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Survival and behaviour of post-smolt Atlantic salmon in coastal habitat with extreme tides

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The early marine migration of 55 Atlantic salmon post-smolts tagged with acoustic transmitters was automatically monitored using 13 to 25 km long arrays of receivers deployed inside the Bay of Fundy, a coastal system on the east coast of Canada. The survival of post-smolts from groups with short- and long-term transmitters in coastal habitat up to 10 km from the river was 92 to 100%, indicating a successful transition to salt water and departure. Migration for 68 to 77% of post-smolts followed a direct route and it was rapid (transit time usually <12 h). Post-smolts initially migrated in a south to south-west direction (*i.e.* orientation towards the mouth of the bay) and they were aggregated near the coast. Post-smolts with long-term transmitters were monitored 20 km from the river where they continued to be aggregated, moving near the coast through a 'common corridor', and their survival to that point was at least 84%. Post-smolts from both groups travelled heading out of the coastal system during ebb tides. Flood tides interrupted migration, and they caused changes in travel direction and delays in departure for post-smolts not leaving by a direct route. Monitoring of coastal habitat inside the Bay of Fundy intercepted 62% of migrating post-smolts with long-term transmitters returning after an initial absence of 2 to 22 days. Returning post-smolts displayed a resident behaviour, using the habitat monitored inside the Bay of Fundy during July and August.

Key words: Atlantic salmon; behaviour; post-smolt; *Salmo salar*; survival; telemetry.

INTRODUCTION

On leaving the river of origin for their oceanic feeding migration, Atlantic salmon *Salmo salar* L. become post-smolts (Allen & Ritter, 1977). Little is known of the biology of Atlantic salmon as they enter the marine habitat or of the factors that influence their migration because of the difficulties in either finding or capturing post-smolts during this transit period. Mortality is thought to be high during post-smolt migration, especially in the early stages when they are still relatively small (Hansen *et al.*, 2003), but empirical data are lacking. The distribution of post-smolts recaptured at sea has been used to infer migration routes, but only on a macro-scale in the Atlantic Ocean (Reddin & Short, 1991; Reddin & Friedland, 1993; Holm *et al.*, 2000; Holst *et al.*, 2000).

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The potential for using telemetry to monitor young Atlantic salmon at sea was examined by Moore *et al*. (2000). They found that studies to date have been limited to habitat where tagged fish were monitored through narrow passages (*e.g*. rivers, estuaries and fjords). The majority of fish tracking studies have focussed on observations about the behaviour of the target species (Moore *et al*., 1995; Lacroix & McCurdy, 1996; Lyse *et al*., 1998), with no empirical data on migration success or survival. Recently, telemetry was used successfully to monitor the survival of Atlantic salmon post-smolts in a coastal system in relation to the presence of numerous Atlantic salmon farms and herring *Clupea harengus* L. weirs (Lacroix *et al*., 2004*a*), but fish were again monitored leaving through narrow passages out of the system. Monitoring tagged fishes in open marine and coastal systems offers a greater challenge than in partially enclosed areas. Lacroix & Voegeli (2000) proposed an approach using acoustic telemetry to provide a measure of survival in open marine systems. This involved the deployment of arrays or longlines of closely spaced automated receivers at intervals along the migration route that could intercept the passage of any migrant tagged with a transmitter and provide a measure of survival along the route. Automated monitoring based on this approach was used by Comeau *et al*. (2002) to successfully monitor the migration pattern of cod *Gadus morhua* L. in the open sea.

In this study, several intercepting arrays of closely-spaced automated receivers were used to monitor Atlantic salmon after they entered the coastal habitat and as they moved out of the inner Bay of Fundy on the east coast of Canada. The goals were to measure the migration success or survival of post-smolts in an open coastal system, and to document their migration route and behaviour patterns, especially in relation to hydrographic conditions and tidal flow. Trites & Garrett (1983) described the Bay of Fundy as a coastal system with the largest tides in the world and with extremely strong tidal currents, especially in the inner bay where the study was conducted.

MATERIALS AND METHODS

SMOLT TAGGING AND RELEASE

In 1999, electronically-tagged Atlantic salmon smolts released at the head of tide *c*. 0·5 km inside the Big Salmon River were automatically monitored after they left the river and entered the Bay of Fundy, a 320 km long bay that flows into the Gulf of Maine [Fig. 1(a)]. The Big Salmon River drains into the inner Bay of Fundy where the tidal range is at least twice as large as in the outer bay. Monitoring was at the narrowest point, where the main body of the bay was 50 km wide and where the transition from the inner to the outer bay began.

Two groups of smolts with different origins, representing different management practices used to conserve and enhance the population, were tagged and then released on separate dates based on their availability. Group 1 were collected as large wild parr by electrofishing in tributaries of the Big Salmon River in October 1998 and then held in a hatchery. They were from the 'live gene bank' established to preserve the genetic base of this Atlantic salmon stock. Group 2 were hatchery-reared first generation S2 offspring of

