Migration and swimming depth of Atlantic salmon kelts *Salmo salar* in coastal zone and marine habitats

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ABSTRACT: Factors influencing the migration and swimming depth of Atlantic salmon kelts *Salmo salar* L. within the York Estuary and Gaspé Bay (Québec, Canada), and in the Gulf of St. Lawrence between Gaspé Bay and the Strait of Belle Isle (Newfoundland, Canada) were studied using acoustic telemetry. In 2006 and 2007, a total of 49 kelts were tagged with acoustic transmitters equipped with depth sensors, released in the river delta leading into the estuary, and tracked using a fixed receiver array within the estuary and the bay. A large variation in migratory behavior existed, with some kelts making a direct, strongly oriented traverse across the estuary and bay, and others showing multiple changes in orientation. There was long-term residence (typically several weeks) in the river delta and rapid migration once kelts reached the estuary and bay resulting from seaward swimming, with a net seaward movement even on a flood tide. Diving was more frequent during daytime. It was hypothesized that diving may have been related to feeding and/or the identification of more temporally consistent sub-surface salinity gradients or current flow directions. The patterns of migration within the coastal zone were similar to those identified for smolts, implying a universal pattern of coastal zone migratory behavior in both smolts and kelts. Migration speed within the marine habitat was dependent on date of departure from Gaspé Bay, which in turn was dependent on the length of time kelts had remained in the delta. It was hypothesized that extended feeding within the delta allowed kelts to improve their physical condition, enabling them to migrate more rapidly in the marine habitat.

KEY WORDS: Telemetry · Migration · Diving · Atlantic salmon kelts

INTRODUCTION

Postspawning survival rates are quite variable among salmonid fishes, with *Salvelinis* and *Salmo* species exhibiting relatively high survival, due to their ability to restore lost somatic energy reserves and to escape exploitation (Niemelä et al. 2000). Atlantic salmon *Salmo salar* kelts, defined as salmon that spawned the previous autumn (Allan & Ritter 1977), return to the marine environment usually during the spring following the fall spawning period (Bardonnet & Baglinière 2000, Niemelä et al. 2000). Surviving kelts

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may make annual returns to rivers for repeat spawning, and given that the fecundity of repeat spawners tends to be greater than that of first-time spawners, repeat spawning may mitigate individual years of reproductive failure and contribute towards genetic diversity (Ducharme 1969, Niemelä et al. 2000). It has thus been suggested that stock management measures should be implemented to protect kelts during their seaward migration (Niemelä et al. 2000).

Very little is known about the coastal zone and marine ecology of salmon kelts (Reddin et al. 2004) and the few published accounts available are not consistent. Some authors have identified kelt migration as being nocturnal (Bendall et al. 2005 for sea trout *Salmo trutta* kelts), while Östergren & Rivinoja (2008) found that sea trout migration tended to occur during daytime. In the case of Atlantic salmon kelts, Scruton et al. (2007) reported nocturnal migration, whereas no diurnal patterns were observed by Hubley et al. (2008). Bendall et al. (2005) found that sea trout migration tends to occur on the ebb tide. These authors also showed the dependency of migration speed on river discharge and temperature, but were unable to separate the 2 variables because of their co-dependence. Several studies have shown the importance of diving in adult salmon (reviewed by Reddin et al. 2004). Most have shown that salmon mainly occupy surface or near-surface waters, with periodic descents to deeper waters: Karlsson et al. (1996) for Baltic salmon; Westerberg (1984), Doving et al. (1985), Reddin et al. (2004), Hubley et al. (2008), Halttunen et al. (2009) for Atlantic salmon. For Pacific salmon, diving has been related to diel period, with increased diving during daytime (Walker et al. 2001), but there has been some inconsistency among the results of different authors. Periodic excursions to deeper waters have been related to feeding, thermoregulation, determining orientation for migration, and/or olfactory exploration (Westerberg 1984, Wada & Ueno 1999). It has been hypothesized that diving during daytime may also be related to avoidance of avian predators such as osprey *Pandion haliaetus* and bald eagle *Haliaeetus leucocephalus* (Reddin et al. 2004, Hubley et al. 2008).

Acoustic telemetry has been an effective method for describing fish migration patterns and inferring mechanisms of migration. The procedure involves tagging individuals with ultrasonic transmitters (Voegeli et al. 1998) and monitoring their movement using acoustic receivers, either moored in fixed linear arrays (e.g. Finstad et al. 2005, Lacroix et al. 2005) or through mobile tracking (e.g. Thorstad et al. 2004, Økland et al. 2006). Given that fish detections by widely-spaced fixed receiver arrays or periodic mobile tracking are generally sparse, these methods provide, at best, comprehensive descriptions of migratory pathways and behavior. If, however, multiple receivers are moored in close enough proximity, fish positions may be interpolated to provide relatively uninterrupted records of individual behavior over large areas and extended periods of time (Hedger et al. 2008b). Atlantic salmon smolts have been particularly well studied using various telemetry techniques (Martin et al. 2009, and references therein) but a similar effort has not been invested in the kelt life-stage, with certain notable exceptions such as Hubley et al. (2008) and Halttunen et al. (2009). In both of these studies, receivers were separated by relatively large distances, limiting the ability to determine fine-scale movements, and were only placed within river and coastal zone environments, thereby forgoing their applicability in determining marine movements. The potential for improved telemetry studies will increase with developments in the infrastructure of telemetry configurations associated with the Ocean Tracking Network (Holden 2006).

In this paper, acoustic telemetry was used to monitor the migration of wild Atlantic salmon kelts within a fine-scale fixed receiver array in an estuary-coastal embayment system. The influence of physical habitat characteristics on movement patterns and swimming depth was examined. The main objectives were (1) to quantify kelt migration patterns within the estuary-coastal embayment system at a finer spatial and temporal scale than has been previously achieved, (2) to determine the factors controlling the seaward migration and swimming depth, (3) to determine the migratory (active swimming vs. passive drifting) and orientation mechanisms, and (4) to compare the migration patterns with those of previous studies of smolts in the same study area to determine if behavioral consistency exists across life-stages.

