns of anadromous bull trout in the Hoh River, Washington. *Transactions of the American Fisheries Society* **136**, 1–11.
- Brett, J. R. (1965). The relation of size to rate of oxygen consumption and sustained swimming speed of sockeye salmon (*Oncorhynchus nerka*). *Journal of the Fisheries Research Board of Canada* **22**, 1491–1501.
- Bystriansky, J. S., Frick, N. T., Richards, J. G., Schulte, P. M. & Ballantyne, J. S. (2007). Wild Arctic char (*Salvelinus alpinus*) upregulate gill Na⁺,K⁺–ATPase during freshwater migration. *Physiological and Biochemical Zoology* **80**, 270–282.
- Castonguay, M., FitzGerald, G. J. & Côté, Y. (1982). Life history and movements of anadromous brook charr, *Salvelinus fontinalis*, in the St-Jean River, Gaspé, Québec. *Canadian Journal of Zoology* **60**, 3084–3091.
- Collins, A. B., Heupel, M. R. & Motta, P. J. (2007). Residence and movement patterns of cownose rays *Rhinoptera bonasus* within a south-west Florida estuary. *Journal of Fish Biology* **71**, 1159–1178.
- Curry, R., van de Sande, J. & Whoriskey, F. (2006). Temporal and spatial habitats of anadromous brook charr in the Laval River and its estuary. *Environmental Biology of Fishes* **76**, 361–370.
- Dadswell, M. J. (2009). Ocean migration of diadromous fishes in a changing global environment preamble. In *Challenges for Diadromous Fishes in a Dynamic Global Environment* (Haro, A., Smith, K., Rulifson, R., Moffitt, C., Klauda, R., Dadswell, M., Cunjak, R., Cooper, J., Beal, K. & Avery, T., eds), pp. 251–253. Bethesda, MD: American Fisheries Society Symposium **69**.
- Dempson, J. B. (1995). Trends in population characteristics of an exploited anadromous arctic charr, *Salvelinus alpinus*, stock in northern Labrador. *Nordic Journal of Freshwater Research* **71**, 197–216.
- Dempson, J.B. & Kristofferson, A.H. (1987). Spatial and temporal aspects of the ocean migration of anadromous Arctic char. In *Common Strategies of Anadromous and Catadromous Fishes* (Dadswell, M., Klauda, R., Moffitt, C., Saunders, R., Rulifson, R. & Cooper, J., eds), pp. 340–357. Bethesda, MD: American Fisheries Society Symposium **1**.
- Dutil, J.-D. (1986). Energetic constraints and spawning interval in the anadromous Arctic charr (*Salvelinus alpinus*). *Copeia* **1986**, 945–955.
- Gulseth, O. & Nilssen, K. (2000). The brief period of spring migration, short marine residence, and high return rate of a northern Svalbard population of Arctic char. *Transactions of the American Fisheries Society* **129**, 782–796.
- Gulseth, O., Nilssen, K., Iversen, M. & Finstad, B. (2000). Seawater tolerance in first-time migrants of anadromous Arctic charr (*Salvelinus alpinus*). *Polar Biology* **24**, 270–275.

- Gyselman, E. C. (1994). Fidelity of anadromous Arctic char (*Salvelinus alpinus*) to Nauyuk Lake, N.W.T., Canada. *Canadian Journal of Fisheries and Aquatic Sciences* **51**, 1927–1934.
- Halfyard, E. A., Gibson, A. J. F., Ruzzante, D. E., Stokesbury, M. J. W. & Whoriskey, F. G. (2012). Estuarine survival and migratory behaviour of Atlantic salmon *Salmo salar* smolts. *Journal of Fish Biology* **81**, 1626–1645. doi: 10.1111/j.1095-8649.2012.03419.x
- Hubley, P. B., Amiro, P. G., Gibson, A. J. F., Lacroix, G. L. & Redden, A. M. (2008). Survival and behaviour of migrating Atlantic salmon (*Salmo salar* L.) kelts in river, estuarine, and coastal habitat. *ICES Journal of Marine Science* **65**, 1626–1634.
- Jákupsstovu, S. H.i. (1988). Exploitation and migration of salmon in Faroese waters. In *Atlantic Salmon: Planning for the Future* (Mills, D. & Piggins, D., eds), pp. 458–482. London: Croom Helm.