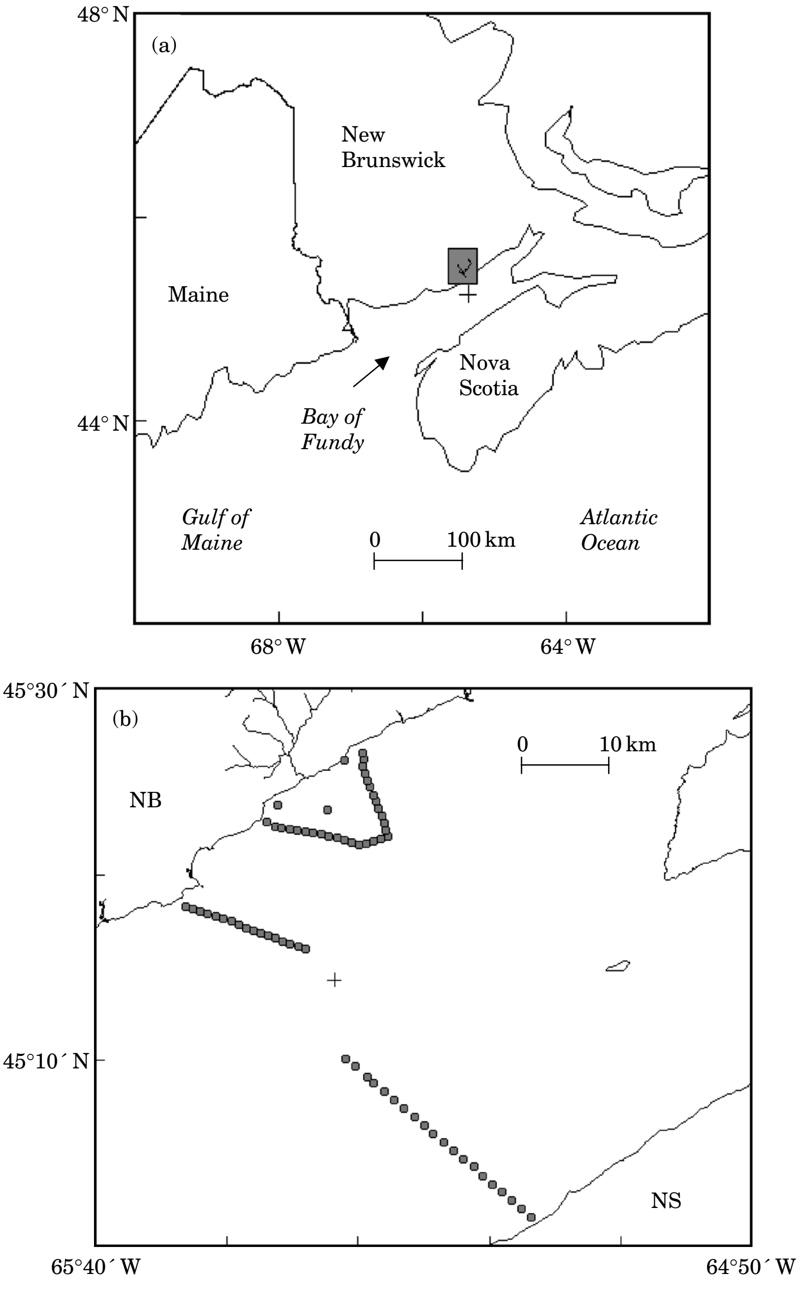

FIG. 1. Maps showing: (a) the location of the Bay of Fundy and Big Salmon River (■) where tagged Atlantic salmon smolts were released and (b) the location of the three coastal monitoring arrays (■) deployed to detect the movements of post-smolts. The position of Quaco Ledge (+) is shown in both maps for cross reference.

wild Big Salmon River brood-stock bred in captivity. Release dates (3 June for group 1 and 15 June for group 2) were within the timing of the smolt migration which in the Big Salmon River usually extends into June (G.L. Lacroix, unpubl. data).

The smolts were surgically implanted with individually coded acoustic transmitters (8 mm diameter V8 series, Vemco Ltd.) as described by Lacroix *et al.* (2004*b*), except that a clove oil solution (40 to 80 mg l^{-1}) was used as an anaesthetic. Transmitters were programmed with random code repetition (range, 30 to 60 s) to reduce the potential overlap in transmission of codes when two or more tags were simultaneously close to a receiver and, thereby, increase the probability of detection (Lacroix & Voegeli, 2000).

Smolts tagged in group 1 ($n = 29$; mean ± s.d. fork length, L_F, 17·3 ± 0·94 cm and mean ± s.d. mass, M, 45·9 ± 7·4 g) were smaller than those of group 2 ($n = 31$; 23·5 ± 1·1 cm and 116·8 ± 16·9 g) (t-test, d.f. = 58, $P < 0{\cdot}05$), but their condition factors (K, $K = 100 M L_F^{-3}$) did not differ (mean ± s.d., K, 0·88 ± 0·04 for group 1 and 0·90 ± 0·05 for group 2) (t-test, d.f. = 58, $P > 0{\cdot}05$). Smaller transmitters were used in group 1 than in group 2 (*i.e.* 28 *v.* 32 mm) to keep the transmitter size, in relation to fish size, within acceptable limits established by Lacroix *et al.* (2004*b*) for tag retention and long-term survival. Different battery options were used to achieve this difference in transmitter size and, as a result, group 1 had transmitters of shorter expected duration than group 2 (*i.e.* 3 to 4 weeks *v.* 8 to 10 weeks).

AUTOMATED MONITORING OF POST-SMOLTS

The departure of tagged smolts from the river was monitored using two automated receivers (VR20, Vemco Ltd.), one moored on the bottom just inside and the other just outside the river mouth. These were used to establish the time at which smolts from both groups started their marine migration. Twenty four of 29 smolts from group 1 and all 31 smolts from group 2 were confirmed to have left the river by sequential monitoring at both receivers. The five smolts from group 1 that did not leave the river were found by searching with a portable receiver (VR60, Vemco Ltd.); they were stranded and died in an intertidal habitat within the estuarine portion of the river.

