



## Atlantic salmon post-smolt migration routes in the Gulf of St. Lawrence

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The migration of Atlantic salmon (*Salmo salar*) post-smolts from the Rivière Saint-Jean on the north shore of the Gulf of St. Lawrence (Canada) was studied during 2009 and 2010. Salmon from rivers in this region spend  $\geq 2$  years at sea before returning to spawn, and are believed to migrate to ocean feeding areas off Greenland. To determine residency time in the nearshore environment, and to define the migration routes of post-smolts, tagged post-smolts were tracked passively in Jacques Cartier Strait and at the two exits of the Gulf of St. Lawrence to the Atlantic Ocean (Cabot Strait and the Strait of Belle Isle). Post-smolts moved rapidly south in the nearshore area; two of them were detected 45 km south of the estuary exit, suggesting that they were moving towards the centre of the Gulf of St. Lawrence. One tagged post-smolt was detected exiting the Gulf of St. Lawrence via the Strait of Belle Isle after 44 d and exhibited a minimum swimming speed of  $14.4 \text{ km d}^{-1}$ . There was no apparent linkage between the detection patterns of post-smolts and surface water temperatures or surface water currents close to shore. Post-smolts, however, appeared to orient to higher salinity.

**Keywords:** Acoustics, Atlantic salmon post-smolt, marine migration, migration pathways in the Gulf of St. Lawrence, orientation, salinity gradient.

### Introduction

Throughout its range, the Atlantic salmon (*Salmo salar*) expresses a wide variation in life history characteristics including age and size at maturity, fecundity, and migration patterns (Hutchings and Jones, 1998). However, most populations are anadromous, undertaking feeding migrations to sea. Juvenile salmon starting their migration to sea are termed smolts. Once the smolts enter the saltwater environment, they are termed post-smolts. Despite evidence suggesting that the highest rates of salmon smolt and post-smolt mortality occur in the marine environment (Cairns, 2001), very little is known about the behaviour and movements of post-smolts in the ocean.

Evidence from age analysis and tag recaptures suggests that North American salmon post-smolts from anadromous populations emigrate to the Labrador Sea and West Greenland by early autumn of their first year at sea (Reddin and Short, 1991; Reddin and Friedland, 1999). They then overwinter in the Labrador Sea and off the Grand Banks (Reddin, 1986). Recently, it has also been suggested that some Atlantic salmon of North American origin circulate within the North Atlantic subpolar gyre (Dadswell *et al.*, 2010).

Historical mark-and-recapture data indicate that post-smolts from rivers on the north shore of the Gulf of St. Lawrence may follow the coast eastward and use the Strait of Belle Isle as the major pathway during their emigration to the North Atlantic (Dutil and Coutu, 1988). However, post-smolts originating from rivers farther south on the Gaspé Peninsula were recaptured near both the Strait of Belle Isle and Cabot Strait (Caron, 1983). Post-smolts from the Miramichi, Restigouche, and Cascapedia rivers have been detected passing through the Strait of Belle Isle as well (F. Whoriskey, pers. comm.). Thus, post-smolts on the way to feeding areas off Greenland may exit the Gulf of St. Lawrence either to the north via the Strait of Belle Isle or to the south through Cabot Strait.

Post-smolts have been observed in the nearshore environment (within 4 km of the coast) along the north shore of the Gulf of St. Lawrence in Quebec between mid-August and mid-September, and in smaller numbers until mid-October (Caron, 1983; Dutil and Coutu, 1988). Rapid growth rates of post-smolts during that period have been documented (Dutil and Coutu, 1988). Based on yearly variations in length gain, Friedland *et al.* (1999) suggested that the slowest growing post-smolts remained

in the Gulf longer. However, in some years, the post-smolts remaining in the Gulf grew at similar rates to post-smolts that feed in the open ocean, indicating that the Gulf might be part of a post-smolt nursery.

Post-smolts are found at sea surface temperatures ranging from 7 to 14°C (LaBar *et al.*, 1978; Holm *et al.*, 2000, 2003). Also, post-smolts appear to favour the highest salinity values available to them (McInerney, 1964; Straty, 1974; Holm *et al.*, 2003), and it has often been suggested that post-smolts follow the main prevailing surface current (Jonsson *et al.*, 1993; Holm *et al.*, 2000; Holst *et al.*, 2000; Dadswell *et al.*, 2010), while their local movements can be influenced by tidal currents (Holm *et al.*, 2003; Lacroix and Knox, 2005; Lacroix *et al.*, 2005). Like other marine epipelagic fishes, Atlantic salmon post-smolts could benefit from travelling with currents to save energy, thereby maximizing their growth (Hansen *et al.*, 1993; Dadswell *et al.*, 2010).

The goals of this research were to (i) determine the residency period of post-smolts from the Rivière Saint-Jean in the nearshore environment; (ii) define migratory routes within the Gulf of St. Lawrence and to the Gulf exits; and (iii) identify the linkages between migratory patterns of post-smolts and physical oceanic variables, including surface water temperatures, salinity, and currents.

## Material and methods

### Trapping and tagging of smolts

In 2009 and 2010, smolts migrating downstream were captured with a rotary screw fish trap (E. G. Solutions, Corvallis, OR, USA) located 19 km upstream of the mouth of the Rivière Saint-Jean (50°17'0"N 64°20'10"W), on Québec's north shore, Canada. The trap was checked every morning, and smolts longer than 13.1 cm and heavier than 20.0 g were implanted with an acoustic transmitter (V9-6L model, Vemco/Amirix Inc., Halifax, NS, Canada, battery life: 55 d in 2009 and 74 d in 2010, power output of 146 dB). The transmitters were uniquely coded and programmed to emit signals at a frequency of 69.0 kHz at randomly determined intervals varying from 20 to 60 s.

