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Behavioural transition during the estuarine migration of wild Atlantic salmon (*Salmo salar* L.) smolt

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Abstract – Ultrasonic telemetry and hydrodynamic modelling were used to study the migratory behaviour of 54 wild Atlantic salmon (*Salmo salar*) smolt captured in freshwater during their downstream migration and tracked in 2 years through a shallow estuary system. A high-density, fixed array of receivers provided detailed spatial and temporal resolution of behaviour in the second year of study. Smolt migration in the river occurred mostly at night and downstream migration was slower during the day. In the estuary, smolt moved seaward on ebbing tides and landward on flooding tides. The effect of current velocity was greater during the night than during the day. We documented for the first time that current velocity and diurnal period only accounted for approximately one-third of the variation in smolt ground speeds in the estuary, indicating that smolt movements were far less passive than previously reported. Smolt energetic status had no effect on smolt swimming behaviour or migratory performance. With an increase in salinity, smolt seaward movements during flooding tides were more frequent, and overall seaward ground velocity increased. The increase in salinity experienced by the smolt during their migration through the leading edge of saltwater intrusion thus induced a behavioural transition from a more passive, fluvial migration to a more active- and seaward-oriented migration.

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Key words: orientation behaviour; sonic tracking; hydrophone array; swimming speed

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Introduction

As they migrate from river to sea, Atlantic salmon (*Salmo salar* L.) smolt leave a relatively uniform fluvial habitat characterised by freshwater and unidirectional currents to traverse an estuarine environment characterised by increasing salinity and variable current directions. Once in the estuary, smolt also face a new field of predators (Blackwell & Juanes 1998; Dieperink et al. 2002). Given that smolt have variable and low-energy reserves after smoltification and during downstream migration (Stefansson et al. 2003), a strategic compromise may be necessary. On one hand, smolt may drift passively with currents, limiting energy expenditure but spending more time in the estuary and thus increasing the risk of predation. On the other hand, they may expend more energy, thus increasing the risk of exhaustion, in active-oriented swimming and reduce transit time in the estuary (Holm et al. 2003). Individual energy status may thus influence the choice of migratory tactic. Given the possibility of significant mortality in estuaries (see Mills 2003), it is imperative to understand the mechanisms employed by Atlantic salmon smolt during this early stage in the marine migration.

Acoustic telemetry has been an effective method for monitoring fish migration patterns. This involves tagging individuals with ultrasonic transmitters (Voegeli et al. 1998), and monitoring their movement using acoustic receivers, either moored in fixed linear arrays

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(Finstad et al. 2005; Lacroix et al. 2005) or through mobile tracking (McCleave 1978; Økland et al. 2006). However, as fish detections by widely spaced fixed hydrophone arrays or periodic mobile tracking are generally few and far between, these methods provide, at best, comprehensive descriptions of migratory pathways and behaviour. If on the other hand multiple receivers are moored in close enough proximity, fish positions may be interpolated to provide relatively uninterrupted records of individual behaviour over large areas and extended periods of time (Hedger et al. 2008b). Such detailed descriptions also require the recording of environmental characteristics at similarly small spatial and temporal scales to understand the environmental control of migratory orientation. As the deployment of sufficient instrumentation to measure such characteristics as current speed and direction, salinity and temperature at small scales can be prohibitively expensive, the development of hydrodynamic modelling procedures to predict point values of environmental characteristics within the model's domain provides a promising alternative to elucidate fish migratory behaviour.

A variety of acoustic telemetry studies conducted over the past 35 years in different systems using both wild and hatchery-reared smolt has provided a general overview of migratory pattern with some conflicting and indirect evidence concerning the relative importance of passive and active components of migratory behaviour. The migration of salmon smolt in the freshwater fluvial habitat is mostly nocturnal and has been qualified as having a strong component of passive drift (see Ibbotson et al. 2006) with swimming oriented with the flow (Fängstam 1993; Davidsen et al. 2005). In the estuarine habitat, smolt tend to move with tidal currents (e.g., Lacroix et al. 2004b, 2005), but considerable behavioural variation has been documented. Moore et al. (1995) found that smolt generally maintained position during the day in an estuary independently of tidal phase whereas Gudjonsson et al. (2005) did not detect any effect of tidal phase or light intensity on smolt movement. In fjord systems, smolt movements have been related to the swimming activity of the fish rather than to water currents, this swimming being slightly oriented towards the sea (Thorstad et al. 2004; Økland et al. 2006). Net seaward movement of smolts during ebb tides and little or random movement at slack water and during flood tides have been observed in smolts migrating through the freshwater–tidal section of some rivers and estuaries (Labar et al. 1978; McCleave 1978; Tytler et al. 1978; Moore et al. 1995). These authors argued that smolt migration was largely passive at that stage. Observations further downstream suggest more active-oriented behaviour and greater swimming speeds in more saline environments (Labar et al. 1978; Moore et al. 1995, 1998; Lacroix & McCurdy 1996). Also, smolt may no longer attempt to maintain position during the day in a more saline environment (Moore et al. 1995). Finally, Hedger et al. (2008a) demonstrated active seaward-oriented migration in Gaspé Bay, Québec, Canada, by smolt which had previously traversed the estuary of the York River. Together, these results suggest that there may be a behavioural transition somewhere in the estuarine environment with more passive behaviour in rivers and more active-oriented behaviour and greater swimming speeds in more saline environments, as originally hypothesised by Stasko et al. (1973). However, no detailed quantitative evaluation of this apparent transition in individual behaviour has yet been presented. In addition, the role of individual energetic status in determining smolt migratory behaviour has not been documented.

In this study, we determined the influence of environmental variables on the spatial and temporal migration patterns of wild Atlantic salmon smolt within the York River and York Estuary, Québec, Canada, using sonic tags and a fixed acoustic receiver array. We focused on current speed and salinity (both measured and predicted by a validated hydrodynamic model), diurnal period and smolt characteristics (body mass and condition factor). We aimed to determine the relative importance of passive and active processes underlying the migration and the influence of individual energetic status on migratory behaviour. We also aimed to test the hypothesis that a behavioural transition occurs as individual smolt migrate into the estuarine transition zone (where freshwater first mixes with seawater) and to identify the environmental control of any such transition.