The initial migration of post-smolts from both groups away from the river mouth was monitored using an array of 32 automated receivers (single-frequency VR1, Vemco Ltd.) deployed 800 m apart (starting <400 m from shore) to surround an area 5 to 10 km from the river as shown in Fig. 1(b). The spacing ensured overlap in detection range between receivers based on *in situ* range tests conducted at different times during the study and under varied conditions. The receivers were suspended 15 to 20 m below the surface using buoys moored as described by Lacroix & Voegeli (2000). The area was continuously monitored until 29 June and during this period searches for transmitters were made within the perimeter of the array using a boat equipped with hydrophone and portable receiver.

The continued migration of post-smolts from group 2 further out of the bay was then monitored using a 13 km long array of 17 VR1 receivers (deployed 800 m apart) that extended out from the New Brunswick coast *c.* 20 km from the river [Fig. 1(b)]. This array, deployed on 12 June, was not used to monitor fish from group 1 released earlier.

The possibility that post-smolts stayed within the confines of the Bay of Fundy for some extended period was then examined. The basis for this hypothesis was the recapture of a few post-smolts in coastal fisheries inside the bay reported by Jessop (1976). Monitoring was done using the receivers extending from the New Brunswick coast and, starting on 30 June, by an additional 25 km long array of 20 VR1 receivers deployed 1300 m apart extending from the Nova Scotia coast [Fig. 1(b)]. The two arrays monitored for the presence of post-smolts from group 2 with the long-term transmitters during July and August. The data stored in the receivers, suspended 20 m below the surface from fixed moorings, were downloaded weekly without moving the position of the receiver.

The stored data indicated that, when passing through a monitoring array, individual post-smolts were detected either simultaneously or in a continuous sequence at several adjacent receivers (*e.g.* a mean of 4·5 and 7·6 receivers at the array 5 to 10 km from the river for groups 1 and 2, respectively, and a mean of 5·4 receivers at the array 20 km from the river mouth for group 2). Their identification code was recorded many times at each receiver (*e.g.* a mean of 414 and 147 transmissions at the array 5 to 10 km from the river for groups 1 and 2, respectively, and a mean of 70 transmissions at the array 20 km from the river mouth for group 2). Code reception at individual receivers occurred in blocks, on average six to 12 blocks, that represented periods of continuous detection. These data indicated a high efficiency of monitoring arrays to intercept tagged post-smolts. The greater spacing of receivers in the array along the Nova Scotia coast (1300 *v.* 800 m) did not reduce the number of receivers at which a tagged post-smolt was detected (mean 4·3 receivers) or the number of codes received during passage (mean 65·4 transmissions) compared to the array along the New Brunswick coast (*t*-test, d.f. = 47, $P > 0{\cdot}05$).

Maps of the sequential position of each post-smolt were produced by combining data from all receivers. Migration success was determined from confirmed movements away from a sector bounded by an array. This was considered to be equivalent to survival if those post-smolts that were not detected leaving a sector were assumed to have died within that sector. This assumption was probably justified based on the high efficiency of monitoring arrays, especially where the array enclosed an area. The times of last detection at the river mouth and of first detection at a receiver within each marine array were used to calculate transit times and the sites of first detection at sea were used to establish travel directions away from the river. To examine behaviour in relation to tidal flow direction, the travel direction of migrating post-smolts (*i.e.* heading into or out of the bay) was established for each continuous segment of migration or travel vector between two or more receivers within an array (groups 1 and 2) or between arrays (group 2) that was completed during the ebb or flood segment of a tidal cycle or during a change in the direction of tidal flow. Stage and direction of tide was established using monitoring times and the tides and currents data at the Canadian Hydrographic Service harmonic station nearest to the monitoring location (*i.e.* either St Martins on the New Brunswick side of the bay or Margretsville on the Nova Scotia side).

RESULTS

Post-smolts survival was very high for both groups monitored to leave the area 5 to 10 km from the river (Table I), and it did not differ between groups (χ^2, d.f. = 1, $P > 0{\cdot}05$). Only two fish, both from group 1, were not monitored leaving the area nor were they monitored later or further away. One of the post-smolts was found during searches, and it was repeatedly detected (12 to 29 June) near the same location inside the perimeter of the array. No movements indicative of either a live post-smolt or an active predator were observed. The other fish was last detected just outside the river mouth where avian predators such as cormorants *Phalacrocorax* spp. and gulls *Larus* spp. were abundant.

TABLE I. Survival and transit time of tagged Atlantic salmon post-smolts from two groups through coastal habitat in the Bay of Fundy

Monitoring location	Group 1	Group 2
Smolts leaving river (*n*)	24	31
Post-smolts leaving the coastal habitat 5 to 10 km from the river		
Survival (%)	92	100
Mean ± S.D. transit time (days)	0·50 ± 0·91	0·46 ± 0·35
Post-smolts leaving the coastal habitat 20 km from river		
Survival (%)	n.d.	84
Mean ± S.D. transit time (days)	n.d.	1·74 ± 2·61

n.d., not determined for group 1 (see text for explanation).

Most smolts entered the bay during an ebb tide (83% and 94% of for groups 1 and 2, respectively, with no difference between groups; χ^2, d.f. = 1, $P > 0{\cdot}05$), soon after high tide (mean 0·9 and 1·9 h after high tide for groups 1 and 2, respectively, with no difference between groups; t-test, d.f. = 47, $P > 0{\cdot}05$). The few smolts that entered during the flood tide did so near the end of the cycle (mean 1·7 h before high tide for both groups) when the tidal current would have been 'slacking'. Tagged fish were therefore exposed to ebb tide currents as they left the river or soon thereafter. As a result, post-smolts initially headed in a south to south-west direction within the bay as they left the river, and many travelled along or near the coast (represented by 60° and 240° vectors in Fig. 2). The distributions were aggregated (the hypothesis that there was uniform distribution between 60° and 240° was rejected, G-test for goodness of fit, d.f. = 5, $P < 0{\cdot}01$), and the travel vector means (212° and 186° for groups 1 and 2, respectively) or distributions did not differ between groups (Watson's U^2 test and χ^2 test, d.f. = 5, $P > 0{\cdot}05$).