The extent of kelt migrations at sea is not well known. In the maritime provinces of Canada, there appear to be 2 migratory tactics: consecutive-year spawning of fish that reside in coastal waters for a short period of time, and alternate-year spawning of fish that may migrate much further to the Labrador Sea between Canada and Greenland (Ritter 1989). In Québec, ~80% of repeat spawners are alternate-year spawners that migrate out of the Gulf of St. Lawrence, possibly to avoid cold winter temperatures in the Gulf, and the remaining ~20% are composed of fish that stay in the gulf to spawn the same year (Ministère des Ressources Naturelles et de la Faune du Québec, unpubl. data). Atlantic salmon kelts originating in rivers of the north shore of the Gulf of St. Lawrence have been observed at river mouths in the vicinity of the Strait of Belle Isle (Colombani et al. 1998). This suggests that salmon kelts from some Québec rivers may migrate to the Labrador Sea, as do Atlantic
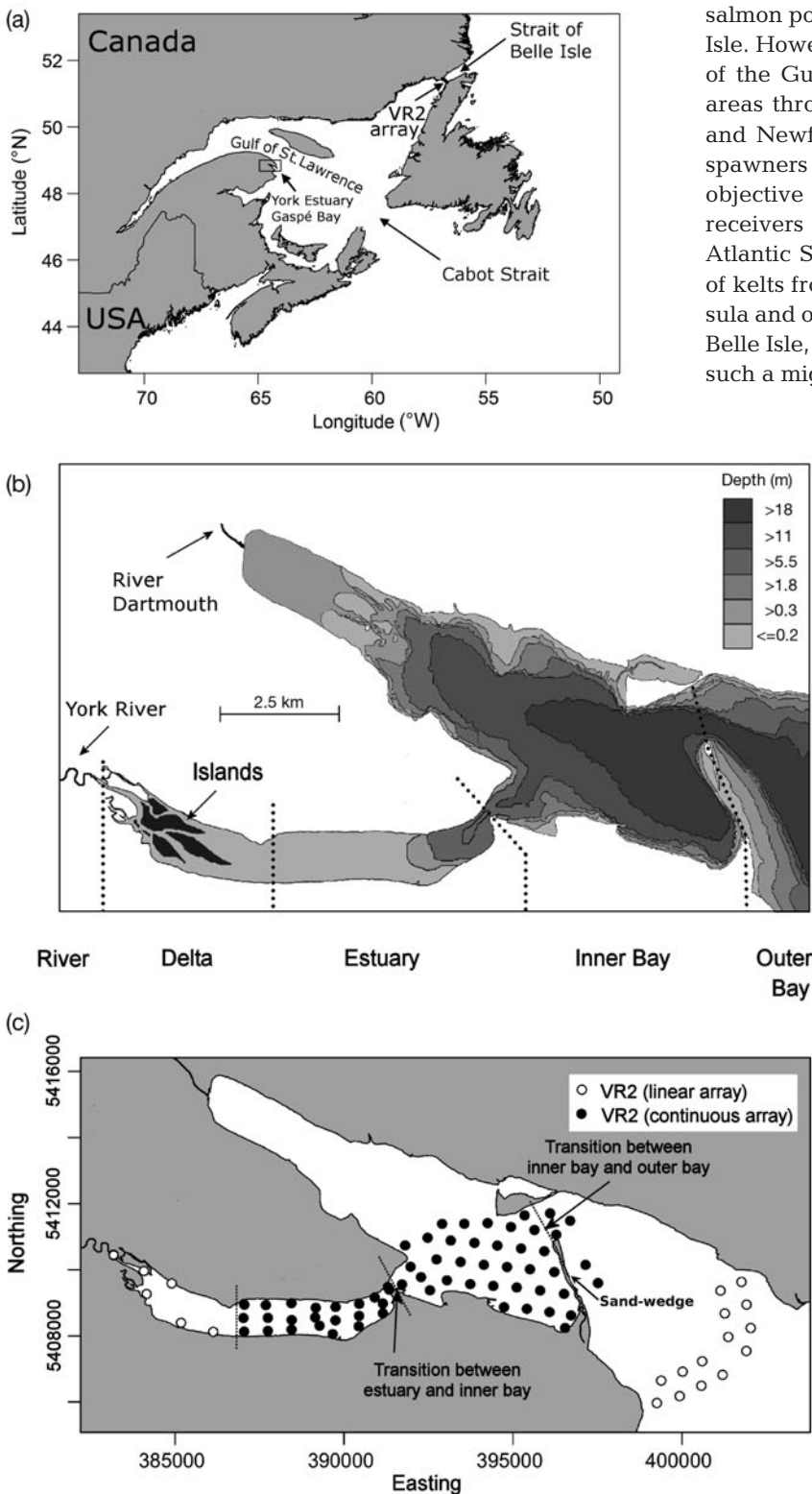
Fig. 1. The study area showing (a) Gaspé Bay and the Strait of Belle Isle; (b) bathymetry of the coupled estuary-coastal embayment system, York Estuary and Gaspé Bay; and (c) the receiver array in 2006 (in Universal Transverse Mercator coordinates). The Labrador Sea is north-east of the Strait of Belle Isle

salmon post-smolts (Caron 1983), via the Strait of Belle Isle. However, stocks in the more south westerly rivers of the Gulf of St. Lawrence may migrate to offshore areas through the Cabot Strait, between Nova Scotia and Newfoundland: the route preferred by first-time spawners to these rivers (Belding 1940). Thus, a final objective of this study was to exploit a fixed array of receivers moored in the Strait of Belle Isle by the Atlantic Salmon Federation to detect any movements of kelts from the more south westerly Gaspésie peninsula and out of the Gulf of St. Lawrence via the Strait of Belle Isle, and to assess the time required to undertake such a migration.