Smolts were anaesthetized with 0.2 ml of clove oil in 1000 ml of river water, and surgery protocols (instruments used, incision, and wound closure) were similar to those of Wagner *et al.* (2011). Transmitter weight (2.9 g in air) was <12% of fish body weight. Smolts of the size used in this study are not believed to be adversely affected by the tagging procedure (Brown *et al.*, 1999; Connors *et al.*, 2002). After surgery and recovery from anaesthesia, smolts were transported to a holding cage in the river. In 2009, smolts were released 3 km upstream of the trap at dusk ~11 h post-surgery, and in 2010, smolts were released before noon (local time) 100 m below the smolt wheel 4 h post-surgery.

A total of 44 smolts were tagged between 14 and 25 June 2009, and 49 smolts were tagged between 3 and 21 June 2010. In each year, some of the tags used were programmed to extend battery life. Twenty-four of the 44 tags implanted in 2009 and 24 of the 49 tags implanted in 2010 were programmed to turn off 20 d (2009) or 14 d (2010) following their activation and to stay off for 60 d (2009) or 50 d (2010). On the 61st or 51st day, respectively, the tags reactivated for the remainder of the battery life (33 d in 2009 and 60 d in 2010). The remaining tags (20 in 2009 and 25 in 2010) were programmed to emit continuously once activated until the battery died. As a result, tag-estimated end-of-life dates were

spread between 8–19 August and 6–15 October in 2009, and between 16 August–3 September and 1–19 November in 2010.

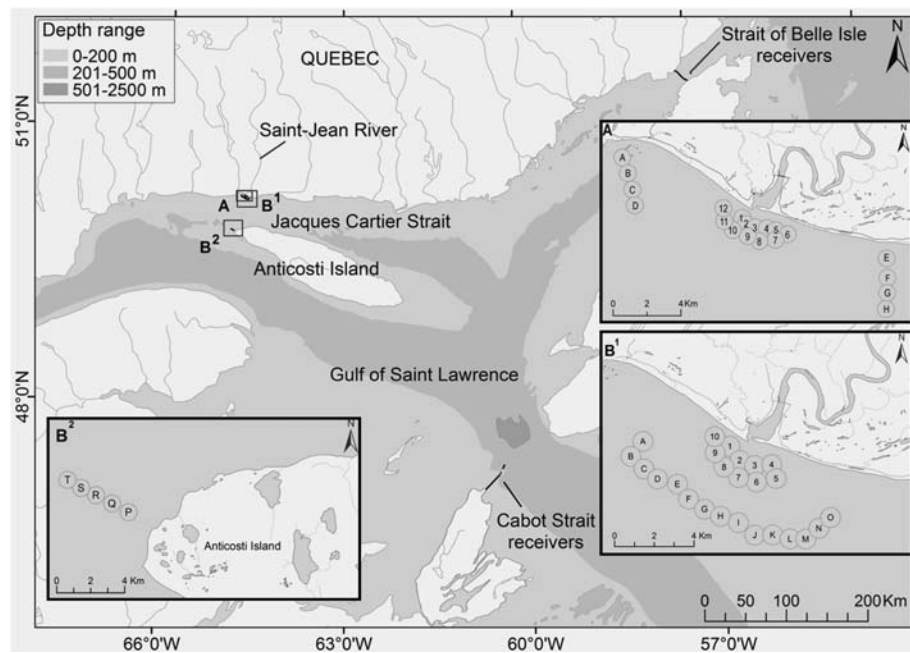
### Receiver deployments and tracking area

Hydroacoustic receivers (Vemco/Amirix Inc. Halifax, VR2 and VR2W models) with estimated directional detection ranges of 513 m radius under calm conditions or 497 m for 1.5–3.1 m s<sup>-1</sup> current (calculated by Vemco, [www.vemco.com](http://www.vemco.com)) were used for this study (Figure 1). Coastal receivers were attached to a line and suspended 4–7 m below the surface, with one surface float (three floats were used where currents were stronger) and a 20 kg trawl anchor. To maintain the receiver in the water column, it was attached to a sinking rope fitted with a swivel, which in turn was attached to a floating line leading down to the anchor. The swivel was made of nylon (544 kg breaking strength) and would break free in case of entanglement by a whale.

Receivers were in place in Jacques Cartier Strait (the stretch of water between Québec's north shore and Anticosti Island; Figure 1), between 13 June and 22 July 2009 (20 receivers) and between 28 May and 30 July in 2010 (30 receivers). Each year, some receivers were deployed in the shape of two arcs, 1 and 2 km around the river mouth to obtain a mean compass direction of swimming orientation for each post-smolt departing the river. During 2009, however, three of the receivers (No. 2 and No. 5 on the first array and No. 8 on the second array) malfunctioned (Figure 1), creating gaps in the array. In 2009, to capture possible post-smolt movements along the coast, two receiver lines of four receivers each were placed perpendicular to the shore, 9 km on either side of the river mouth and extending 4 km offshore (Figure 1).

The deployment scheme in 2010 was adjusted after analysis of detection patterns in 2009. During 2010, the inner two receiver-arc arrays were repeated in the deployment scheme, but a third array (composed of 15 receivers) was added ~4 km off the coast in the hope of further refining estimates of mean compass direction for post-smolt movements, consisting of three points (arrays 1, 2, and 3). An array composed of five receivers was deployed off the western point of Anticosti Island, but unfortunately one of them was lost (receiver R; Figure 1). During the second half of July, two receivers of the third array off the Rivière Saint-Jean (G and N) detached from their anchors (the rope was later found lacerated from excessive rubbing against the anchor). Both of these receivers remained attached to their buoys and were retrieved by a local fisherman after an estimated 2 weeks of drift, 1.6 km west and 0.8 km south of the Bouleau River estuary, 80 km west of the Rivière Saint-Jean.

The northern exit of the Gulf of St. Lawrence (Strait of Belle Isle) was fitted with an array of 22 receivers deployed by the Atlantic Salmon Federation (ASF). This array was operational between 18 June and 13 September 2009 and 17 June and 15 October 2010. An unexpected marine seismic survey took place during 2009 in the Strait of Belle Isle. Because this survey probably would have moved or damaged the receivers, we removed all the receivers from the Strait at an earlier date than the programmed transmitter death. In the southern exit of the Gulf of St. Lawrence (Cabot Strait), the Ocean Tracking Network (OTN), headquartered at Dalhousie University, deployed 31 receivers (during autumn of 2009 and early spring 2010) in a continuous line between Cape Breton, Nova Scotia, and Saint-Paul Island, with six additional receivers positioned in a line running 5 km northeast of the island (see Figure 1).