Study area: York River and York Estuary

The York River, located on the north-eastern coast of the Gaspé Peninsula, Québec, Canada (48.85°N, 64.45°W) (Fig. 1), flows into the shallow York Estuary (mean depth = 2–3 m). Depth increases nearer to the outlet in the eastern part of the estuary, where a channel of several 100 m in width and >10 m in depth is found. Water circulation within the estuary is driven by tides, wind and river discharge. A salinity gradient exists between the freshwater input from the York River and brackish water input from the inner bay of Gaspé, with the influence of freshwater discharge being particularly great during spring snowmelt, when discharge may exceed 80 $m^3 \cdot s^{-1}$. The shallow depth of the estuary prevents strong thermal and salinity stratification throughout much of the estuary, although there may be a thin layer of relatively warm surface water of riverine origin overlying colder, more saline water of maritime origin

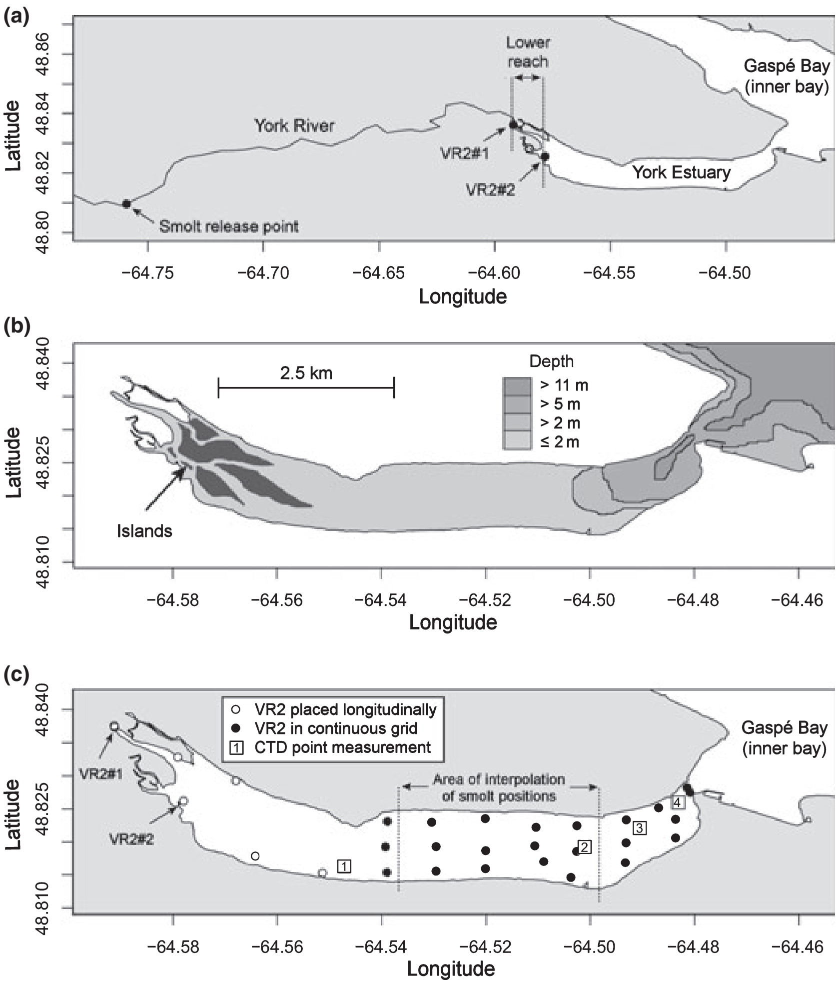

Fig. 1. Study site. (a) General view of the study site showing York River and the smolt release site, the two westernmost receiver clusters and the York Estuary; (b) bathymetry of the York Estuary; (c) positions of the VR2s (points) and CTD point measurements (squares).

in the deeper eastern part of the estuary (reviewed by Hedger et al. 2008a). Smolt migrate from the river to the marine environment in the spring and early summer (May, June).

Methods

Smolt capture, tagging and tracking

A total of 5163 and 2790 wild Atlantic salmon smolt were collected 16 km upstream from the river mouth in the York River between 30 May and 10 June 2005 and between 20 May and 5 June 2006 respectively with a Pennsylvania trap net and a smolt wheel. Large numbers of smolt were sampled to monitor the smolt run on this river for management purposes and to obtain a sufficient number of the largest smolt for the implantation of coded short-term internal transmitters (Vemco Division, Amirix Systems Inc., Halifax, Canada, V9-6L model, 9 × 20 mm, 3.3 g in air, 20–50 s burst rate, 69 kHz frequency, 53-day life span). The choice of the largest smolt minimised the risk of mortality from the surgical implantation of the transmitters. In 2005 and 2006, 24 and 30 smolt respectively were anaesthetised by immersion in a 40 mg·l^{-1} clove oil solution for 5–10 min. A longitudinal ventral incision was made, the transmitter was inserted into the body cavity and three to four silk points were made to close the incision. All instruments were sterilised with a chlorhexidine gluconate 0.05% solution (Bax-edin; Omega Laboratories Ltd, Montreal, Canada) prior to use. Gills were irrigated with freshwater throughout the surgery. After surgery, smolt were kept in a holding tank with flowing fresh water and were released after 2–3 h, several metres downstream of the capture trap. All fish had recovered from the tagging procedure and were active at release. Mean fork length and mass of tagged smolt were 152 mm (range = 142–177 mm) and 31.5 g (range = 27.1–43.4 mm) respectively. Mean condition factor [100 × mass (kg) × fork length (mm)$^{-3}$] was 0.885 (range = 0.782–0.988). Transmitter mass and length represented an acceptable proportion of fish mass (mean proportional mass = 10.25%, range = 7.47–13.41%; mean proportional length = 13.16%, range = 11.30–14.08%), according to Brown et al. (1999) and Lacroix et al. (2004a).