MATERIALS AND METHODS

Study area. The principal study area was a coupled estuary-coastal embayment system, York Estuary and Gaspé Bay, located on the north eastern coast of Gaspésie, Québec, Canada (48.85°N, 64.45°W) (Fig. 1a). For the purpose of this study, the system is divided into 4 regions: (1) delta (at the transition between the estuary and the York River that flows into it); (2) estuary; (3) inner bay; and (4) outer bay (Fig. 1b). The delta stretches for several km from the York River, and its flow and water quality characteristics are dominated by the discharge from the river: tidal effects are absent, water is fresh, and temperature varies on a diel basis. The estuary is shallow, with a mean depth of ~3 m, but depth increases to >10 m in a narrow trench separating the estuary from Gaspé Bay. Salinity and temperature within the estuary are controlled by the balance between freshwater input from the river into the delta (the discharge of which varies greatly on an annual basis, predominantly due to floods in May from snowmelt) and the intrusion of water of greater salinity into the estuary from Gaspé Bay. The coastal embayment, Gaspé Bay, is composed of 2 distinct regions: a partially enclosed inner bay and an open outer bay. The inner bay is wide (>4 km) and shallow (a maximum depth of 25 m) relative to its length (~10 km). It is separated from the outer bay by a sand-wedge, which is submersed at high tide. There is a relatively deep channel in the north (~1 km in

width and 20 m in depth) where the bulk of the inter-change of water between the inner and outer bays occurs. Gaspé Bay is typically vertically stratified in summer, with a surface layer of warm low-salinity water of riverine origin overlying a layer of colder saline water of maritime origin (Carrière 1973, Koutitonsky et al. 2001), although stratification may disappear for brief periods on a non-periodic basis. A horizontal salinity gradient generally exists across the bay, but this salinity gradient is not temporally persistent, and there may be localized (both spatially and temporally) reversals in the local salinity gradient due to the interaction between inputs of freshwater and surface eddying (Hedger et al. 2008b).

York River is a major salmon river, supporting an annual run of ~1750 adult salmon. Spawning grounds are located between 10 and 80 km upstream. Approximately 27% of spawners are grilse (having spent 1 yr at sea), the rest are multi sea-winter salmon. Of these latter fish, 55% have spent 2 yr at sea, 30% have spent 3 yr at sea and 15% are repeat spawners (Ministère des Ressources Naturelles et de la Faune du Québec, unpubl. data). Downstream migration of kelts occurs in April and May, with kelts migrating through the estuary and coastal embayment into the Gulf of St. Lawrence.

Kelt capture, tagging and tracking. Migration patterns of Atlantic salmon kelts were studied using 49 kelts (24 in 2006; 25 in 2007) tagged with coded ultrasonic transmitters equipped with pressure sensors to record the swimming depth (Vemco Ltd, V9P-2L model, 47×9 mm, 6.4 g in air, random burst rate 20 to 50 s, frequency 69 kHz, life time 150 d). Kelts were captured by sport angling (baited hook) near to the intersection of the York River and the river's delta from 26 April to 1 May 2006 and 2 to 4 May 2007. Mean fork length and weight of the tagged kelts were 70 cm (range: 49.5 to 109.5) and 2.5 kg (range: 0.8 to 8.5) in 2006 and 80.4 cm (range: 54.1 to 106) and 4.0 kg (range: 0.8 to 9.0) in 2007 (Table 1). Kelts shorter than 63 cm were probably grilse (n = 18), and kelts longer than 63 cm were probably 2 or 3 sea-winter fish (n = 31) (Ministère des Ressources Naturelles et de la Faune du Québec, unpubl. data).

A standard surgical procedure was used for transmitter implantation, which included anaesthesia (5 to 10 min, 45 mg l^{-1} clove oil solution), disinfection (0.05% chlorexidin solution), body cavity incision (2 to 3 cm long anterior from the pelvic girdle), suturing (3 to 4 simple interrupted sutures, Prolene 8685H, 2 to 0 absorbable monofilament, FS (Franklin Silverman) cutting needle; Summerfelt & Smith 1990), and antibiotic

Table 1. *Salmo salar.* Fork length (FL), weight (W), and number of detections of Atlantic salmon kelt registered by the receiver array in the coupled estuary-coastal embayment system, York Estuary and Gaspé Bay, and in the Strait of Belle Isle in 2006 and 2007

Tag#	FL (mm)	W (kg)	No. detections	Tag#	FL (mm)	W (kg)	No. detections
	2006				2007		
2006-1	53	1	6680	2007-1	78	3	12765
2006-2	81.8	3.9	4934	2007-2	87.3	4.6	4338
2006-3	95	5.9	1251	2007-3	106	9	4835
2006-4	82	3.3	528	2007-4	59	1.5	5520
2006-5	78.5	3.1	555	2007-5	58	1.2	15763
2006-6	86.5	3.5	3967	2007-6	78.3	3.5	23184
2006-7	56	1	819	2007-7	101.5	8.4	3781
2006-8	78.5	3.4	861	2007-8	84.7	4.4	3955
2006-9	80	3.5	3297	2007-9	79	3.1	1686
2006-10	109.5	8.5	4715	2007-10	79.8	3.1	4606
2006-11	49.5	0.8	7367	2007-11	60.5	1.6	38423
2006-12	60.5	1.4	7517	2007-12	87.5	4.4	4575
2006-13	58.8	1.3	2607	2007-13	101.5	7.6	14758
2006-14	79	3.4	2549	2007-14	54.1	0.9	8221
2006-15	59	1.4	6638	2007-15	98.8	7.3	17541
2006-16	71.7	2.2	3885	2007-16	81	4.1	4794
2006-17	56	1	4910	2007-17	82	3.7	2768
2006-18	58.8	1.3	4930	2007-18	80.5	3.2	9266
2006-19	51.8	0.8	783	2007-19	96	7.1	4595
2006-20	78	3.5	2906	2007-20	85.5	4	9174
2006-21	84	4.1	7576	2007-21	84.5	3.9	792
2006-22	57	1.1	0	2007-22	56	0.8	1886
2006-23	59	1.2	1388	2007-23	78	3.3	0
2006-24	57	1.2	2794	2007-24	94.5	6.1	4518
				2007-25	57.5	1.3	1071

injection (oxytetracycline, 55 mg kg^{-1} of fish weight; Summerfelt & Smith 1990).