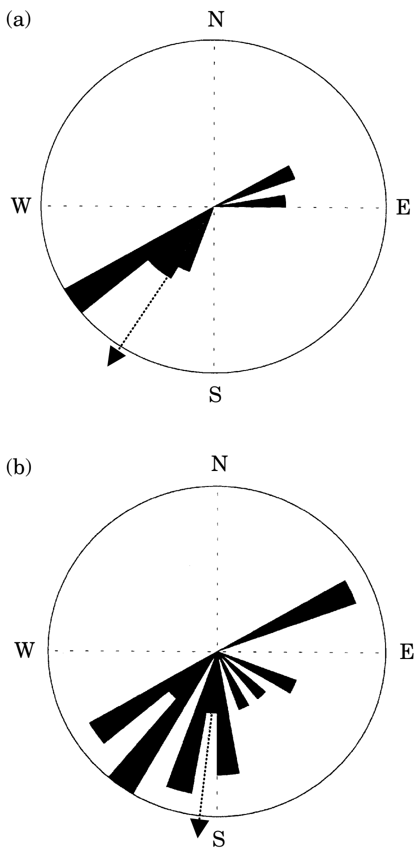

FIG. 2. Vector rose plots of the initial direction of travel of post-smolts monitored after entering the bay from: (a) group 1 and (b) group 2. The river mouth is at the centre of the compass rose, the shoreline extends along the 60° and 240° vectors, and the vector mean is shown (···▶).

Post-smolts from both groups migrated away from the river rapidly with no difference in mean transit time (Table I; *t*-test, d.f. = 51, $P > 0{\cdot}05$), and 44% of them reached the array 5 to 10 km from the river before the ebb tide turned. Transit times were <12 h for 71% and <24 h for 94% of post-smolts from both groups. Post-smolts usually continued to move rapidly away from the area, with 75% leaving within 24 h based on their time of last detection at the array. Others were delayed for several days (maximum 10·5 days) before departing, during which time they were repeatedly monitored within the area.

The survival of post-smolts from group 2 continued to be high as they migrated further out of the bay, moving through the monitoring array 20 km away along the New Brunswick coast (Table I). No estimate was obtained for group 1 at this array because of their early release date and departure (*i.e.* before deployment of the array). The five post-smolts from group 2 that were not detected passing this array were never detected again after they had left the area 5 to 10 km from the river. They either passed by outside of the monitoring array, leaving by a different route than the majority of post-smolts monitored, or they died before reaching the array (*i.e.* in the area between the two monitoring arrays).

As they headed further away from the river, post-smolts from group 2 continued to be aggregated close to the New Brunswick coast (the hypothesis that there was a uniform distribution among receivers was rejected, *G*-test for goodness of fit, d.f. = 5, $P < 0{\cdot}05$), with most fish leaving through a 'common corridor' *c.* 2·5 to 5 km from shore [Fig. 3(a)]. These post-smolts continued to migrate rapidly (Table I). Transit times, from entry into the bay, were <48 h for 81% of post-smolts. Several fish were slower (maximum 13·9 days) because they had been delayed within the area monitored near the river. Post-smolts then either departed without delay (69% leaving in <24 h), or they were detected in the area for several days (maximum 4·6 days) before leaving. Those fish that 'lingered' were monitored moving back-and-forth between arrays 5 to 10 km and 20 km from the river during this period.

Two distinct behaviour patterns became apparent when comparing transit times and sequential position plots for individual post-smolts: 1) rapid migration along a direct path away from the areas monitored [Fig. 4(a)], and 2) delayed migration with back-and-forth movements within the areas monitored [Fig. 4(b)]. Post-smolts that left rapidly migrated by following a relatively direct path away from the river. This included 77 and 68% of post-smolts from groups 1 and 2, respectively, monitored in the area near the river (with no difference between groups, *t*-statistic for test of equality of arcsine transformed percentages, $P > 0{\cdot}05$), and then 50% of post-smolts from group 2 monitored further away. Post-smolts that were delayed were repeatedly monitored moving either within or between the areas monitored before departing.

The direction of travel of post-smolts during monitored intervals was closely linked to the direction of tidal flow, both for fish that migrated directly and those that moved extensively within the area monitored (Table II). These intervals represented average travel distances of 5 to 10 km between receivers. When moving out of the bay post-smolts did so predominantly during an ebb tide or during a change from flood to ebb tide, and none did so against a flood tide. Travel intervals when post-smolts moved into the bay occurred during flood tides or during a change from ebb to flood tide and none occurred during an