Migration of sonic-tagged smolt was monitored in the estuary by an array of 11 fixed acoustic receivers in 2005 and 30 fixed acoustic receivers in 2006 (Vemco, VR2 model) (the configuration for 2006 is shown in Fig. 1). Of the 30 receivers in 2006, seven were placed longitudinally in the far western part of the estuary; the remaining 23 were placed in a continuous grid designed to ensure continuous coverage in the central and eastern part of the estuary (mean separation distance between neighbouring receivers = 332 m). Transmitter detection range varied between 200 and 700 m but was mainly 300–400 m (Hedger et al. 2008a).

Analysis of the telemetry data

Riverine migration

The overall success of detection for tagged smolt from the release site to VR2#1 was 81%. A total of 16 smolt out of 24 (2005) and 28 smolt out of 30 (2006) were detected at VR2#1. Of the eight transmitters not detected by the receiver array in 2005, four were detected later in the summer during a mobile acoustic telemetry survey made in the river. Two of these transmitters were detected multiple times in the same area and, of these, one was recovered from the substrate 2 km upstream from the release site. A total number of 8439 and 10385 contacts were recorded by the acoustic receiver array in 2005 and 2006 respectively in the riverine part of the study area. The mean number of contact per smolt per acoustic receiver was 87.90 in 2005 and 92.72 in 2006.

Total riverine transit time was calculated from the release site situated 16 km upstream to the first cluster of receivers (VR2#1). We also calculated transit time between the westernmost mooring site (VR2#1) and a second site (VR2#2) located 1.6 km downstream on the margin of the estuary in 2005 and 2006 (Fig. 1) to examine the effect of diurnal period, discharge and smolt characteristics on migratory behaviour upon entry into the estuary. These mooring sites (VR2#1 and VR2#2) were composed of three and two receivers respectively, to compensate for the short detection range in the river. The departure (VR2#1) and arrival (VR2#2) signals were associated with the central position of each VR2 cluster at these sites.

Estuarine migration

The overall success of migration for smolt that entered the estuary and migrated through the entire length of the estuary was 95%. A total of 15 smolt out of 16 (2005) and 27 smolt out of 28 (2006) were detected throughout the entire estuary. In 2005, one smolt was lost but the location could not be estimated because of the coarser grid configuration. In 2006, one smolt (#3234) migrated only as far as the westernmost row of the continuous grid and was not detected further. A total of 3136 and 95706 contacts were recorded by the acoustic receiver array in 2005 and 2006 respectively in the estuarine part of the study area. In 2005, few contacts were recorded as only five VR2s were located in the estuary and four of these formed a transect across the eastern part of the estuary where the smolt were migrating quickly. The mean number of contacts per smolt per acoustic receiver was 26.13 in 2005 and 43.26 in 2006.

Smolt movements were estimated in the continuous part of the array in 2006 (Fig. 1). It was not possible to interpolate smolt paths in 2005 because of the coarser configuration of the array during that year. Smolt positions were estimated using cross-validated local polynomial regression (Becker et al. 1988), implemented in R (http://www.r-project.org) using the Friedman's supersmoother (Friedman 1984). For each smolt, a local polynomial model was fitted to the detections from the georeferenced receiver array, establishing separately the relationship between easting and northing as a function of time (10-min time interval) throughout its detection period in the acoustic receiver array (Hedger et al. 2008b).

Smolt ground velocities were determined for every estimated position as the distance between two successive positions divided by the 10-min interval. Given the west–east linear configuration of the York River estuary, only the x-component (i.e., west–east component) of the smolt and current flow velocities was considered. A positive value of the x-component indicated a seaward movement (directed towards the east) and a negative value indicated a landward movement (directed towards the west). Estimated positions that were not related to detections recorded by a receiver within a 5-min interval were considered unreliable and were not included in the analysis. All estimated positions west of 64.537°W or east of 64.498°W (Fig. 1) were excluded because of unreliable positioning when smolt were outside or close to the border of the grid.

Transit time of migration across the estuary was estimated for each fish in 2005 and 2006. The transit time was estimated from the last detection at VR2#1 to the last detection at the receiver at the outlet of the estuary. The transit time for the continuous grid of receivers was also estimated in 2006 from the time of the first estimated position to the time of the last estimated position (between the two vertical dashed lines; Fig. 1).

Environmental characteristics

Mean daily discharge data for the York River were obtained from a flow gauge operated by the Québec provincial government. Temperature within the river near the VR2#1 station was measured using a

VEMCO thermograph. Diurnal periods were determined as day and night based on sunset and sunrise local-time predictions.

Tidal elevation was predicted using the WTides software package (http://www.wtides.com). The accuracy of this prediction was verified by comparing predicted values with measured values from a tide gauge. Wind data were obtained from an on-site Vantage Pro2 anemometer (Davis Instruments, Hayward, CA, USA), which provided a continuous record at 30-min intervals.

Point measurements of temperature and salinity were made using a SEACAT Profiler CTD at low and high tide on six dates (3, 12, 14 and 24 July, and 1 and 7 August 2006) at four positions within the estuary (Fig. 1). Current measurements were made in 2005 using Lagrangian drifters released (one on 16 June 2005, six on 17 June 2005) within the estuary, near to the channel separating the estuary from the inner bay of Gaspé. A GPS mounted on each buoy determined its position at 5-min intervals. Drifters were left within the estuary for between 20 and 100 min.

Circulation within the estuary was modelled using the finite volume hydrodynamic model MOHID (Silva et al. 2002; Braunschweig et al. 2003; Trancoso et al. 2005). This model uses the Navier–Stokes primitive equations with the Boussinesq and hydrostatic assumptions. The model was run in a 2D mode because the estuary was shallow. The General Ocean Turbulence Model was used to determine horizontal eddy viscosity. The spatial domain was extended from the estuary through the inner part of Gaspé Bay and some of the outer bay. The model had a grid configuration of 124 cells by 108 cells (x and y domains). Cell size was 156 m in the x-domain and 162 m in the y-domain. The time step was 15 s. The model was initiated with a homogeneous salinity of 25 psu and temperature of 10 °C. Validation of the model simulation was achieved by comparing predicted velocities and salinities with those measured in the estuary (using drifters and CTDs respectively).