Migration of the transmitter-tagged kelts was monitored by a fixed receiver array (Vemco Ltd, VR2 model) consisting of: (1) a series of receivers placed longitudinally along the river's delta (7 receivers in 2006; 8 receivers in 2007); (2) a continuous array in the estuary, in the inner bay, and on the western margin of the outer bay (62 receivers in 2006; 63 receivers in 2007); (3) a linear array in the outer bay placed from one coast to the other (14 receivers in 2006 and 2007); and (4) a linear array in the Gulf of St. Lawrence, in the Strait of Belle Isle between the Newfoundland and Labrador coasts (22 receivers in 2007) (Fig. 1a). The configuration in the coupled estuary-coastal embayment system for 2006 is shown in Fig. 1c; the configuration for 2007 was almost identical. Receivers in the continuous array were moored on a near-hexagonal grid designed to ensure complete spatial coverage, with a mean distance between neighboring receivers of 570 m. The maximum range of the transmitter within the inner bay was ~650 m, giving considerable overlap in the receiver detection ranges (Hedger et al. 2008a); therefore, the configuration of receivers in the continuous array in the estuary and the inner bay was suitable for the use of non-parametric regression for the interpolation of kelt positions. Receivers outside of the continuous array (in the upper estuary and in the linear arrays in the outer bay, and in the Strait of Belle Isle) were not used for interpolating kelt positions because it was found that they provided only intermittent coverage of only some of the kelts. The Belle Isle linear array, operated by the Atlantic Salmon Federation, was used to monitor migration beyond the coupled estuary-coastal embayment. The mean distance between neighboring receivers located in this linear array was 933 m.

Analysis of the telemetry data. Firstly, the residence time of each kelt in each region (delta, estuary, inner bay and outer bay) was determined. Residence time per region was defined as the time period between first detection in that region to first detection in the subsequent region downstream. Then, within the continuous array (estuary and inner bay), kelt locations were interpolated using kernel smoothing; the rationale being that this could provide a fine-scale interpolation of kelt locations allowing fine-scale patterns and their causes to be identified. A normal kernel (bandwidth = 30 min) was used because this has been shown to produce less error than the box kernel (Hedger et al. 2008a). For each kelt, the location was estimated at 10 min intervals (separately in easting and northing dimensions) from the coordinates of the receivers detecting the transmitter signals. Ground speed was then determined as the distance between successive estimated positions over the time difference (10 min).

Characterization of the physical habitat. Continuous measurements of York River discharge were obtained from a flow gauge stationed in the river in 2006 and 2007. Tidal phase was predicted throughout the time that kelts were within the estuary-coastal embayment system using the WTides software package (www.wtides.com), with the prediction verified by measurements within the inner bay. Continuous measurements of water temperature were made during both study years using a thermograph stationed at the mouth of the river delta (depth = 1 m) and in the inner bay (depths = 1, 9 and 18 m) near to the center of the continuous receiver array.

Vertical profiles of current direction and speed were obtained in 2006 using an Acoustic Doppler Current profiler (ADCP) at depths of 0.0, 2.7, 8.0 and 13.3 m. The thermograph and ADCP data were used to determine temporal variation in water temperature and water velocity in the inner bay as a function of depth. Vertical profiles of salinity were obtained from point measurements made using SEACAT Profiler Conductivity-Temperature-Depth (CTD) dataloggers (SeaBird Electronics Inc.) in July and August 2006. These profiles were obtained too late in the year to be directly used in modeling environmental controls on kelt migration and swimming depth, but they provided contextual information that could be used in the interpretation of any established relationships.

Statistical analysis. Regional differences in kelt residence times were determined using ANOVA. The relationship between kelt residence time in each region and environmental and kelt characteristics was determined using stepwise linear modeling. Predictors were (1) mean discharge from the York River throughout kelt residence in each region, (2) mean water temperature throughout kelt residence in each region, and (3) fork length. Residence times were firstly log transformed to achieve a normal distribution. For the delta and inner bay, temperatures were obtained from the respective thermographs; for the estuary (lying between the delta and the inner bay), the means of the delta and inner bay thermograph temperatures were used. York River discharges were used as a proxy for all discharges into the bay, as discharges from the other river flowing into this bay (River Dartmouth) had a similar intra-annual pattern.

The effects of environmental characteristics and kelt characteristics on kelt seaward ground speed (interpolated at 10 min intervals) and depth (using data directly obtained from the receivers) were determined using linear mixed-effects modeling. The lme(nlme) function of the open-source package R (Hornik 2009) was used. Seaward kelt ground speed (the *x*-component of kelt ground speed: positive when directed towards the sea in the east and negative when directed

towards the land in the west) was normally distributed so it could be used as a response variable without a transformation; a log transformation was applied to depth to achieve near-normality. For depth, all observations where the water column depth was <2 m were removed because these shallow waters prevented descent to greater depths, which would have biased the analysis of the effect of predictor variables. Predictor variables were chosen as those being the most likely to affect seaward ground speed and depth. Fixed effects were (1) diel period (daytime vs. night), (2) tidal phase (ebb vs. flood), (3) time (the fractional Year Day: e.g. Year Day = 2.5 is the date at noon on 2 January), and (4) fork length. The individual fish was used as a random effect. A first-order autoregressive model was used to account for the within-group autocorrelation. Fixed effects were then successively removed from each model (from those having least significance to those having most significance) if their removal did not cause a significant reduction in explanatory power.

Relationships between the time taken to migrate across the marine habitat (from Gaspé Bay to the Strait of Belle Isle) and fork length, date of departure from the bay, and residence time within each region of the coupled estuary-coastal embayment were determined by Spearman's rank correlation.