**Figure 1.** Location of hydroacoustic receiver arrays in the Gulf of St. Lawrence in the Jacques Cartier Strait in 2009 (a) and in 2010 (b<sup>1</sup>); at the western point of Anticosti Island (b<sup>2</sup>; in 2010 only); in the Strait of Belle Isle (both years), and in the Cabot Strait by the OTN (in 2010 only). Receivers in arrays a, b<sup>1</sup>, and b<sup>2</sup> are indicated by letters or numbers, and detection ranges of 500 m radius are indicated with a circle. Recording thermometers (minilogs, Vemco) were attached 4–7 m below the water surface at receivers No. 5 and No. 10 in 2009 (a) and at receivers A, E, I, M, and R in 2010 (b<sup>1</sup> and b<sup>2</sup>).

### Post-smolt residency period calculations, detection patterns, and compass direction determinations

Residency periods in the nearshore environment were calculated as the time between the first and last detection on nearshore environment receivers. In 2010, the third (outermost arc from the estuary) array was divided into three sections each containing five receivers (receivers A–E to the west, F–J in the centre, and K–O to the east) to determine if the detections of smolts crossing this arc were randomly distributed ( $\chi^2$ ).

The direction taken by each smolt in the marine environment was determined. The successive compass directions travelled by each post-smolt from the mouth of the estuary (64°20'11"W 50°16'58"N) to the first location of detection on the first array, and from the last detection location on the first array to the first detection on the second array were estimated using a map and the coordinates of the receiver positions as an approximation for the location of post-smolts. If a post-smolt was not detected at the second receiver array or was detected only by the second array and not the first, then the compass direction from the estuary to the first or the second array, as appropriate, was determined. If a post-smolt was detected by two neighbouring receivers of the same array within a 10 min interval, then the post-smolt was assumed to be in the overlapping zone of the two receivers' respective range. In that case, the compass direction for this post-smolt was determined using the middle point between the two receiver positions as the actual position of the fish, rather than either of the two receivers that had detected the tag. A post-smolt was considered detected if it was detected once (one hit) or more at each location.

The mean of these successive compass directions was calculated for each smolt. A rose diagram showing the mean direction across

the first two arc arrays was constructed for each year of study using the R statistical 'circular' package (<http://www.r-project.org/>). Rayleigh's test was used to calculate the overall mean of direction per year, and circular analysis of variance (ANOVA) using a high concentration *F*-test (Stephens, 1972) was used to compare the means of directions between the two study years. In 2010, calculation of mean compass directions included data on the directions of post-smolts travelling through the third receiver array.

### Surface currents

The direction and speed of the nearshore currents at the time that post-smolts were last detected at the first and second receiver arrays off the Rivière Saint-Jean were approximated by correlating the time and day of the post-smolt passage to the nearest hourly tide direction and speed provided by the Atlas of Tides and Currents of the Mingan Archipelago–Gulf of St. Lawrence (2003–2012)–for Sector 1 (St. Lawrence Global Observatory, 2011a). The number of times the tidal direction matched the mean direction of post-smolt movement was determined.

### Water temperatures and surface salinity

Surface water temperatures 5–7 m below the surface were recorded (°C) to the nearest first decimal with temperature loggers (Vemco/Amirix Inc. Minilogs) attached directly below the receiver. Water temperature was recorded every 30 min from 13 June to 22 July at receivers No. 5 and No. 10 in 2009 (Figure 1) and receivers A (29 May–30 July), E, I, M, and R (1 June–30 July) in 2010 (Figure 1). Each datalogger was attached on the rope directly below the receiver, 5–8 m below the surface. Daily mean water temperatures were calculated and compared using univariate ANOVA. Surface water samples were

collected during 2010 in the nearshore environment during flood tides (30 July and 12–14 August 2010) and during ebb tides (23 August 2010). Five water samples were collected at the Anticosti Island receiver line on an ebbing tide on 4 August 2010. Salinity values were measured with a salinometer (Yellow Springs Instrument Co., Yellow Springs, OH, USA; Model 33) at these locations (Table 1). Water samples were not taken during the time of the smolt run, but rather during the following month. However, we expect that the direction of the freshwater outflow and nearshore salinity fluctuations, regulated by the predictable tidal rhythmic flow, would be relatively consistent except for a slight decrease in the extent of the freshwater surface area over-time, which would vary with the volume of river discharge. Because there was no difference in the mean of surface salinity between the two samples taken during flood tides, mean salinity values were calculated when more than one sample was available for the same location. As a result, salinity values were available for 20 and 19 positions for flood and ebb tides, respectively (Table 1). These salinity values were used to generate isohalines through bivariate interpolations using the package 'Akima' in the R statistical programming interface (<http://www.r-project.org/>) (Akima, 1978). Two graphs were generated, one for flood tide and one for ebb tide.

## Results

### Detection patterns and direction of movement off the Rivière Saint-Jean

During 2009, 25 of the 44 tagged smolts (56.8%) that exited the estuary were detected by at least one of the receivers located off the mouth of the Rivière Saint-Jean. No detections occurred at the two arrays perpendicular to the shore, located 9 km on either side of the estuary (Figure 1). A total of 23 post-smolts

were detected crossing the first receiver array (~1 km from the estuary exit). Sixteen post-smolts were detected by the second receiver array; however, two of them (tags 57812 and 57868) were not initially detected at the first array. The receivers positioned at the centre of the first (receiver No. 3) and second (receiver No. 9) arrays detected the most post-smolts, with 14 and 12 post-smolts detected (Figure 2a). This was 31.8 and 27.3%, respectively, of the 44 individuals first released in freshwater, and 56.8 and 48.0%, respectively, of the 25 smolts detected in the marine environment. One post-smolt (tag 57867) was detected 19 km upriver from its estuary exit 1 d after its last detection at sea by receiver No. 9. The upstream detection, after being detected at sea, was probably due to a predation event, possibly by an upstream migratory anadromous brook trout (*Salvelinus fontinalis*) that had ingested the smolt. Post-smolts were detected within the first two receiver arrays for a mean time of 36 min (s.d. = 41 min, range: 1–188 min,  $n = 23$ ).