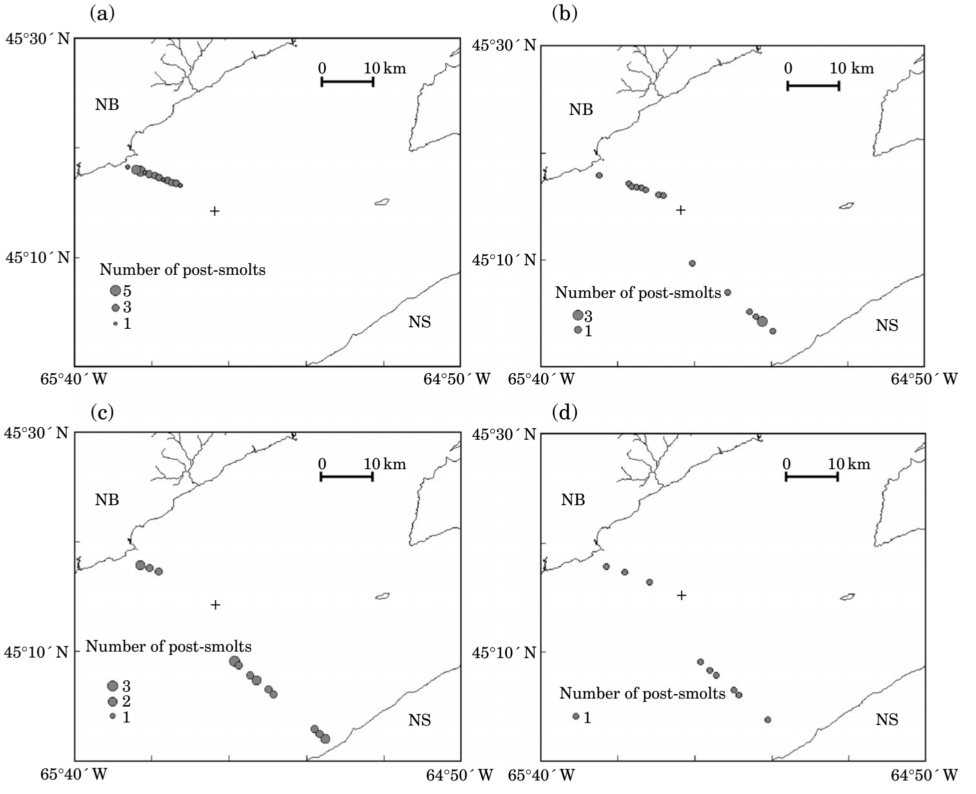

FIG. 3. Position of post-smolts from group 2 along the monitoring New Brunswick and Nova Scotia arrays: (a) when they first moved out of the bay, (b) when some post-smolts first moved back to the area monitored, (c) when some moved out of the area for a second to fourth time and (d) when some moved back to the area for a second to third time. The position of Quaco Ledge (+) is shown in all maps for cross reference.

ebb tide. The behaviour patterns observed during flood and ebb tides were different (d.f. $= 7$, $P < 0{\cdot}005$), but there was no difference in response between the two groups of post-smolts (based on a multi-way *G*-test of independence and interaction for data in Table II, d.f. $= 2$, $P > 0{\cdot}05$).

A resident behaviour pattern was recorded for many of the post-smolts with long-term transmitters. Instead of continuing their seaward migration, 16 of the 26 post-smolts from group 2 that were moving out of the bay (*i.e.* 62%) were later monitored returning to one of the arrays extending from each coast [Fig. 3(b)]. The returns were evenly distributed between both sides of the bay, with an aggregation *c.* 6 to 8 km from shore on the Nova Scotia side. This first return occurred mostly during July, 2 to 22 days after post-smolts had first left the area (mean ± S.D. time period $11{\cdot}0 \pm 7{\cdot}9$ days). The wide range in time periods indicated that while some post-smolts had remained nearby others may have travelled farther away. No returns from group 1 were recorded, probably because of the use of short-term transmitters in this group and their early release date (*i.e.* transmitters would have stopped transmitting by the time that returning post-smolts were monitored in July).

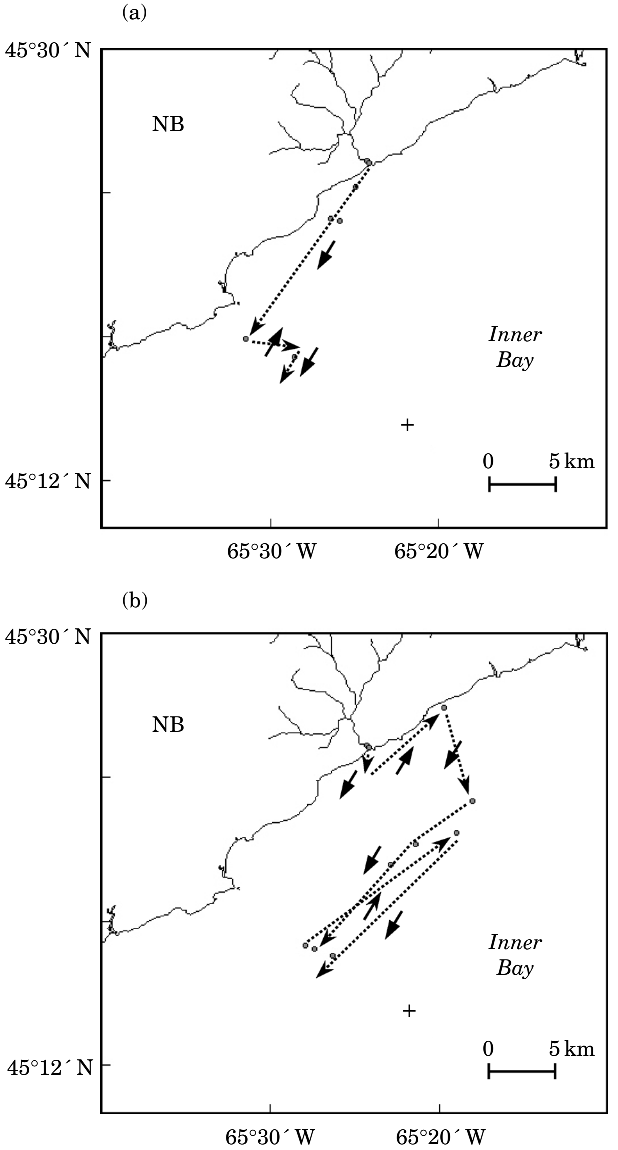

FIG. 4. Examples of sequential migration routes (···➤) followed by post-smolts: (a) that left the area rapidly by a direct path and (b) that were delayed and left the area by a less direct path. The direction of tidal flow during each monitored segment is shown (⟶).