A longitudinal transect was traced equidistant from both banks of the estuary between the mouth of the York River and the outlet of the estuary at the inner bay of Gaspé. Current velocities (x-component) and salinities experienced by the fish were determined from the association between the spatiotemporal position of the fish and the predicted current velocities and salinities located in the nearest cell of the hydrodynamic model output along the transect.

Statistical analysis

Relationships between migration patterns and smolt and environmental characteristics were determined separately for the York River and the York Estuary. Statistics were performed using R (Hornik 2007) unless otherwise specified.

Riverine migration

The median time of day of the transit between VR2#1 and VR2#2 was used to determine the time when smolt migrated from the river into the estuary. A Rayleigh test was performed to test the null hypothesis that the occurrence of movement was random with respect to the time of day (Batschelet 1965). The differences between the time of arrival at VR2#2 and time of departure at VR2#1 were first analysed by t-test with respect to diurnal period, and second by linear modelling with respect to discharge and smolt characteristics (mass and condition factor). Tidal effects in the downstream reach of the river were minimal and thus were not analysed. Data from 2005 and 2006 were pooled.

Estuarine migration

The transit time from VR2#1 to the exit of the estuary was analysed with respect to the riverine transit time (from the release site to VR2#1), smolt mass and smolt condition factor with data from 2005 and 2006 pooled. The transit time through the continuous grid of receivers in 2006 was also analysed with respect to the riverine transit time, smolt mass, smolt condition factor and also with respect to the tidal phase and diurnal period at first detection in the grid.

Only the smolt tracked in 2006 were considered in the analysis within the continuous grid of receivers because the receiver configuration in 2005 was too coarse for the interpolation of smolt positions. In 2006, only smolt that migrated through the entire estuary were used; one smolt (#3234) was thus rejected. A second smolt (#3244) was also rejected because the local polynomial regression gave unreliable patterns due to outlier detections.

A first analysis was performed with all velocity data pooled and transformed into a binomial variable expressing the direction of smolt movement as either "seaward" or "landward". Observed relative frequencies of direction of movement were compared with Pearson's chi-square test in relation to flooding tide and ebbing tide and in relation to upper and lower estuary defined as a binomial value of salinity (upper estuary <2 psu; lower estuary ≥2 psu). This demarcation generally occurred halfway between the entrance to the grid and the exit from the estuary.

The relationships between smolt ground velocity (x-component) and smolt and environmental characteristics were determined using linear mixed modelling in SAS® (proc mixed) (version 9.1; SAS Institute Inc., Cary, NC, USA). Auto-regressive structure (AR1) with individuals as subject was used in the modelling to account for the temporal autocorrelation between repeated measures of smolt ground velocity (one measure every 10 min). The response variable (smolt ground velocity, x-component) was log-transformed to attain best normality (Box–Cox method). The following variables were used as fixed effects: (i) the x-component of predicted current velocity experienced by the fish; (ii) predicted salinity experienced by the fish; (iii) diurnal period; (iv) fish mass; (v) fish condition factor. Interactions between all environmental predictors (current velocity, salinity and diurnal period) were tested. A collinearity test was performed to assure noncollinearity between effects. Numerous models were tested and fitted by maximum likelihood method. The model with the lowest AIC value was selected. Coefficients of the effects were obtained by running the selected model with nonlogged data and the statistical significance of the effects was evaluated with confidence intervals (95%).

Results

Environmental characteristics

River discharge varied greatly throughout the time period that smolt were within the river, decreasing from 46.51 to 16.84 $m^3 \cdot s^{-1}$. A longitudinal gradient in temperature and salinity was observed across the length of the estuary from relatively warm and oligohaline water in the western part at CTD Station No. 1 (mean temperature of upper 2 m = 19.79 °C, mean salinity of upper 2 m = 4.68 psu) to relatively cool and polyhaline water in the eastern part at CTD Station No. 4 (mean temperature of upper 2 m = 16.69 °C, mean salinity of upper 2 m = 23.25 psu).

No evidence of stratification for either temperature or salinity existed at CTD Station No. 1. The estuary was stratified at the other CTD stations, involving a thin layer of relatively warm and oligohaline water in the upper 2 m of the water column (mean temperature = 17.64 °C, mean salinity = 17.82 psu) overlying a layer of cold and polyhaline water beneath this layer (mean temperature = 14.13 °C, mean salinity = 27.20 psu).

Salinity at high tide was greater than that at low tide: mean differences between high and low tide of the upper most 2 m of the water column was 3.01 psu (CTD Station No. 1), 2.14 (CTD Station No. 2), 2.05 (CTD Station No. 3) and 2.45 (CTD Station No. 4).

Model predictions

Current velocity predicted by the hydrodynamic model at the exit of the estuary to the inner bay of Gaspé was not significantly different to that measured using Lagrangian drifters: x-component (Pearson's correlation, $r = 0.86$, $t_{41} = 11.02$, $P < 0.001$); y-component (Pearson's correlation, $r = 0.63$, $t_{41} = 5.32$, $P < 0.001$). Salinity predicted by the model was significantly correlated with measured salinity (Pearson's product–moment correlation: $r = 0.83$, $t_{36} = 9.15$, $P < 0.001$). Given that predicted velocities and salinities were significantly correlated with values measured in the field, the use of these predictions in establishing relationships between smolt migration and environmental characteristics was justified.