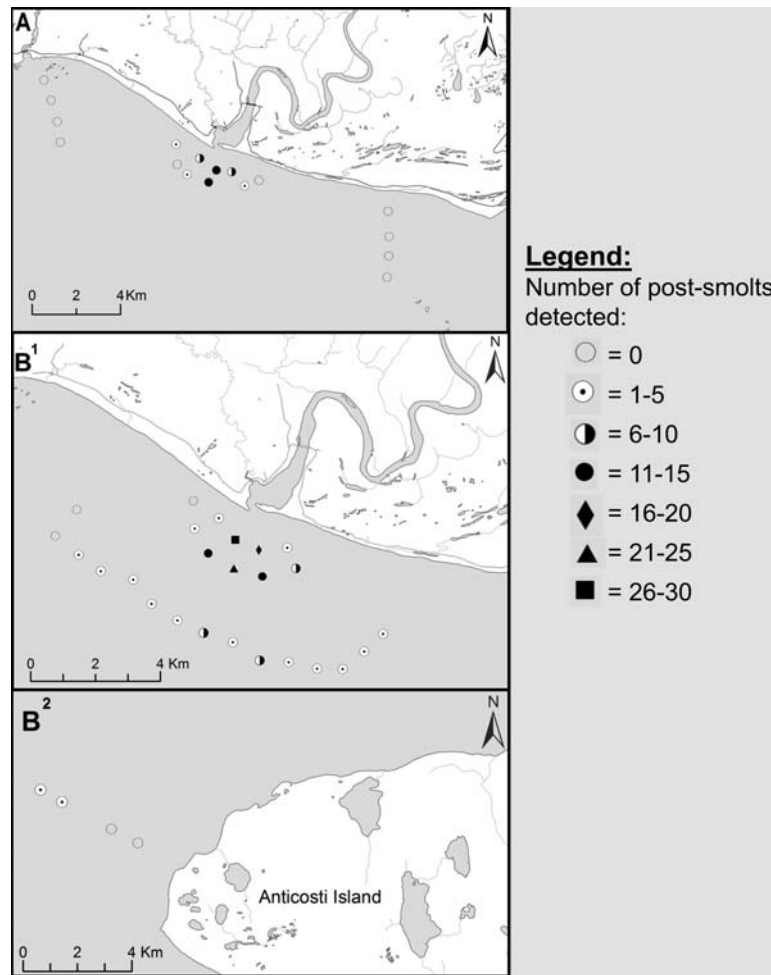
In 2010, 41 (83.7%) of the 49 smolts tagged in freshwater were detected on the nearshore arrays after exiting the Rivière Saint-Jean. A total of 39 post-smolts were detected crossing the first receiver array, 38 post-smolts were detected by the second array, and 36 post-smolts were detected by the third receiver array. Two post-smolts (tags 36216 and 36249) failed to be recorded by the first array, but were later detected at the second and third arrays. Another two post-smolts (tags 36250 and 36208) failed to be detected by the second receiver array, but were recorded moving through the first and third arrays. Tag 36211 was detected at the first and second arrays, failed to be detected at the third array, but was later detected at the Strait of Belle Isle on 23 July 2011. Thus, the minimum numbers of individual post-smolts that crossed the first, second, and third arcs were 41, 40, and 37, making up 83.7, 81.6, and 75.5% of the tagged group, respectively. As in 2009, the receivers positioned in 2010

**Table 1.** Surface salinity from samples collected in 2010.

Water sample location	Latitude	Longitude	Salinity at flood 1	Salinity at flood 2	Mean salinity at flood tide	Salinity at ebb tide
Arc 1	50°16'47"	64°21'02"	25.5	27.6	26.6	24.4
Arc 2	50°16'24"	64°20'37"		21.3	21.3	
Arc 3	50°16'17"	64°19'58"	14.8	10.8	12.8	25.2
Arc 4	50°16'19"	64°19'15"	12.5	18.4	15.5	17.2
Arc 5	50°15'56"	64°19'03"		14.5	14.5	11.8
Arc 7	50°15'57"	64°20'39"	13.0	27.8	20.4	26.2
Arc 9	50°16'36"	64°21'40"	27.8	26.4	27.1	26.2
Arc 10	50°17'3"	64°21'41"	28.8		28.8	
A	50°16'53"	64°24'44"	20.2	16.8	18.5	22.6
B	50°16'28"	64°25'14"	19.2		19.2	
C	50°16'8"	64°24'40"	20.2	15.3	17.8	26.2
E	50°15'44"	64°23'14"		20.4	20.4	21.6
G	50°15'4"	64°22'04"	26.4		26.4	23.0
H	50°14'53"	64°21'23"	26.4	27.4	26.9	
I	50°14'43"	64°20'37"		27.6	27.6	29.2
K	50°14'24"	64°19'09"		28.0	28.0	27.2
L	50°14'18"	64°18'25"	24.5		24.5	
M	50°14'18"	64°17'45"	23.8	20.0	21.9	27.6
N	50°14'36"	64°17'12"	27.8		27.8	
O	50°14'54"	64°16'43"	28.0	25.5	26.8	29.2
AC1	49°53'32"	64°32'11"				28.0
AC2	49°53'48"	64°32'60"				28.0
AC3	49°54'3"	64°33'48"				28.2
AC4	49°54'16"	64°34'32"				27.8
AC5	49°54'31"	64°35'13"				28.6

Averages of salinity values are reported for locations where more than one sample was taken.





**Figure 2.** Number of post-smolts detected at each receiver in 2009 (a) and 2010 (b<sup>1</sup> and b<sup>2</sup>).

at the centre of the first (receivers No. 2 and No. 3) and second (receiver No. 7) arrays detected the most post-smolts, with 26, 20, and 24 post-smolts detected, respectively (Figure 2b<sup>1</sup>).