Post-smolts from group 2 that returned to the monitoring area instead of continuing their seaward migration continued to be detected along the New Brunswick and Nova Scotia arrays throughout July and August [Fig. 3(c), (d)]. Ten post-smolts were monitored leaving a second time after a mean $\pm$ S.D. time period of $15{\cdot}1 \pm 11{\cdot}9$ days, six post-smolts returned a second time after a mean $\pm$ S.D. time period of $8{\cdot}7 \pm 8{\cdot}8$ days and five post-smolts were monitored leaving or returning more than two times after a mean $\pm$ S.D. time period of

TABLE II. Travel direction of tagged Atlantic salmon post-smolts from two groups in a coastal habitat in relation to direction of tidal flow in the Bay of Fundy

Travel direction	Group 1	Group 2
The per cent moving out of the Bay of Fundy during an:		
Ebb tide	76	70
Flood tide	0	0
Changing tide	24	30
n	21	71
The per cent moving into the Bay of Fundy during an:		
Ebb tide	0	0
Flood tide	19	68
Changing tide	81	32
n	16	47

The sample size (*n*) represents the number of travel segments monitored.

8·0 ± 5·8 days. These movements included brief and extended 'forays' (range, 2–36 days), either in a nearby habitat or farther away both inside the bay and out towards its mouth. Returns and departures were based on travel direction established by the monitoring sequence and by tidal flow direction at the time of interception (Table II). As the summer progressed, two to three times more post-smolts were monitored on the Nova Scotia side than on the New Brunswick side of the bay (*t*-statistic for test of equality of arcsine transformed percentages, $P < 0{\cdot}01$) with no difference between departures and returns (χ^2, d.f. = 1, $P > 0{\cdot}05$), but the distributions [Fig. 3(c), (d)] were not different from expected when based on the area monitored by each array (*G*-test for goodness of fit, d.f. = 1, $P > 0{\cdot}05$). Post-smolts from group 2 that were monitored to return to the area a first time and those that continued to show some residency later in the summer (*i.e.* returning a second or third time) were usually those that had initially been delayed and did not leave by a direct path (*e.g.* 81% of those post-smolts delayed >48 h returned).

DISCUSSION

The high early marine survival of tagged Atlantic Salmon post-smolts monitored along their migration route by acoustic telemetry was the first report of survival at this stage in an open marine habitat. It indicated that smolts successfully made the transition to salt water and to the post-smolt stage. In addition, automated monitoring provided a variety of new information for post-smolts or helped clarify some previous observations. A fine scale analysis of movements was used to describe the coastal migration route of post-smolts inside the inner Bay of Fundy. The effect of strong tides on migratory behaviour previously reported for smolts in estuaries was found to persist in the open marine habitat where it resulted in two distinct migratory patterns that influenced distribution and destination. Some post-smolts returned to the area while others apparently continued their migration. The extended presence of some post-smolts inside the Bay of Fundy was determined to reflect a resident behaviour pattern rather than a slow seaward migration from the area. This behaviour was possibly a function of an initial tide-related delay in migration as post-smolts left the coastal area near the river.

The measure of survival was considered to be highly accurate because of the performance of the monitoring arrays with closely spaced receivers. The likelihood of a tagged fish moving through undetected was very low. All fish moving through the array enclosing the area 5 to 10 km from the river were either monitored or accounted for as lost within that area. Because the other two arrays stretching out into the bay from each coast did not completely close off the area, there was a possibility that some fish moved through undetected and that survival was even higher than that observed (*i.e.* >84%). The aggregation of migrating post-smolts along the New Brunswick coast, however, ensured the likelihood that post-smolts were intercepted at the array 20 km from the river.

The mortality that occurred during the first weeks at sea was surprisingly low considering that post-smolts migrated through an open coastal habitat with extreme tidal range and currents (Trites & Garrett, 1983), and with numerous potential predators (marine fishes, mammals and birds). Predation, especially at the post-smolt stage during the first months after leaving the river, has generally been listed as an important source of marine mortality in salmonids (Hansen *et al.*, 2003; Middlemas *et al.*, 2003; Montevecchi & Cairns, 2003). At this stage, post-smolts are still small and easy prey. Lacroix *et al.* (2004*a*) suggested that the abundance of predators near Atlantic salmon farms was a source of the mortality of post-smolts monitored by telemetry in an area of the outer Bay of Fundy. The possibility that tag movement in this study could have reflected that of a predator (*i.e.* other than avian) and not of the target species tagged, as observed by Beland *et al.* (2001) for smolts inside an estuary, was examined and determined to be low. This was based on the assumption that the behaviour and habitat of a potential predator (*i.e.* large marine fish or mammal) would be distinguishable from that of post-smolts for which behaviour patterns, migration routes and transit times were determined.