Average predicted water velocity experienced by the smolt during flooding tides was 0.03 $m \cdot s^{-1}$ (min: 0 $m \cdot s^{-1}$; max: 0.10 $m \cdot s^{-1}$) and during ebbing tides was 0.04 $m \cdot s^{-1}$ (min = 0 $m \cdot s^{-1}$; max = 0.14 $m \cdot s^{-1}$); residual water velocity experienced by smolt was seaward with a mean of 0.01 $m \cdot s^{-1}$. Predicted salinities in the estuary during the smolt migration ranged from 0.04 to 14.26 psu. Predicted salinities within the continuous acoustic receiver grid used for modelling ranged from 0.04 to 7.15 psu.

Riverine migration

Migration from the point of smolt release to VR2#1 took between 0.44 and 3.46 days (mean = 1.31 days). In the lower reach (between VR2#1 and VR2#2), a strong diurnal effect was apparent (Figs 2a,b). The distribution of the occurrence of movement in relation to the time of day was not random (Rayleigh test, $P = 0.0012$); movement occurred more frequently during the night (mean time of transit: 23.00 h) than during the day. Transits across the lower reach were also significantly faster during the night than during the day (Welch two-sample t-test, $t_{11} = -2.700$, $P = 0.010$). Thus, only nocturnal movements were analysed for testing the effects of smolt characteristics and discharge on migratory behaviour in the lower reach of the river. Two smolt that stopped migrating for an abnormally long time at high discharge and during the night were removed from the analysis. A significant effect of discharge was observed at night with smolt transiting faster at greater discharges (Table 1, Fig. 2c). No significant effects of smolt characteristics (mass or condition factor) on transit time were observed.

Estuarine migration

The transit from VR2#1 to the exit of the estuary in 2005 and 2006 took between 0.26 and 4.16 days (mean = 1.91 days). The transit time for this section was not significantly affected by the transit time in the river ($F = 1.228$, $P = 0.275$), smolt mass ($F = 0.032$, $P = 0.859$) or smolt condition factor

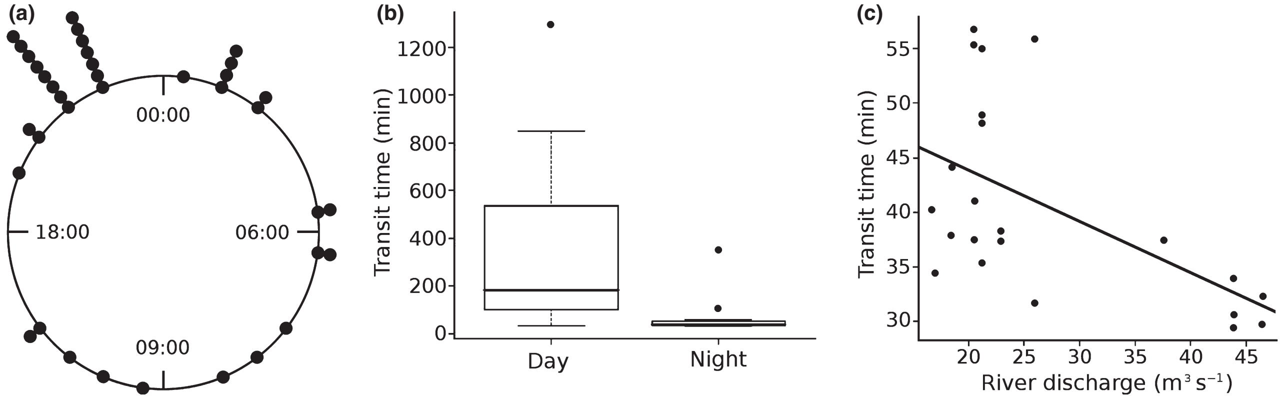

Fig. 2. Migration of smolt through the short downstream reach of the river (1.6 km): (a) the occurrence of transits in relation to median time of the transit; (b) transit time related to diurnal period; (c) time in transit for nocturnal transits as a function of river discharge.

Table 1. Analysis of variance table for the relationship between nocturnal transit time and river discharge, smolt mass and smolt condition factor (CF) through the short downstream reach of the river (between VR2#1 and VR2#2).

Effect	d.f.	Sum of squares	Mean sum of squares	*F*-value	*P*(>*F*)
Discharge	1	531.86	531.86	9.135	0.007
Mass	1	60.05	60.05	1.031	0.323
CF	1	68.03	68.03	1.169	0.294
Residuals	18	1047.97	58.22		

($F = 2.765$, $P = 0.105$). Smolt showed a relatively complex migration pattern within the estuary in 2006 (Fig. 3) with patterns varying between highly oriented migration (e.g., #3245, #3257) to a much-less oriented migration, involving multiple changes in direction (e.g., #3238, #3246, #3259). The transit through the continuous grid of VR2 in 2006 took between 0.09 and 3.42 days (mean = 1.04 days). The transit time within the grid was not significantly affected by the transit time in the river ($F = 0.070$, $P = 0.794$), smolt mass ($F = 0.031$, $P = 0.862$), smolt condition factor ($F = 1.195$, $P = 0.287$), tide state at first detection ($F = 1.518$, $P = 0.232$) or diurnal period at first detection ($F = 1.873$, $P = 0.186$). However, most smolt entered the grid during ebbing tides (25 out of 27 smolt) and most also exited the grid seaward during ebbing tides (25 out of 27 smolt).

The frequency distribution of the direction of smolt movements (landward vs. seaward) was different under flooding and ebbing tides (Pearson's chi-square test, $\chi^2_1 = 132.32$, $P < 0.001$) (Fig. 4). Smolt movements were mostly oriented seaward during the ebbing tide and landward during the flooding tide. The frequency distribution of the direction of smolt movements was also different within the upper versus the lower estuary (Pearson's chi-square test, $\chi^2_1 = 4.948$, $P = 0.026$) with more movements seaward in the lower estuary than in the upper estuary. However, this difference between the upper and lower estuary was only significant during the flooding tide (Pearson's chi-square test, $\chi^2_1 = 14.701$, $P < 0.001$) and not during the ebbing tide (Pearson's chi-square test, $\chi^2_1 = 0.823$, $P = 0.364$).