- Jensen, J.L.A. (2013). The seasonal migratory behavior of sympatric anadromous Arctic charr and brown trout. PhD Thesis, University of Tromsø, Tromsø, Norway.
- Jensen, J. L. A. & Rikardsen, A. H. (2008). Do northern riverine anadromous Arctic charr *Salvelinus alpinus* and sea trout *Salmo trutta* overwinter in estuarine and marine waters? *Journal of Fish Biology* **73**, 1810–1818.
- Jensen, J. L. A. & Rikardsen, A. H. (2012). Archival tags reveal that Arctic charr *Salvelinus alpinus* and brown trout *Salmo trutta* can use estuarine and marine waters during winter. *Journal of Fish Biology* **81**, 735–749.
- Jensen, J. L. A., Rikardsen, A. H., Thorstad, E. B., Suhr, A. H., Davidsen, J. G. & Primicerio, R. (2014). Water temperatures influence the marine area use of *Salvelinus alpinus* and *Salmo trutta*. *Journal of Fish Biology* **84**, 1640–1653. doi: 10.1111/jfb.12366
- Jobling, M., Johansen, S., Foshaug, H., Burkow, I. & Jørgensen, E. (1998). Lipid dynamics in anadromous Arctic charr, *Salvelinus alpinus* (L.): seasonal variations in lipid storage depots and lipid class composition. *Fish Physiology and Biochemistry* **18**, 225–240.
- Johnson, L. (1980). The Arctic charr, *Salvelinus alpinus*. In *Charrs, Salmonid Fishes of the Genus Salvelinus* (Balon, E. K., ed.), pp. 15–98. The Hague: Dr. W. Junk Publishers.
- Johnson, L. (1989). The anadromous Arctic charr, *Salvelinus alpinus*, of Nauyuk Lake, N.W.T., Canada. *Physiology and Ecology, Japan* **1**, 201–227.
- Kessel, S. T., Cooke, S. J., Heupel, M. R., Hussey, N. E., Simpfendorfer, C. A., Vagle, S. & Fisk, A. T. (2014). A review of detection range testing in aquatic passive acoustic telemetry studies. *Reviews in Fish Biology and Fisheries* **24**, 199–218.
- Klemetsen, A., Amudsen, P.-A., Dempson, J. B., Jonsson, B., Jonsson, N., O'Connell, M. F. & Mortensen, E. (2003). Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories. *Ecology of Freshwater Fish* **12**, 1–59.
- Knip, D. M., Heupel, M. R. & Simpfendorfer, C. A. (2012). To roam or to home: site fidelity in a tropical coastal shark. *Marine Biology* **159**, 1647–1657. doi: 10.1007/s00227-012-1950-5
- Lacroix, G. L. & Voegeli, F. A. (2000). Development of automated monitoring systems for ultrasonic transmitters. In *Advances in Fish Telemetry* (Moore, A. & Russell, I., eds), pp. 37–50. Lowestoft: CEFAS.
- Materna, S., Cech, J. Jr. & Hopkins, T. (2000). Diel movements of bat rays, *Myliobatis californica*, in Tomales Bay, California: evidence for behavioural thermoregulation? *Environmental Biology of Fishes* **58**, 173–182.
- McCart, P. J. (1980). A review of the systematics and ecology of Arctic char, *Salvelinus alpinus*, in the western Arctic. *Canadian Technical Report of Fisheries and Aquatic Sciences* **935**, 1–89.
- Miller, B. A. & Sadro, S. (2003). Residence time and seasonal movements of juvenile Coho salmon in the ecotone and lower estuary of Winchester Creek, South Slough, Oregon. *Transactions of the American Fisheries Society* **132**, 546–559.
- Montgomery, W. L., McCormick, S. D., Naiman, R. J., Whoriskey, F. G. & Black, G. (1990). Anadromous behavior of brook charr (*Salvelinus fontinalis*) in the Moisie River, Quebec. *Polskie Archiwum Hydriobiologii* **37**, 43–61.
- Moore, J. W. (1975). Distribution, movements, and mortality of anadromous Arctic char, *Salvelinus alpinus* L., in the Cumberland Sound area of Baffin Island. *Journal of Fish Biology* **7**, 339–348.