Also in 2010, the pattern of post-smolts detected along the 15 receivers of the third array was more fan-shaped than in the inner array arcs, but not evenly distributed among the three equal portions of the array ( $\chi^2 = 11.7$ , d.f. = 2,  $p = 0.003$ ). Seven post-smolts were detected on the westernmost section (on A–E receivers) of this arc array, while 26 and 17 post-smolts were detected on the central (F–J receivers) and eastern (K–O receivers) sections, respectively. However, all but two of the receivers of this array detected at least one post-smolt, with the exceptions being receivers A and B (Figure 1), and the greatest number of smolts detected on the third array occurred near the centre at receivers H and J where seven and ten post-smolts were recorded, respectively (Figure 2b<sup>1</sup>). In 2010, post-smolts were detected within the first two receiver arrays for a mean time of 75 min (s.d. = 96 min, range: 1–432 min,  $n = 40$ ), and within the three receiver arrays for a mean duration of 168 min (s.d. = 135, range: 62–727 min,  $n = 36$ ).

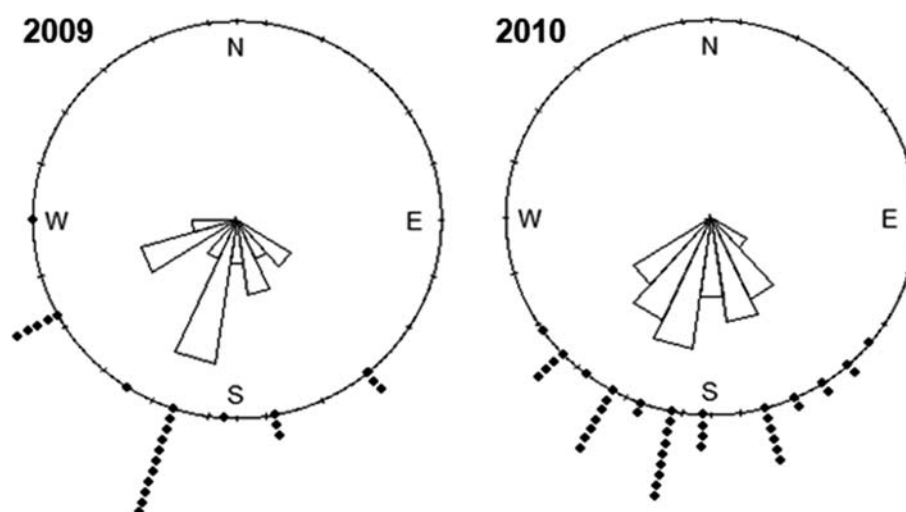
Atypical detection patterns were noticed on the third receiver arc during 2010. Tag 36232 was detected at receiver G on 12 July, 21 d after its previous detection at receiver I; tag 36244 was recorded multiple times between 17 and 28 June at receivers M,

N, and O; and tag 36259 was also recorded multiple times at receiver N between 18 and 30 June 2010. These detections were not included in the analyses because we suspected that these post-smolt detections were suspicious. Causes of atypical patterns could include movement patterns of possible predators such as anadromous brook trout (Curry *et al.*, 2006), milling behaviour (Dempson *et al.*, 2011), or mortality.

The mean direction for post-smolts travelling through the two first arrays within 2 km from the estuary exit was similar between the two years of study (Figure 3; circular ANOVA with high concentration  $F$ -test:  $F = 3.677$ ,  $p > 0.05$ ), with a mean direction south–southwest in 2009 and south in 2010. The mean direction calculated for post-smolt movements through the three receiver arrays in 2010 was  $186.6^\circ$  (south), with a significant Rayleigh's test result testing for non-uniformity ( $p < 0.0001$ ;  $r = 0.885$ ).

#### Detection patterns and movement at Anticosti Island, Cabot Strait, and the Strait of Belle Isle receiver lines

Two post-smolts were detected crossing the west point of Anticosti Island at receiver S (tag 36249) and at receiver T (tag 36251) (Figure 2b<sup>2</sup>). Post-smolt 57249, released on 14 June 2010, was detected off the Rivière Saint-Jean at receiver No. 5 on the second array and receiver O on the third array, and it then took 42 h 21 min to reach receiver S near Anticosti Island, travelling



**Figure 3.** Rose diagrams showing the mean vector of directions recorded for each detected post-smolt in 2009 ( $n = 25$ ) and 2010 ( $n = 41$ ) as it travelled from the estuary through the first two receiver arrays 2 km off the estuary. The circular mean was calculated for each year, and Rayleigh's test of non-uniformity was run, giving an index of concentration ( $r$ ) from 0 to 1. For 2009: mean =  $200.4^\circ$  (south-southwest),  $r = 0.853$ ,  $p < 0.0001$  and for 2010: mean =  $187.3^\circ$  (south),  $r = 0.896$ ,  $p < 0.0001$ .

at a rate of  $27.8 \text{ cm s}^{-1}$  ( $2.0 \text{ bl s}^{-1}$ ). Post-smolt tag 57251, released on 15 June 2010, was detected at receiver No. 4 on the first arc array, receiver No. 5 on the second array, and at receiver O on the third array, then took 148 h 22 min (6.2 d) before being recorded on receiver T off Anticosti Island, giving a minimum travel estimate of  $8.3 \text{ cm s}^{-1}$  ( $0.6 \text{ bl s}^{-1}$ ).

One post-smolt (tag 36211) was detected crossing the Strait of Belle Isle receiver array on 23 July 2010, 44 d after its last detection at receiver No. 6 on the second arc off the Rivière Saint-Jean. The shortest route to the Strait of Belle Isle was  $\sim 630 \text{ km}$  if the post-smolt travelled on the north side of Anticosti Island. Assuming the fish followed the shortest route, travelling rates would have been  $16.6 \text{ cm s}^{-1}$  ( $1.2 \text{ bl s}^{-1}$ ), for a minimum speed of  $14.4 \text{ km d}^{-1}$ . If, however, this post-smolt first moved south of Anticosti Island before turning to the Strait of Belle Isle, then the route would have been at least  $800 \text{ km}$ , with a minimum travelling rate estimated at  $22.2 \text{ cm s}^{-1}$  ( $1.5 \text{ bl s}^{-1}$ ). No post-smolts were detected at the Cabot Strait array, but it is possible that some post-smolts swam out of the Gulf of St. Lawrence on the northern side of Cabot Strait where no receivers were deployed.