RESULTS

Physical habitat characteristics

Surface water temperatures experienced by the kelts increased as they migrated seaward through the estuary-coastal embayment: the mean temperature experienced by the kelts was 4.8°C in the delta (delta bay thermograph), 7.6°C in the estuary (mean of the delta and inner bay thermograph, depth = 1 m) and 9.5°C in the inner bay (inner bay thermograph, depth = 1 m). The inner bay was mainly thermally stratified. During the time that kelts were being detected in the inner bay, mean temperatures recorded by the inner bay thermograph were 9.5°C (depth = 1 m), 4.3°C (depth = 9 m) and 1.9°C (depth = 18 m). Temperatures often varied by several degrees over time periods of several hours, but a significant correlation existed between temperature at a depth of 1 m and temperature at a depth of 9 m during the time that kelts were being detected (Spearman's rank correlation, $\rho = 0.21$, n = 4445, p < 0.001 in 2006; $\rho = 0.48$, n = 4445, p < 0.001 in 2007). Distinct periods of mixing occurred, however, with thermal stratification temporarily disappearing on a non-periodic basis. A trend of increasing temperature with date existed in both years, suggesting the influence of solar forcing. A weak correlation existed

between solar elevation and inner bay surface temperature during the time that kelts were being detected ($\rho = -0.03$, n = 4380, p < 0.001 in 2006; $\rho = -0.05$, n = 4380, p < 0.001 in 2007), from which it can be inferred that much of the variation in water temperature was caused by changes in mixing rates between waters of terrestrial and marine origins.

Surface water temperatures and currents showed higher short-term heterogeneity than sub-surface temperatures and currents. Diel variation in temperature decreased with increasing depth: mean temperature SD = 0.78°C (depth = 1 m); mean temperature SD = 0.31°C (depth = 9 m). The correlation between current velocity and seaward tidal gradient increased with depth in the water column: e.g. for the x-component of current speeds from the ADCP and seaward tidal gradient: Spearman's rank correlation, $\rho = 0.11$, n = 4445, p < 0.001 (depth = 0 m); $\rho = 0.42$, n = 4445, p = <0.001 (depth = 2.7 m); $\rho = 0.67$, p < 0.001 (depth = 8.0 m); $\rho = 0.53$, n = 4445, p < 0.001 (depth = 13.3 m).

Kelt migration and swimming depth in coastal zone habitat

Of the 49 kelts released, 47 were detected by the receiver array (Table 1): one of the undetected kelts (#2007-23) had eroded fins at capture and exhibited considerable bleeding during surgery, suggesting mortality shortly after release. Of the 47 kelts that were detected, 45 were detected in the inner bay, 41 were detected in the western-most part of the outer bay (to the east of the sand-wedge) and 28 were detected crossing the linear array in the outer bay. Of the 13 kelts detected in the Strait of Belle Isle, 7 were not detected by the linear receiver array in the outer bay. As such, the minimum survival rate between release and the outermost transect located in Gaspé Bay exceeded 70%. Within the estuary, greatest detection rates of kelts occurred within the deeper, eastern region near to the inner bay (Fig. 2); within the inner bay, greatest detection rates occurred on the western margin of the sand-wedge. Kelts migrated out of the delta from 5 to 30 May (median = 8 May) in 2006 and from 9 May to 9 June (median = 25 May) in 2007. Patterns of kelt migration within the inner bay varied markedly according to individual (Figs. 3 & 4). Twenty-nine kelts (64% of the sample) showed multiple changes in direction (e.g. #2006-15, #2007-7, #2007-14), 11 kelts (24% of the sample) showed a highly oriented migration towards the sea (e.g. #2006-9, #2007-15, #2007-19) and 5 kelts (11% of the sample) were not detected often enough to determine their migration pattern. No difference existed in fork length (Mann-Whitney U-test, $W = $
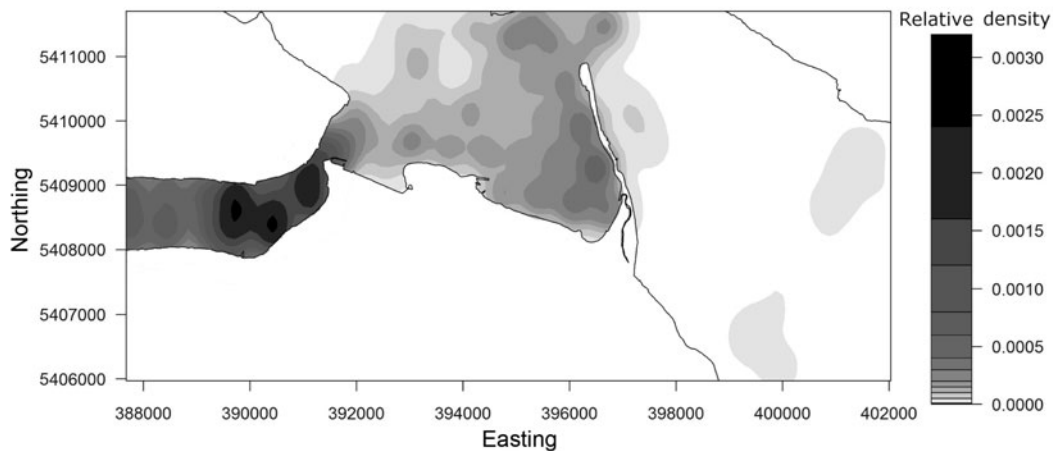
Fig. 2. *Salmo salar.* Density plot of Atlantic salmon kelt detections in the coupled estuary-coastal embayment system, York Estuary and Gaspé Bay in 2006 and 2007. Coordinates are Universal Transverse Mercator

165, n = 38, p = 0.879) as to which pattern the kelts followed. Of the kelts that were detected in the most westerly part of the outer bay, 30 migrated through the deep channel separating the inner and outer bays (e.g. #2006-17) and 11 migrated across the sand-wedge (e.g. #2007-18). Of the 11 kelts that migrated across the sand-wedge, migration occurred when tidal elevation was high (10 migrated during above-mean tidal elevation, and 1 migrated during slightly less than mean tidal elevation). No effect of tidal current direction on migration across the sand-wedge was apparent: 6 migrated during flood tides and 5 migrated during ebb tides.