Differences in rearing history, size and release date between the two groups of post-smolts that were monitored did not result in any differences in initial survival, migration route, transit time or behaviour pattern. This indicated that they were apparently under similar pressures and influences as they entered the bay and migrated away. After departure from the area 5 to 10 km from the river, no comparison was made because only post-smolts from group 2 were monitored. Those from group 1 were released and departed before the arrays further away were deployed, and they had short-term transmitters. As a result, only post-smolts from group 2 were found using the habitat within the Bay of Fundy during July and August. This behaviour was observed for post-smolts that were initially slow in leaving and had the least direct migration routes moving out of the bay. Individual routes revealed common behaviour patterns that were related to tidal flow and surface currents. This diminished the possibility that predators and not returning post-smolts were tracked. Furthermore, the same individuals were monitored repeatedly over weeks or months during which time predators would probably have evacuated an ingested tag, and tag movement would have stopped.

The presence of some post-smolts from group 2 during >2 months in coastal habitat inside the bay was not necessarily anomalous. Neither was it unique to a specific stock complex from the Bay of Fundy as suggested by Verspoor *et al.* (2002). For example, in the northern Gulf of St Lawrence the occurrence of some post-smolts near shore in late summer and their late movement out of coastal reaches was considered to be either a result of late migrant smolts or of the influence of sea temperature on behaviour (Dutil & Coutu, 1988). In the Baltic Sea, extended residence of post-smolts in the Bothnian Sea close to their home stream was reportedly connected with large smolt size and food availability (Salminen *et al.*, 1994; Kallio-Nyberg *et al.*, 1999). Some of these factors may have been implicated in the residency of post-smolts observed in the Bay of Fundy.

Smolts from the Big Salmon River can be late migrants because of the late snowmelt and cold water temperature in the spring, and the hatchery smolts monitored were large in comparison to wild smolts. Post-smolts that remained inside the bay were most often those that were initially delayed in leaving the coastal area by tidal currents. These delays could have influenced synchronization with environmental factors that can affect migration (Kallio-Nyberg *et al.*, 1999). Post-smolts monitored for an extended period inside the bay actually displayed an active resident behaviour where, for some reason, post-smolt migration was interrupted after first leaving the area and they then returned to the area, and then continued to repeat this pattern. The behaviour was different from that of post-smolts migrating out to marine feeding grounds slowly, and it required suitable long-term habitat within the coastal system. The area inside the Bay of Fundy, unlike the habitat throughout most of the Gulf of Maine to the south, was favourable to extended post-smolt residency and survival because of the consistently cold water temperature caused by tidal mixing and advection inside the bay (Smith, 1997).

The influence of tidal currents on post-smolt migration in the open marine habitat was emphasized by the apparent control of tidal flow direction on direction of travel; heading out of the bay mainly during ebb tides, and heading into the bay during flood tides or during a change from ebb to flood. Post-smolts made no headway out of the bay against the flood tide when tidal current could exceed $1\,m\,s^{-1}$ (CHS, 1981). Travel with the tide would have been rapid (*e.g.* after entry into the bay which coincided with the ebbing tide) until a change in tidal flow occurred. Post-smolts then probably had two options. They either continued to swim against the tide (more or less holding their position until the next change in tidal flow direction) or they were transported back (either passively or swimming with the tidal flow). This would have resulted in the two behaviour patterns observed; relatively rapid and direct movements heading out, but at a slower speed than ebb currents, and back-and-forth movements with a delay in departure. This was similar to the effects of tides on smolts in estuaries and entering coastal waters (LaBar *et al.*, 1978; McCleave, 1978; Moore *et al.*, 1995) and on post-smolts migrating out of coastal areas through narrow channels (Lacroix & McCurdy, 1996; Lacroix *et al.*, 2004*a*). This was the first indication that the impact of tides on migratory behaviour persisted in an open marine habitat where it affected migration routes and transit times.

In open water, Jonsson *et al.* (1993) and Holst *et al.* (2000) reported that post-smolt distribution was closely linked to the main surface currents, but that migration was slower than expected using the current as the main transportation vector. Trites & Garrett (1983) determined that surface circulation inside the Bay of Fundy was characterized by an outflow along the New Brunswick coast and a straightforward inflow along the Nova Scotia coast during summer. Some of the outflow also made a counter clockwise turn in the outer portion of the bay joining with the inflow along the Nova Scotia coast. These residual currents probably played a role in the initial orientation of post-smolts (*i.e.* on a course heading straight out of the bay) and their common use of a departure 'corridor' close to the New Brunswick coast. The return of some post-smolts to the area monitored during the summer and their presence along the Nova Scotia coast would also have been favoured by the general circulation in the Bay of Fundy.

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References

Allen, I. R. H. & Ritter, J. A. (1977). Salmonid terminology. *Journal du Conseil International pour l'Exploration de la Mer* **37,** 293–299.

Beland, K. F., Kocik, J. F., vandeSande, J. & Sheehan, T. F. (2001). Striped bass predation upon Atlantic salmon smolts in Maine. *Northeastern Naturalist* **8,** 267–274.

CHS (Canadian Hydrographic Service) (1981). *Atlas of Tidal Currents: Bay of Fundy and Gulf of Maine*. Ottawa: Department of Fisheries and Oceans.

Comeau, L. A., Campana, S. E. & Castonguay, M. (2002). Automated monitoring of a large-scale cod (*Gadus morhua*) migration in the open sea. *Canadian Journal of Fisheries and Aquatic Sciences* **59,** 1845–1850.

Dutil, J. D. & Coutu, J. M. (1988). Early marine life of Atlantic salmon, *Salmo salar*, postsmolts in the northern Gulf of St. Lawrence. *Fishery Bulletin* **86,** 197–212.

Hansen, L. P., Holm, M., Holst, J. C. & Jacobsen, J. A. (2003). The ecology of post-smolts of Atlantic salmon. In *Salmon at the Edge* (Mills, D., ed.), pp. 25–39. Oxford: Blackwell Science Ltd.