### Environmental factors in the nearshore environment: temperature, current, and salinity

In 2009, there were no differences in daily mean temperatures recorded at receiver No. 5 and No. 10 (Table 2, Welch's  $t$ -test:  $t = 0.4245$ , d.f. = 22,  $p = 0.7$ ), when post-smolts were present within the two receiver arrays (17–28 June 2009). The equally spaced temperature loggers deployed on the third receiver array in 2010 (at receivers A, E, I, and M) also did not differ in daily mean water temperatures between 6 and 24 June 2010, when post-smolts were present (Table 2, ANOVA:  $F = 0.3$ , d.f. = 3,  $p = 0.8$ ).

During 2009, 68.0% ( $n = 17$ ) of the post-smolts swam through the receiver arrays off the Rivière Saint-Jean on an ebb tide, while 32.0% ( $n = 8$ ) did so on a flood tide. The observed calculated movement directions of post-smolts passing through the receiver arrays approximately matched the surface water current directions

**Table 2.** Mean of water surface temperatures ( $^\circ\text{C}$ ) recorded every 30 min at each location when post-smolts were present within the two receiver arrays in 2009 (17–28 June) and within the three receiver arrays in 2010 (6–24 June).

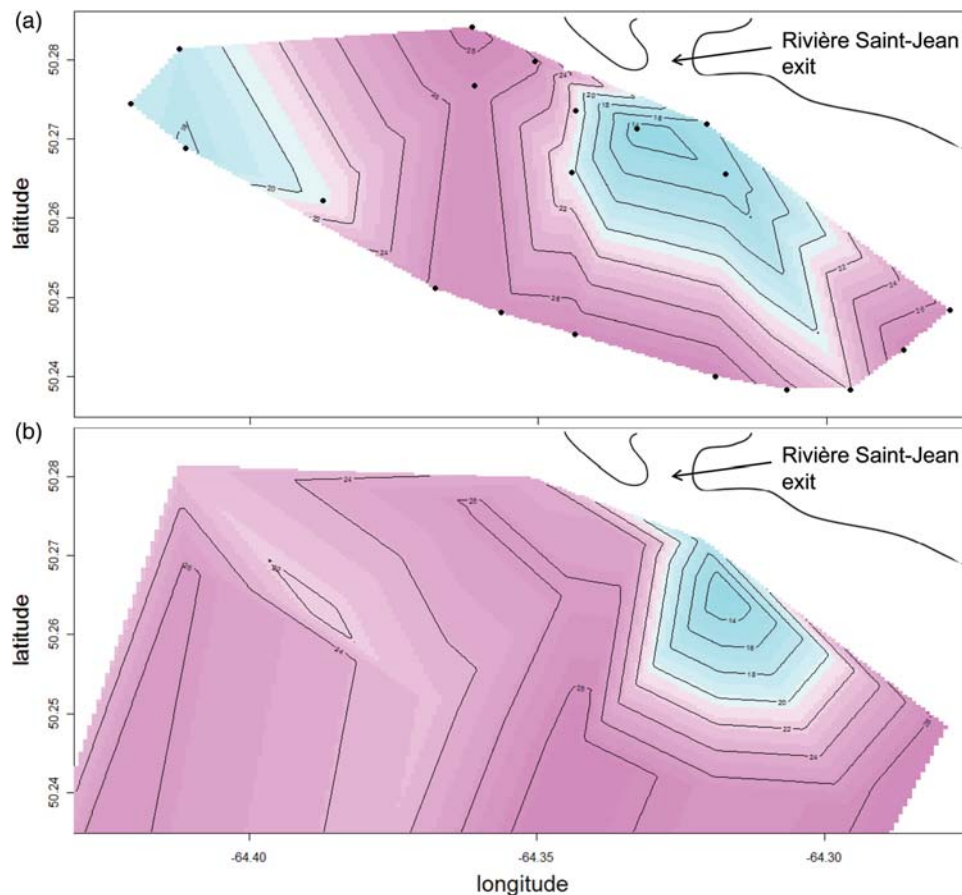
	2009		2010			
	No. 5	No. 10	A	E	I	M
Mean	5.8	5.6	5.0	5.0	4.8	4.7
s.d.	1.6	1.6	1.3	1.3	1.2	1.3
Min	3.2	3.1	3.2	3.2	3.1	2.9
Max	10.2	9.9	7.9	7.9	7.7	7.9
$n$	576	576	912	912	912	912

in six cases (24%). In 2010, the majority (31 of 41) of the tagged post-smolts (75.6%) swam across the receiver arrays off the Rivière Saint-Jean on an ebb tide, while the remainder swam through on a flood tide (24.4%). The direction of the post-smolt movements through the arrays matched the estimated surface water current direction for only two individuals (4.9%).

Off the Rivière Saint-Jean estuary, the lowest salinity ranged from 11.8 (near receiver No. 5) at ebb tide to 12.8 (near receiver No. 3) during flood tide (Figure 4). The highest salinity values ranged from 28.8 at flood tide (near receiver No. 10) to 29.2 during ebb tide (receiver O). Surface salinity along the Anticosti Island receiver line ranged from 28.0 closest to the island to 28.6 offshore (5 km away from the island).

### Discussion

Post-smolts exiting the estuary of the Rivière Saint-Jean showed a significant directional movement south and south-southwest during the two years of the study. This held true across the multiple estuary receiver arrays that had been deployed at increasing distances from the river exit, although the post-smolts dispersed more as they transited the outermost array. A 6 year study of post-smolt coastal movements in Narraguagus Bay, Maine, USA, also documented post-smolts moving south-southwest as they exited the river (Kocik et al., 2009). Dempson et al. (2011) observed



**Figure 4.** Isohalines of surface salinity during flood tide (a) and ebb tide (b) obtained through bivariate interpolations from the salinity values observed at the sampled sites (dark circle), with blue colours indicating freshwater and pink indicating saline water (sites on the Anticosti line taken during ebb tide only are not shown on the map).

annual changes in migration routes over a 3 year study of post-smolts travelling out of a 50 km long fjord in southern Newfoundland.