Kelt swimming depth was mainly near the surface, but kelts exhibited a wide range of depth-use patterns during their migration (Fig. 5). Within the estuary, most kelts remained in near-surface waters (48.9% of detections occurred when kelts were within 1 m of the surface and 99.1% of detections occurred when kelts were within 5 m of the surface), but there were some instances of kelts migrating at the bed of the water column throughout the estuary (e.g. #2007-17) and 21% of the 47 kelts dived to depths >2 m when migrating along the trench separating the estuary from the inner bay (Fig. 5; e.g. #2006-14, #2006-18). Within both the inner and outer bay, kelts were again mostly observed within the near-surface layer (80.7% of detections occurred when kelts were within 1 m of the surface and 96.8% of detections occurred when kelts were within 5 m of the surface), but diving occurred, either periodically with individual dives lasting several min separated by several hours (e.g. #2007-14), or in clusters of individual dives extending for periods lasting as long as several hours (e.g. #2007-10, at the transition between the estuary and bay). The vast majority of dives lasted for short periods of time: >83% lasted for <1 min; >99% lasted for <10 min; the longest dive

lasted for ~23 min. Not all kelts dived while migrating across the inner bay. Diving was observed in 40% of 45 kelts detected within the inner bay, although the number of kelts diving may have been greater than this because there were occasional gaps in detections of some kelts. Kelts that dived experienced a large range of temperatures and, to a lesser degree, salinities: temperatures of ~9 to 9.5°C when migrating through the surface layer and of ~4 to 5°C at depths of ~9 m; salinities of ~25 psu in the surface layer (≤1 m) and ~28 psu in the sub-surface layer (>1 m) (from the CTD point samples from 2006).

Factors controlling kelt migration and swimming depth in coastal zone habitat

Kelt residence time per region decreased significantly as kelts moved through the estuary-coastal embayment system towards the sea (Fig. 6) (ANOVA, $F_{1,176}$ = 123.90, p < 0.001): delta ($\overline{X}$ = 16.32 d, N = 45), estuary ($\overline{X}$ = 1.32 d, N = 44), inner bay ($\overline{X}$ = 0.67 d, N = 41), outer bay ($\overline{X}$ = 0.23 d, N = 28). In the delta, kelt residence time was positively related to mean water temperature and fork length (Table 2). In the estuary and the inner bay, kelt residence time was negatively related to mean discharge and mean water temperature.

The mean absolute ground speed derived from the interpolated kelt positions increased as kelts moved through the system (ANOVA, $F_{2,7216}$ = 114.75, p < 0.001): estuary ($\overline{X}$ = 20.5 cm s^{-1}), inner bay ($\overline{X}$ = 31.6 cm s^{-1}), outer bay ($\overline{X}$ = 46.7 cm s^{-1}). Tidal phase was the only significant variable affecting seaward ground speed in the mixed-effects model (p < 0.001) with faster seaward ground speed during ebb tide. This model explained 44.8% of the variation in seaward
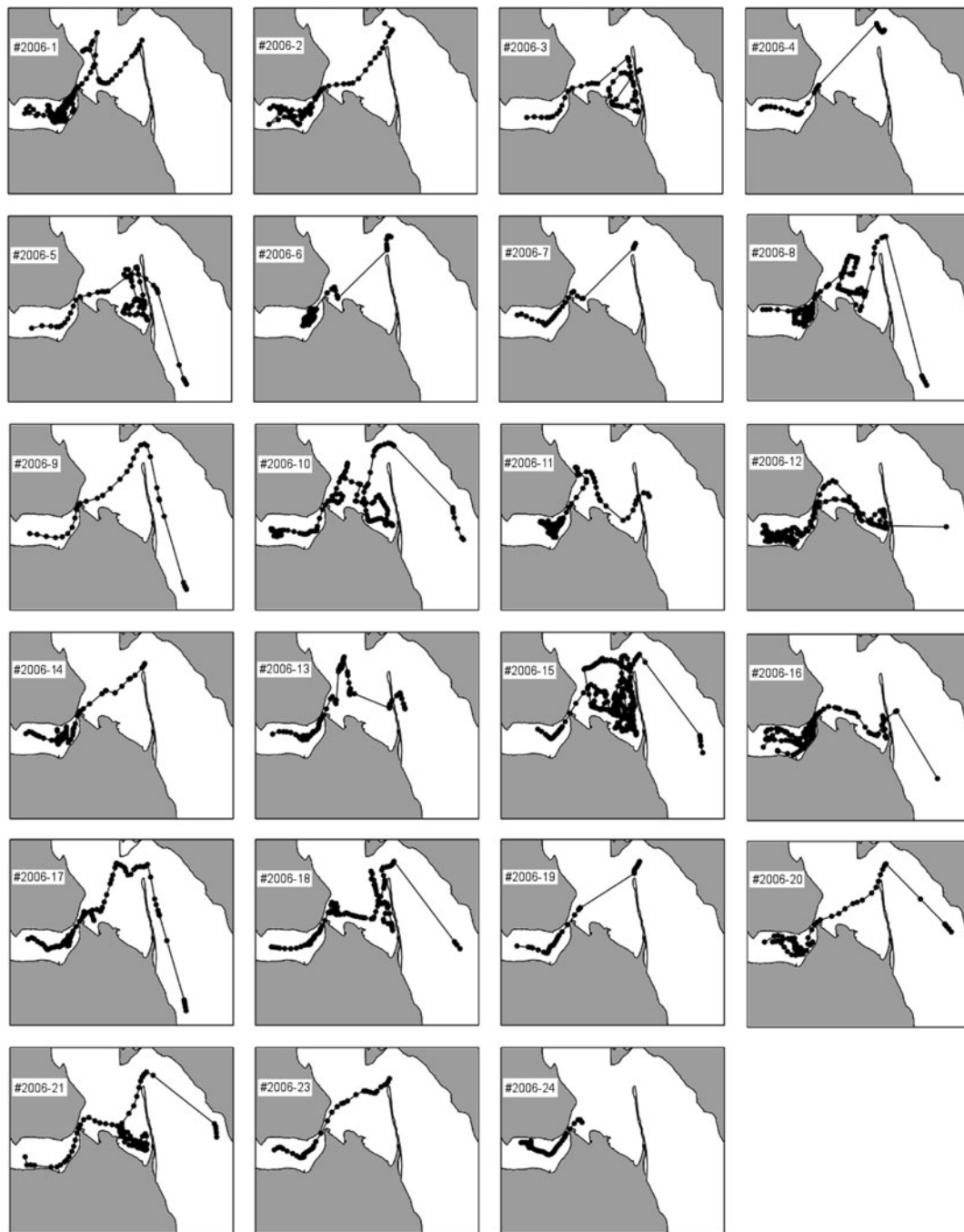
Fig. 3. *Salmo salar.* Kelt migration patterns in 2006 interpolated using kernel smoothing (time interval = 10 min). Kelts migrate seaward (from the western margin of the York Estuary towards the east). Points indicate interpolated positions. For clarity, points are joined by lines