- Moore, J.-S., Harris, L. N., Tallman, R. F. & Taylor, E. B. (2013). The interplay between dispersal and gene flow in anadromous Arctic char (*Salvelinus alpinus*): implications for potential for local adaptation. *Canadian Journal of Fisheries and Aquatic Sciences* **70**, 1327–1338. doi: 10.1139/cjfas-2013-0138
- Morris, C. & Green, J. M. (2012). Migrations and harvest rates of Arctic charr (*Salvelinus alpinus*) in a marine protected area. *Aquatic Conservation: Marine and Freshwater Ecosystems* **22**, 743–750.
- Power, G. (1980). The brook charr, *Salvelinus fontinalis*. In *Charrs: Salmonid Fishes of the Genus Salvelinus* (Balon, E. K., ed.), pp. 141–203. The Hague: Dr W Junk bv Publishers.
- Rikardsen, A. & Amundsen, P.-A. (2005). Pelagic marine feeding of Arctic charr and sea trout. *Journal of Fish Biology* **66**, 1163–1166.
- Rikardsen, A., Diserud, O., Elliott, J., Dempson, J., Sturlaugsson, J. & Jensen, A. (2007). The marine temperature and depth preference of Arctic charr (*Salvelinus alpinus*) and sea trout (*Salmo trutta*), as recorded by data storage tags. *Fisheries Oceanography* **16**, 436–447.
- Spares, A. D., Stokesbury, M. J. W., O'Dor, R. K. & Dick, T. A. (2012). Temperature, salinity and prey availability shape the marine migration of Arctic char, *Salvelinus alpinus*, in a macrotidal estuary. *Marine Biology* **159**, 1633–1646.
- Sprules, W. (1952). The Arctic char of the west coast of Hudson Bay. *Journal of the Fisheries Research Board of Canada* **9**, 1–15.
- Swanson, H. & Kidd, K. (2009). A preliminary investigation of the effects of anadromous Arctic char on food web structure and nutrient transport in coastal Arctic lakes. In *Challenges for Diadromous Fishes in a Dynamic Global Environment* (Haro, A., Smith, K., Rulifson, R., Moffitt, C., Klauda, R., Dadswell, M., Cunjak, R., Cooper, J., Beal, K. & Avery, T., eds), pp. 465–483. *American Fisheries Society Symposium* **69**.
- Trotter, P. C. (1989). Coastal cutthroat trout: A life history compendium. *Transactions of the American Fisheries Society* **118**, 463–473.
- Tsukamoto, K., Miller, M.J., Kotake, A., Aoyama, J. & Uchida, K. (2009). The origin of fish migration: the random escapement hypothesis. In *Challenges for Diadromous Fishes in a Dynamic Global Environment* (Haro, A., Smith, K., Rulifson, R., Moffitt, C., Klauda, R., Dadswell, M., Cunjak, R., Cooper, J., Beal, K. & Avery, T., eds), pp. 45–61. *American Fisheries Society Symposium* **69**.
- Uchida, K., Kaneko, T., Yamaguchi, A., Ogasawara, T. & Hirano, T. (1997). Reduced hypoosmoregulatory ability and alteration in gill chloride cell distribution in mature chum salmon (*Oncorhynchus keta*) migrating upstream for spawning. *Marine Biology* **129**, 247–253.
- VanGerwen-Toyne, M., Lewis, C., Tallman, R. F. & Martin, Z. (2013). Information to support the assessment of Arctic char (*Salvelinus alpinus*) in the Sylvia Grinnell River, Nunavut, 2009–2011. *DFO Canadian Science Advisory Secretariat Science Response Document* **2013**.

Electronic Reference

- Reddin, A. M., Broome, J., Keyser, F., Stokesbury, M. J. W., Bradford, R., Gibson, J. & Halfyard, E. (2014). Use of animal tracking technology to assess potential risks of tidal turbine interactions with fish. In *Proceedings of the 2nd International Conference on Environmental Interactions of Marine Renewable Energy Technologies (EIMR2014)*, Stornoway, Scotland, 28 April – 02 May 2014. Available at http://tethys.pnnl.gov/sites/default/files/attachments/EIMR2014_8114_Redden.pdf (last accessed 3 March 2015).