Furthermore, the tagged post-smolts in this study moved rapidly away from the coast once they entered the marine environment in both years. Post-smolts departing the Rivière Saint-Jean took ~1 h or less to leave the 2 km zone (2009 and 2010) and <3 h to leave the 4 km zone around the estuary (in 2010). No post-smolts detected at the third array in 2010 were logged back at the second array, indicating that movements seaward were without direction reversals, as might be occasioned by foraging bouts. This observation is contrary to the findings of Dutil and Coutu (1988), who reported nearshore post-smolt residency of several months along the northern coast of the Gulf of St. Lawrence. Dempson *et al.* (2011) also observed extended residency in a fjord of southern Newfoundland with extensive back-and-forth movements.

Other researchers have associated rapid emigration of post-smolts with environmental cues. In Norway and Iceland, post-smolts were observed rapidly leaving the nearshore environment and orienting towards warmer and more saline water (Holm *et al.*, 2000; Holst *et al.*, 2000; Gudjonsson *et al.*, 2005). No significant water temperature variations were observed off the Rivière Saint-Jean, hence no linkage between post-smolt directional

movements and warmer water temperatures could be made. However, the mean near-surface water temperatures measured in the marine environment during this study ranged between 4.8 and 5.8°C. Spring cold surface water temperatures (5–7°C) have been correlated with poor survival of post-smolts compared with a warmer optimal range (8–10°C) in the North Sea (Friedland *et al.*, 1998). Across the Atlantic Ocean, post-smolts appear to favour optimal surface temperatures ranging from 7 to 14°C (LaBar *et al.*, 1978; Holm *et al.*, 2000; Holm *et al.*, 2003). Hence, it is possible that the cold water temperatures present in the nearshore environment in this study site may have stimulated post-smolts to pursue their migration offshore to seek optimal temperatures. Records of sea surface temperatures in the Gulf of St. Lawrence indicate that, in spring, the warmest areas (6–10°C seasonal means) are located in the western half of the Gulf (from Anticosti Island to northern Nova Scotia). In summer, however, it is the southern half of the Gulf (from the Gaspé Peninsula to Cabot Strait) that is characterized by the warmest mean water temperatures ranging from 15 to 18°C, while the northern half (including the water surrounding Anticosti Island) presents summer mean temperatures optimum to post-smolts ranging from 11 to 14°C. The warmest sea surface temperatures in autumn range from 8 to 10°C and are restricted to south (Prince Edward Island) and southeastern (Newfoundland) areas

of the Gulf (St. Lawrence Global Observatory, 2011b; Zhai *et al.*, 2011).

Despite the hourly local variation in water current speed and direction reported by the St. Lawrence Global Observatory in the nearshore coastal environment in the vicinity of the Rivière Saint-Jean, residual water currents in Jacques Cartier Strait are known to flow west (El-Sahb, 1976; Drinkwater and Gilbert, 2004). An unintended empirical test of this occurred when two buoys and receiver mounts (receiver G and N) from our arrays detached from their respective anchors 2 weeks apart and drifted to the same location to the west. The post-smolts, however, travelled south–southwest from the estuary to the second array, subsequently fanning out to a more dispersed south–southwest to southeast direction by the time they crossed the third array. Therefore, the great majority (76% in 2009 and 95% in 2010) of the smolts did not follow the putative dominant nearshore currents occurring during their initial migration in the Gulf of St. Lawrence.

Surface salinity interpolation data for the nearshore environment near the Rivière Saint-Jean revealed that irrespective of whether the tide was ebbing or rising, the freshwater input from the river flowed south–southeast. However, during ebb tides, the freshwater area was more concentrated and defined (e.g. smaller surface area), while during the flood tide, it was dispersed over a larger area as the rising tide pushed the freshwater back towards shore (Figure 4). Despite the tidal influence on surface salinity, most of the freshwater outflow from the Rivière Saint-Jean affected salinities on the eastern half of the first two receiver arrays. However, this effect had mostly dissipated at the outermost third receiver array (Figure 4), except for a small area of less saline surface water probably influenced by another freshwater input west of the third array where receivers A, B, and C were deployed. It is accepted that increases in salinity not only influence the timing of sea entry, but may also assist migrating salmon to orient towards the open ocean (McInerney, 1964; Thorpe, 1994; Holm *et al.*, 2000; Lacroix and Knox, 2005). Within the first 2 km off the Rivière Saint-Jean, post-smolts oriented south and not west, where surface salinity appeared greatest. However, detection rates on the third array were not random, and the highest numbers of detections occurred where salinity measurements were the highest, with lower detection rates on the westernmost side of the array where salinity values were the lowest. The spatial scale of the study was large. It was, therefore, difficult to determine conclusively what environmental variables affected the orientation of the salmon in the Gulf.

Our results do not support the generalization that post-smolts from this region stay close to shore to feed and gain weight and energy before migrating out of the Gulf of St. Lawrence, although this could occur in years when inshore prey availability was high (see Caron, 1983; Dutil and Coutu, 1988; Friedland *et al.*, 1999). Our study did not attempt to quantify prey availability. However, the Gulf of St. Lawrence supports a productive ecosystem regulated by physical factors, such as seasonal freshwater discharge and weather patterns, which in turn are affected by yearly variations (Maps *et al.*, 2011). The phytoplankton and zooplankton biomass varies spatially and temporally within the Gulf, with primary production blooms starting earlier (spring) in the northeast Gulf and the Magdalen shallows, and later (summer) in the lower St. Lawrence estuary (Mei *et al.*, 2010). Primary production density and locations possibly affect the distribution of post-smolts, whose growth rates are accelerated and sustained at high

levels, commencing as soon as they leave the riverine environment (Dutil and Coutu, 1988; Friedland *et al.*, 1999). Also, many predators, such as northern gannets (*Morus bassanus*), which are known to feed on post-smolts (Montevecchi *et al.*, 2002), were observed while deploying the receivers at sea. Predator presence and abundance in the area may incite post-smolts to leave the coastal zone rapidly upon entrance to the marine environment.