Among the linear mixed models that tested for the effects of environmental variables and fish characteristics on smolt ground velocity (*x*-component), the selected model included current velocity, diurnal period, salinity and the interaction between current velocity and diurnal period. The model explained 33% of the variance in smolt ground velocity ($r^2 = 0.33$). Although the intercept showed a bias towards positive values (seaward), this was not statistically significant. All effects in the selected model were significant except for the diurnal effect, which was significant only when in interaction with current velocity (Table 2). The selected model showed a significant positive effect of current velocity on the movement of smolt (ß = 1.3875) with smolt moving mostly seaward on ebbing tides and mostly landward on flooding tides (Fig. 5). Although no difference could be observed for diurnal period alone, the interaction between diurnal period and current velocity had a weak but significant effect (Fig. 6). Current velocity had a positive effect for both the day and night, but the effect was stronger at night (ß = 1.7798) than during the day (ß = 0.9952). Salinity also had a significant positive effect on the movement of smolt (ß = 0.0309), with seaward smolt ground velocity increasing as salinity increased (Fig. 7). No collinearity was detected between current velocity and salinity. The linear mixed modelling did not show salinity modifying the relationship between smolt ground velocity and current velocity or that smolt mass or

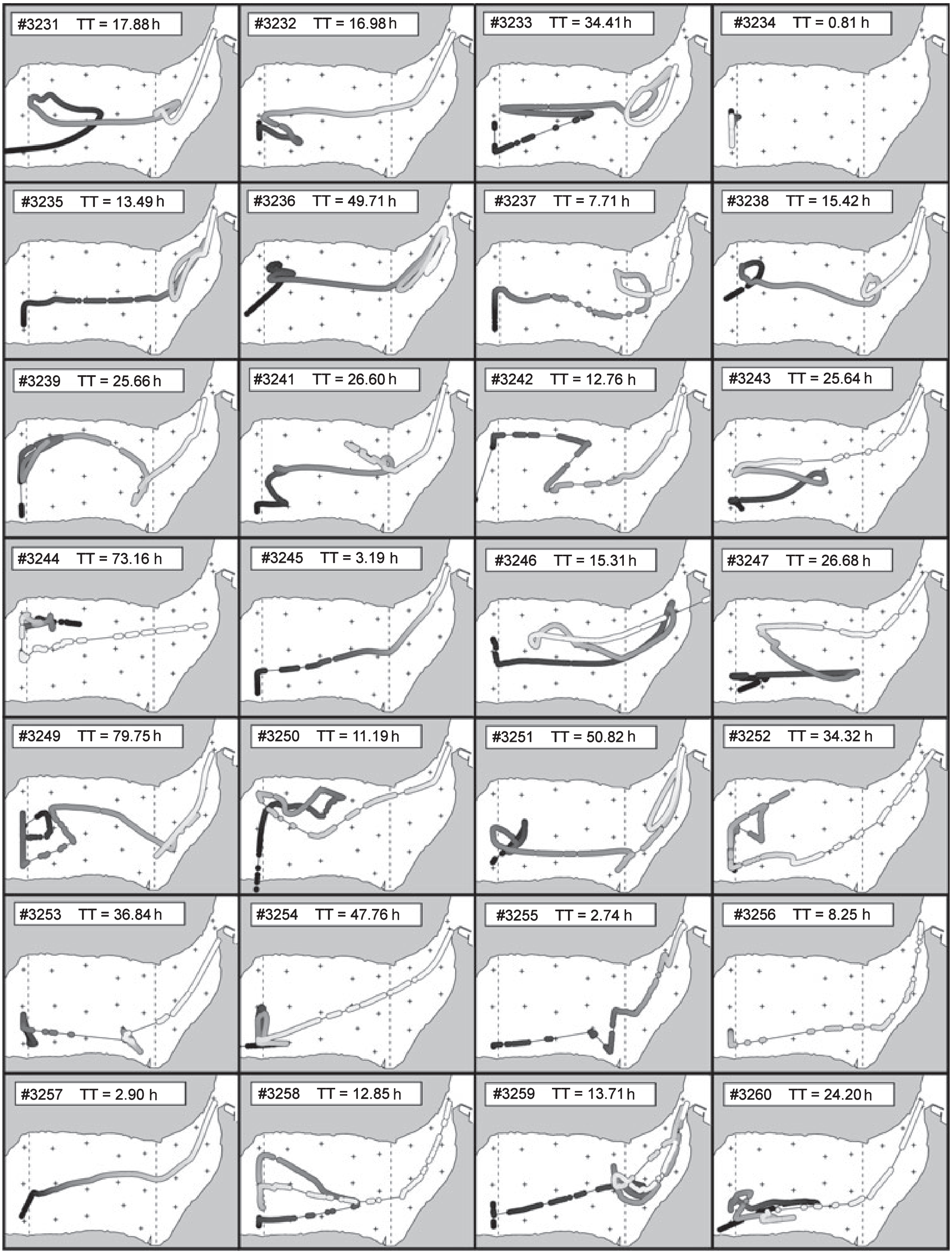

Fig. 3. Interpolated smolt tracks through the fixed array. Gray-tone gradation in the smolt paths varies from black (initial detection in the continuous array) to white (final detection). Thin lines are straight line tracks where no interpolated positions were available. Only data located between the vertical dashed lines were included in the analysis. Fish no. (#) was that of the V9-6L transmitter code; transit time (TT) was the time period between first and last detection of the smolt within the continuous array of acoustic receivers.