Holm, M., Holst, J. C. & Hansen, L. P. (2000). Spatial and temporal distribution of post-smolts of Atlantic salmon (*Salmo salar* L.) in the Norwegian Sea and adjacent areas. *ICES Journal of Marine Science* **57,** 955–964.

Holst, J. C., Shelton, R., Holm, M. & Hansen, L. P. (2000). Distribution and possible migration routes of post-smolt Atlantic salmon in the North-east Atlantic. In *The Ocean Life of Atlantic Salmon: Environmental and Biological Factors Influencing Survival* (Mills, D., ed.), pp. 65–74. Oxford: Fishing News Books.

Jessop, B. M. (1976). Distribution and timing of tag recoveries from native and nonnative Atlantic salmon (*Salmo salar*) released into Big Salmon River, New Brunswick. *Journal of the Fisheries Research Board of Canada* **33,** 829–833.

Jonsson, N., Hansen, L. P. & Jonsson, B. (1993). Migratory behaviour and growth of hatchery-reared post-smolt of Atlantic salmon *Salmo salar*. *Journal of Fish Biology* **42,** 435–443.

Kallio-Nyberg, I., Peltonen, H. & Rita, H. (1999). Effects of stock-specific and environmental factors on the feeding migration of Atlantic salmon (*Salmo salar*) in the Baltic Sea. *Canadian Journal of Fisheries and Aquatic Sciences* **56,** 853–861.

LaBar, G. W., McCleave, J. D. & Fried, S. M. (1978). Seaward migration of hatchery-reared Atlantic salmon (*Salmo salar*) smolts in the Penobscot River estuary, Maine: open-water movements. *Journal du Conseil International pour l'Exploration de la Mer* **38,** 257–269.

Lacroix, G. L. & McCurdy, P. (1996). Migratory behaviour of post-smolt Atlantic salmon during initial stages of seaward migration. *Journal of Fish Biology* **49,** 1086–1101.

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.

Lacroix, G. L., McCurdy, P. & Knox, D. (2004*a*). Migration of Atlantic salmon post-smolts in relation to habitat use in a coastal system. *Transactions of the American Fisheries Society* **133,** 1455–1471.

Lacroix, G. L., Knox, D. & McCurdy, P. (2004*b*). Effects of implanted dummy acoustic transmitters on juvenile Atlantic salmon. *Transactions of the American Fisheries Society* **133,** 211–220.

Lyse, A. A., Stefansson, S. O. & Fernö, A. (1998). Behaviour and diet of sea trout post-smolts in a Norwegian fjord system. *Journal of Fish Biology* **52,** 923–936.

McCleave, J. D. (1978). Rhythmic aspects of estuarine migration of hatchery-reared Atlantic salmon (*Salmo salar*) smolts. *Journal of Fish Biology* **12,** 559–570.

Middlemas, S. J., Armstrong, J. D. & Thompson, P. M. (2003). The significance of marine mammal predation on salmon and sea trout. In *Salmon at the Edge* (Mills, D., ed.), pp. 43–60. Oxford: Blackwell Science Ltd.

Montevecchi, W. A. & Cairns, D. K. (2003). Predation on post-smolt Atlantic salmon by gannets: research implications and opportunities. In *Salmon at the Edge* (Mills, D., ed.), pp. 61–77. Oxford: Blackwell Science Ltd.

Moore, A., Potter, E. C. E., Milner, N. J. & Bamber, S. (1995). The migratory behaviour of wild Atlantic salmon smolts in the estuary of the River Conwy, North Wales. *Canadian Journal of Fisheries and Aquatic Sciences* **52,** 1923–1935.

Moore, A., Lacroix, G. L. & Sturlaugsson, J. (2000). Tracking Atlantic salmon post-smolts in the sea. In *The Ocean Life of Atlantic Salmon: Environmental and Biological Factors Influencing Survival* (Mills, D., ed.), pp. 49–64. Oxford: Fishing News Books.

Reddin, D. G. & Friedland, K. D. (1993). Marine environmental factors influencing the movement and survival of Atlantic salmon. In *Salmon in the Sea and New Enhancement Strategies* (Mills, D., ed.), pp. 79–103. Oxford: Fishing News Books.

Reddin, D. G. & Short, P. B. (1991). Postsmolt Atlantic salmon (*Salmo salar*) in the Labrador Sea. *Canadian Journal of Fisheries and Aquatic Sciences* **48,** 2–6.

Salminen, M., Kuikka, S. & Erkamo, E. (1994). The divergence in the feeding migration of Baltic salmon (*Salmo salar* L.); the significance of smolt size. *Nordic Journal of Freshwater Research* **69,** 32–42.

Smith, P. C. (1997). Vertical exchange processes in the Gulf of Maine. In *Proceedings of the Gulf of Maine Ecosystem Dynamics Scientific Symposium and Workshop, RARGOM Report 97-1* (Wallace, G. T. & Braasch, E. F., eds), pp. 69–104. Hanover, NH: Regional Association for Research on the Gulf of Maine.

Trites, R. W. & Garrett, C. J. R. (1983). Physical oceanography of the Quoddy Region. In *Marine and Coastal Systems of the Quoddy Region, New Brunswick* (Thomas, M. L. H., ed.). *Canadian Special Publication of Fisheries and Aquatic Sciences* **64,** 9–34.

Verspoor, E., O'Sullivan, M., Arnold, A. L., Knox, D. & Amiro, P. G. (2002). Restricted matrilineal gene flow and regional differentiation among Atlantic salmon (*Salmo salar* L.) populations within the Bay of Fundy, eastern Canada. *Heredity* **89,** 465–472.