ground speed within the estuary and inner bay. In both the estuary and the inner bay, mean seaward ground speed was positive on both ebb and flood tides: ebb tide ($\overline{X}$ = 14.5 cm s^{-1}), flood tide ($\overline{X}$ = 3.9 cm s^{-1}).

Kelt depths became significantly shallower as kelts traversed the system (ANOVA, $F_{2,63979}$ = 691, p <

0.001): estuary ($\overline{X}$ = 1.28 m), inner bay ($\overline{X}$ = 0.82 m), outer bay ($\overline{X}$ = 0.75 m). Diel period was the only significant variable affecting kelt swimming depth (p < 0.001) selected by the mixed-effects model, with greater depths occurring during the day. This model explained 89% of the variance in depth. Mean and maximum
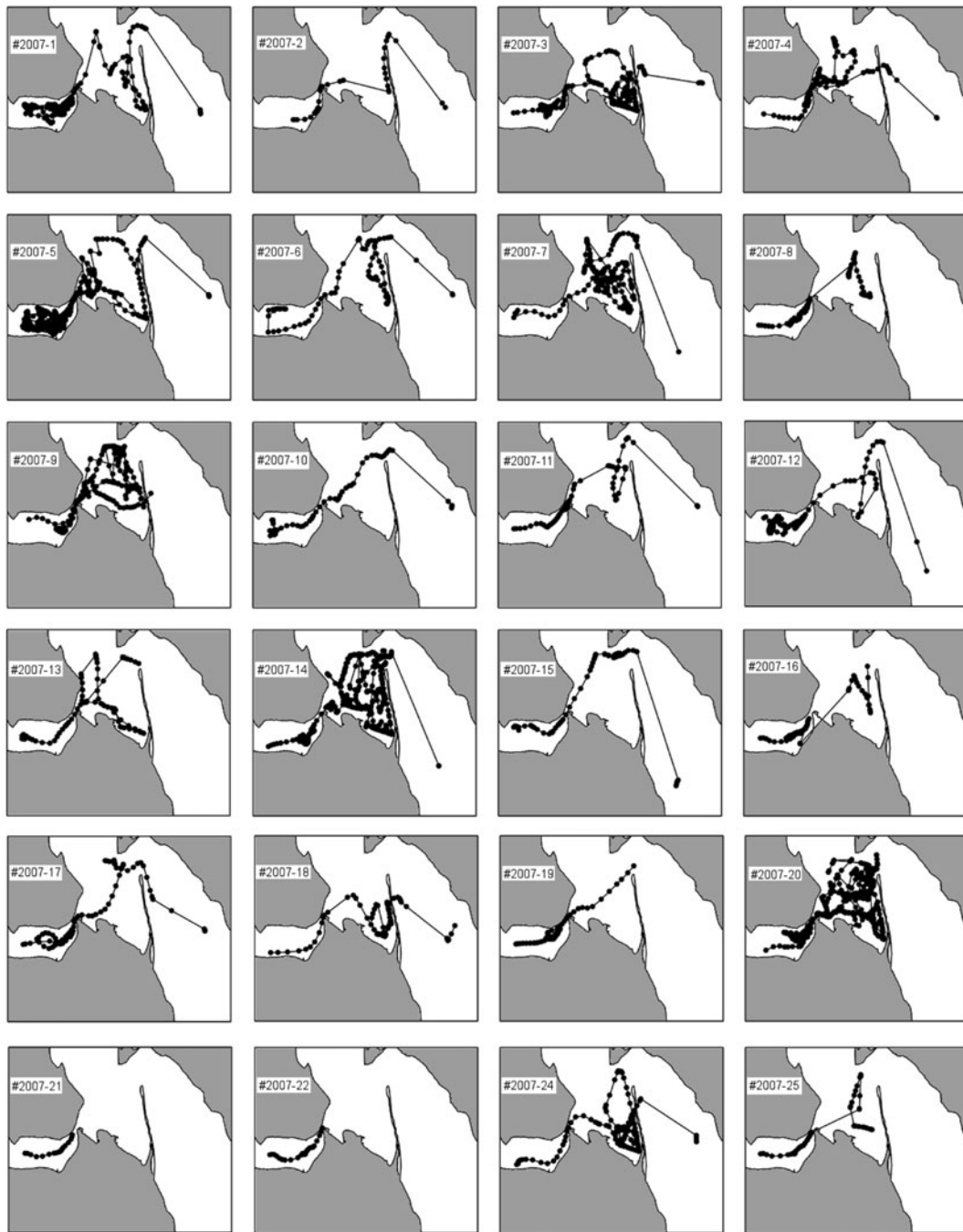
Fig. 4. *Salmo salar.* Kelt migration patterns in 2007 interpolated using kernel smoothing (time interval = 10 min). Kelts migrate seaward (from the western margin of the York Estuary towards the east). Points indicate interpolated positions. For clarity, points are joined by lines

depth during daytime was greater than that during night in the estuary ($\bar{X}_{Day}$ = 1.81 m, $\bar{X}_{Night}$ = 0.75 m; $max._{Day}$ = 16.9 m, $max._{Night}$ = 10.7 m), in the inner bay ($\bar{X}_{Day}$ = 0.99 m, $\bar{X}_{Day}$ = 0.79 m; $max._{Day}$ = 41.0 m, $max._{Night}$ = 9.0 m) and in the outer bay ($\bar{X}_{Night}$ = 0.97 m, $\bar{X}_{Day}$ = 0.63 m; $max._{Night}$ = 15.0 m, $max._{Night}$ = 7.0 m).