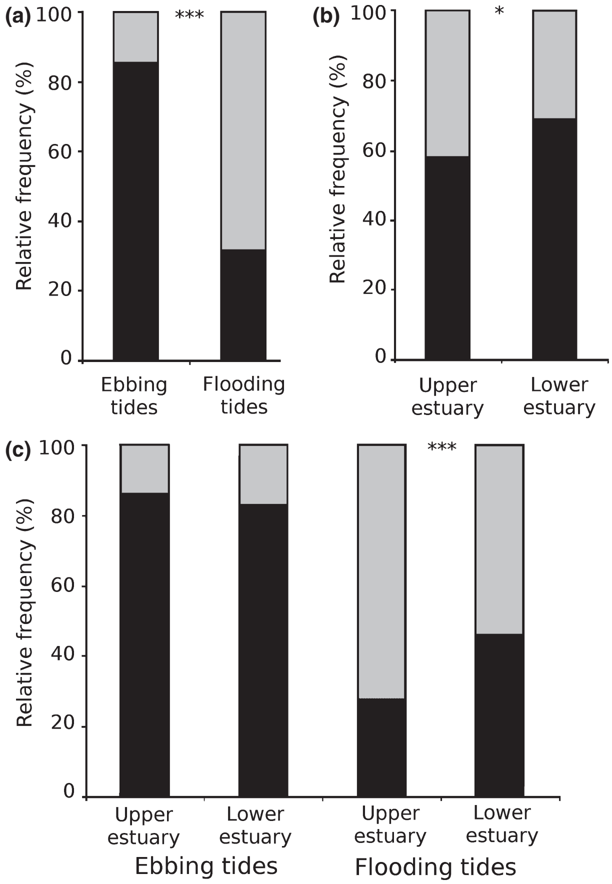

Fig. 4. Relative frequency of seaward (black columns) and landward (grey columns) movements: (a) during ebbing tides vs. flooding tides; (b) within the upper estuary versus the lower estuary; (c) within the upper estuary versus the lower estuary under flooding or ebbing tides. Distributions are statistically different at $P < 0.05$ (*) and $P < 0.001$ (***).

Table 2. Selected linear model coefficients (β), standard error (SE) and confidence intervals for smolt ground velocity (x-component) in the estuary.

Effect	β	SE	95% CI
Intercept	0.0161	0.0162	−0.0174 to 0.0495
Current velocity (x)	1.3875	0.1251	1.1422 to 1.6328*
Salinity	0.0309	0.0048	0.0215 to 0.0402*
Intercept (day)	0.0193	0.0165	−0.0151 to 0.0538
Intercept (night)	0.0128	0.0168	−0.0222 to 0.0478
Current velocity (x), day	0.9952	0.1291	0.7419 to 1.2484*
Current velocity (x), night	1.7798	0.1606	1.4648 to 2.0948*

Coefficients with confidence intervals that did not overlap zero (*) were considered statistically significant.

condition factor had an effect on smolt ground velocity. Finally, no salinity-induced change in diurnal behaviour was seen.

Discussion

The continuous coverage of smolt positions from the dense VR2 grid, alongside a thorough modelling of

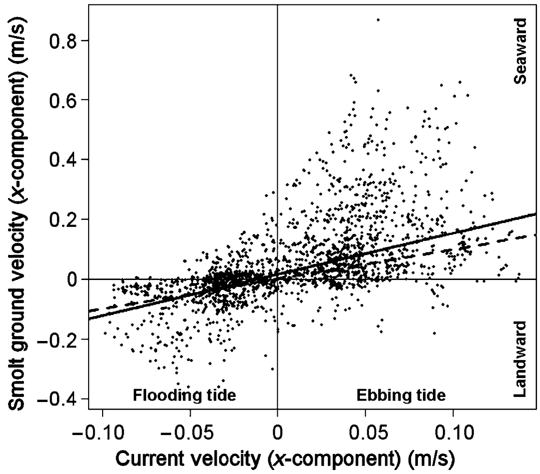

Fig. 5. Relationship between smolt ground velocity (x-component) and predicted current velocity. Points represent pooled individual observations. The solid line represents the intercept and coefficient obtained from the multiple regression model (intercept = 0.0161, coefficient = 1.3875). The dashed line represents the predicted relationship in the case of passive drift with the current (intercept = 0, coefficient = 1).

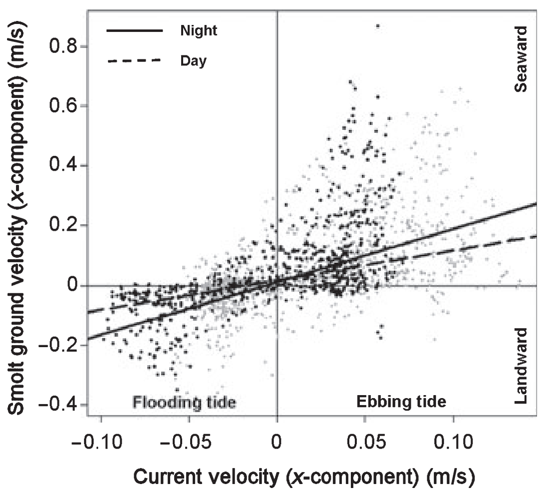

Fig. 6. Relationship between smolt ground velocity and predicted current velocity during night and day. Points in background represent pooled data for night (black points) and day (grey points). The lines represent the intercept and coefficient obtained with the multiple regressions model for the night (solid line; intercept = 0.0128, coefficient = 1.7798) and day (long dashed line; intercept = 0.0193, coefficient = 0.9952).

environmental characteristics over fine spatial and temporal scales and a mixed-effects modelling approach for examining covariate relationships provided an unprecedented description of the swimming behaviour of Atlantic salmon smolt migrating through an estuarine transition zone. As in previous studies, a mixture of both active and passive behaviour was documented. However, we documented for the first time that current velocity and diurnal period only

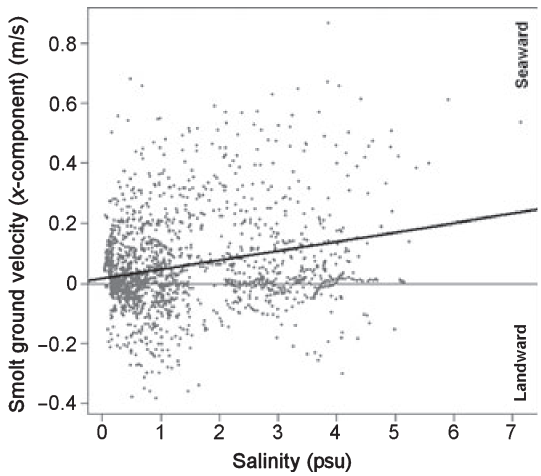

Fig. 7. Relationship between smolt ground speed and predicted salinity. Points in background represent pooled data. The line represents the intercept and coefficient obtained from the multiple regression model (intercept = 0.0161, coefficient = 0.0309).