The results of this study showed that a consistently observed migratory pathway to the south was not correlated with surface water temperatures or surface water currents in the nearshore environment. Instead, post-smolt movements were rapid and away from the shore to areas where local measured salinity values tended to be highest.

Greater freshwater outflow during spring would decrease inshore surface salinities, causing post-smolts to swim rapidly offshore to access higher salinities (Straty, 1974). Nearshore salinities would be expected to rise later in the year as the annual spring freshwater discharge peak subsided. Also, the discharge of organic matter with the freshwater outflow along the nearshore zone probably reduces primary productivity in spring (Maps *et al.*, 2011; Mei *et al.*, 2011). Consequently, feeding opportunities in that zone would be reduced in spring and improve again later in summer.

Other factors may influence post-smolt movements. For instance, salmonids may imprint on the geomagnetic field of their natal river, which would help them find their river of origin during spawning migration (Lohmann *et al.*, 2008). If so, it is likely that they sense the geomagnetic field upon their first oceanic migration as well, and use it to navigate to feeding grounds. Similarly, in salmonids, the sense of smell plays an important role in homing (Brannon, 1982; Hasler and Scholz, 1983), and thus may also play a role in the orientation of migrating post-smolts. Finally, post-smolts may also follow emigrating kelts of their native river as the latter swim to feeding grounds after overwintering in the river. For instance, in the Rivière Saint-Jean, a kelt was detected crossing the Anticosti Island line in 2010 and then was detected crossing the Strait of Belle Isle receiver line 40 d later travelling at an approximate rate of 16.5 km d<sup>-1</sup> (Lefèvre and Whoriskey, 2010). Despite the fact that kelts are capable of swimming much faster than juveniles, the post-smolt detected at the Strait of Belle Isle in this study travelled almost as fast (14.4 km d<sup>-1</sup>); thus, further research investigating the learning of migration routes by conspecific salmon should be pursued.

Two post-smolts were detected on a limited receiver array positioned off Anticosti Island 41 km southwest past our outermost receiver array around the river estuary. Assuming straight-line travel routes, these fish moved at rates varying from 8.3 to 27.8 cm s<sup>-1</sup>. Despite this variation, these travel rates indicated sustained and directed movements of the fish toward the centre of the Gulf of St. Lawrence in the period following their entry to sea. During the study, no post-smolts were detected at Cabot Strait, and only one post-smolt was detected crossing the Strait of Belle Isle array (in 2010). This post-smolt took 44 d to complete the migration, travelling at speeds comparable with the two post-smolts mentioned above, between 16.6 cm s<sup>-1</sup> (or 14.4 km d<sup>-1</sup>) and 22.2 cm s<sup>-1</sup> depending on the possible pathways. Interestingly, post-smolts originating from other rivers of the Gulf of St. Lawrence (namely the Miramichi, Cascapedia, and Restigouche rivers) have also been detected crossing the Strait of Belle Isle, 30–50 d following their estuary departure (F.



Whoriskey, pers. comm.), but in greater proportion (~20% of tagged individuals) compared with what was observed for the Rivière Saint-Jean (F. Whoriskey, pers. comm.). Kocik *et al.* (2009) reported similar speeds ranging from 19 to 29 cm s<sup>-1</sup> between 10 and 15 km offshore. Also, Lacroix and McCurdy (1996), while working in a macro-tidal estuary, recorded much faster speeds ranging between 64 and 267 cm s<sup>-1</sup> in the Chamcook Channel of the Bay of Fundy.

Failure to detect post-smolts at the Gulf's exits could mean that post-smolt mortality in the Gulf was high, that the transmitter batteries expired, or that the receivers were removed (Strait of Belle Isle only) before the acoustically tagged post-smolts entered the Atlantic Ocean. The post-smolts also could have left the Gulf through the northern part of Cabot Strait, where no receivers were deployed at the time of this study. To date, only two post-smolts from two different rivers in Quebec entering into the Gulf were reported to have probably used Cabot Strait to enter the Atlantic Ocean. One of these two was tagged on the Gaspé Peninsula (originating from the Saint John River), and the other was marked in the Cascapedia River near Quebec's border with New Brunswick. They were recaptured near Cabot Strait at Cape Broyle (on the eastern coast of Newfoundland) and off Cape Breton, respectively (Caron, 1983). Lastly, it may also be possible that at least some post-smolts do not leave the Gulf of St. Lawrence and instead confine their ocean movements and growth there. However, this latter possibility seems unlikely because the winter water temperatures drop below 0°C in most areas of the Gulf of St. Lawrence or stay between 0 and 1°C in the Cabot Strait region, which would either be lethal to post-smolts or would not allow them to maintain the constant growth that we observed when reading the scales (which show growth patterns) of returning adults. However, surface water temperatures in the northern area of Cabot Strait and along the south-eastern coast of Newfoundland stay relatively warm until the end of autumn (Zhai *et al.*, 2011), making it possible for post-smolts to delay their entrance to the Atlantic Ocean until later in the year, assuming suitable nursery areas in the Gulf were present (e.g. Friedland, 1999). Future research is required to distinguish which (if any) of these explanations accounts for the observed telemetry patterns of post-smolts in the Gulf. To elucidate post-smolt migration, researchers should continue to tag salmon and track post-smolt movements at the exits of the Gulf of St. Lawrence. The Strait of Belle Isle and Cabot Strait should be equipped along their entire length with acoustic telemetry equipment left in place until at least the end of November. In parallel, prey availability studies should be conducted in the Gulf of St. Lawrence in summer and autumn. Surface trawl surveys should be conducted in areas of high prey availability in an attempt to capture post-smolts and during different seasons to estimate the spatio-temporal distribution of salmon juveniles in the Gulf of St. Lawrence.

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