accounted for approximately one-third of the variation in smolt ground velocities in the estuary, indicating that smolt movements were far less passive than previously reported. We demonstrated that smolt significantly increased their seaward movements against the flooding tide when exposed to saline waters and, for the first time, we demonstrated a significant relationship between smolt seaward ground speed and salinity. These observations provided direct behavioural evidence to support the hypothesis that relatively small increases in salinity early in the estuarine migration induce a shift in the behaviour of smolts to an increasingly active and seaward-oriented migration. Contrary to our initial prediction, smolt energetic status had no detectable effect on smolt swimming behaviour or migratory performance. This last observation is somewhat mitigated by the fact that only the largest smolt were selected for tag implantation.

Nocturnal migratory movements in the river showed the effect of passive displacement because migration speed was positively related to water discharge, although differences between day and night indicated that smolt resisted downstream movement during the day. In the estuary, smolt ground speed was also related to current velocities. Smolt exhibited bi-directional movements in the estuary, moving mostly seaward during ebbing tides and mostly landward during flooding tides. This positive effect of currents on smolt movements in estuaries has been noted in previous studies (e.g., Moore et al. 1995, 1998; Lacroix et al. 2004b) and has been interpreted as the passive displacement of smolt drifting with the flow. However, if smolt behaviour were purely passive, their displacement could be largely explained by current velocity. In our model, environmental characteristics only explained 33% of the variance and therefore smolt behaviour could not be considered as largely passive. Also, assuming that there was a positive rheotactic response in the river (e.g., Davidsen et al. 2005), this behaviour extended to the estuary so that smolt swam in the same direction as the water current independently of its direction. This is supported by our observation of a strong relationship between smolt movements and current velocity during the night.

Smolt movements clearly became seaward biased while in the lower estuary (salinity ≥2 psu). An increase in the frequency of smolt seaward movements and an increase in smolt ground velocity were observed as the smolt migrated through the estuary and experienced increased salinity. Hedger et al. (2008a) also observed that higher salinities in the inner part of Gaspé Bay enhanced smolt seaward movements and that the behaviour was highly active and mostly independent of water currents.

The increasing seaward bias observed during migration in the estuary suggests active swimming coupled with a preferred direction, implying a compass mechanism (Dodson 1988). In the inner part of Gaspé Bay, salinity gradients had a weak effect on swimming direction but salinity had a strong positive effect on swimming speed when smolt were oriented seaward, also indicative of a compass mechanism (Hedger et al. 2008a). In an estuary, the superposition of orthokinesis on a preferred compass bearing represents a robust mechanism whereby smolt would swim faster seawards when experiencing greater salinity regardless of the direction of tidal flow.

Circadian behaviour was observed in both the river and estuary. In the river, transits occurred mostly during the night. The maintenance of position during the day may have been associated with predator avoidance or prey identification (see Ibbotson et al. 2006). In the estuary, the relationship between the currents and smolt movement was also stronger nocturnally. During the night, smolt moved with the current flow at greater velocities than during the day regardless of current direction. We suggest that the circadian behaviour observed in the estuary is an extension of the behaviour observed in the river, so that smolt would show migratory behaviour during the night and nonmigratory behaviour during the day. However, smolt were not strictly maintaining position during the day and we observed that movement with the flow occurred even in daylight in the estuary. This is concordant with the observations of Moore et al. (1995) who showed that, in estuaries, smolt were moving with the current during the night and were mostly keeping position during the day but were still being displaced by the current. As smolt appeared to be maintaining position during the day in riverine habitat, it is not clear why smolt would move with the current during the day once in the estuary. Smolt might be unable to keep position because of increased buoyancy associated with smoltification (Pinder & Eales 1969) and more dense saline water. Alternatively, they might have to shift their feeding behaviour from a stationary positioning to a more active and mobile feeding mode, making them more subject to water displacement.

Moore et al. (1995) observed that the effect of the diurnal period on the behaviour of smolt was abandoned as the smolt reached the lower part of Southampton Estuary (UK), so that smolt would no longer hold position during the day. In contrast, our results revealed that circadian behaviour was maintained throughout the estuary regardless of the increase in salinity. Hedger et al. (2008a) also observed that a circadian behaviour was preserved even further seaward in the study area (the inner part of Gaspé Bay) where smolt orientation was more diffuse during the day and more seaward oriented during the night. Therefore, our observations of smolt behaviour within the estuarine transition zone are consistent with those shown for smolt behaviour within the adjacent coastal embayment. Smolt feeding and growth is important early in the marine phase (Andreassen et al. 2001) and smolt (at least in an aquaculture setting) are known to feed visually during daylight (Jorgensen & Jobling 1993). Therefore, smolt may be feeding during the day throughout their seaward migration through the York estuary and the inner part of Gaspé Bay.

To conclude, our observations of smolt migrating through the estuarine transition zone have provided a far more complete picture of their migratory behaviour than provided by earlier studies. Based on earlier work, smolt migrations had been qualified as including (i) a strong tidal component to the direction of smolt migration, the movement being predominantly with the direction of flow, and (ii) a selective ebb tide transport, including a minor nocturnal component while in the estuary and limited directed swimming, either with or against the current, when the lower portion of an estuary was reached (Lacroix et al. 2004b). Although we observed a strong tidal component in smolt ground speed, seaward orientation was more frequent in the lower estuary than in the upper estuary with the most significant increase in seaward movements observed during the flooding tide. The relationship between currents and smolt movement was strongly nocturnal. Directed swimming was far more important than previously inferred, with ground speed increasing with increasing salinities. The behavioural transition from one involving a component of passive drift to one that is more active, consisting of directed swimming, appears to occur at the leading edge of salt-water intrusion.

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