Kelt migration and swimming depth in marine habitat

In 2006, none of the tagged kelts were detected in the Strait of Belle Isle, but the receivers were deployed late in the season on 10 July so kelts may have passed
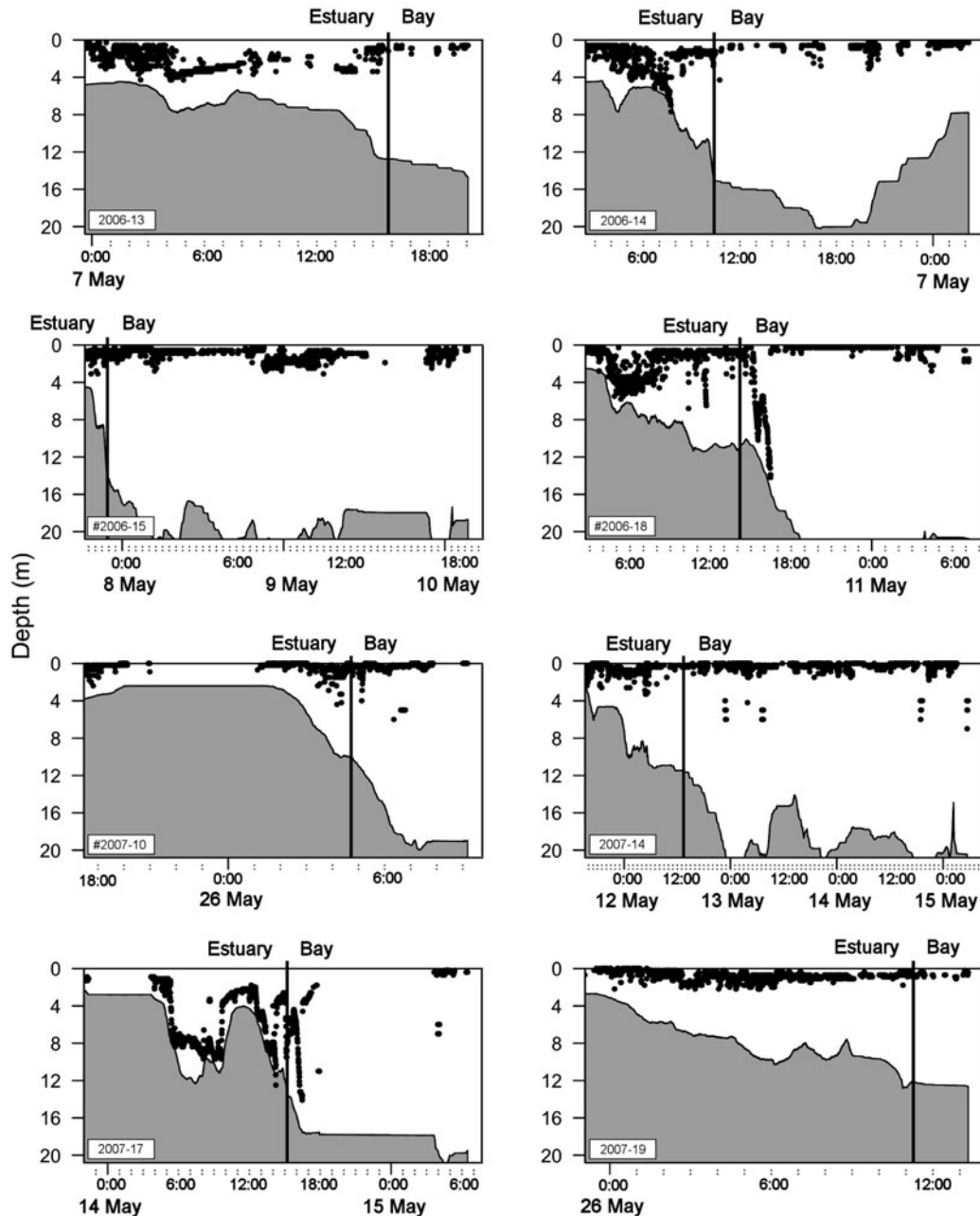
Fig. 5. *Salmo salar*. Depth plots of 8 Atlantic salmon kelts in the York River estuary and the Gaspé bay. The bed of the estuary and bay is shown by the filled gray area

through the strait before the deployment. Thirteen kelts were detected in the Strait of Belle Isle in 2007. In that year, kelts had left Gaspé Bay from 11 May to 10 June and were detected in the Strait of Belle Isle from 1 to 15 July. Kelts covered a distance of 639 to 650 km in the open sea in a mean time period of 45 d (range: 27 to 62 d) at a mean ground speed of 15 km d^{-1} (range: 10 to 24 km d^{-1}). No relationship existed between marine ground speed and length (Spearman rank correlation, $\rho = 0.26$, $n = 13$, $p = 0.378$) or time taken to migrate

across the inner and outer bays ($\rho = 0.18$, $n = 13$, $p = 0.595$). However, a strong positive relationship existed between marine ground speed and date of departure from Gaspé Bay ($\rho = 0.877$, $n = 13$, $p < 0.001$). The mean ground speed was 11 km d^{-1} (range: 10 to 12, $n = 3$) for kelts leaving in early May, 15 km d^{-1} (range: 13 to 18, $n = 7$) for kelts leaving at the end of May, and 22 km d^{-1} (range: 18 to 24, $n = 3$) for kelts leaving in early June. A strong positive relationship also existed between marine ground speed and kelt residence time in the

delta (ρ = 0.807, n = 13, p < 0.001). No significant relationship was found for any other region of the coupled estuary-coastal embayment.

Kelt swimming depth in the Strait of Belle Isle occurred mainly in the near-surface water (78% of the 144 detections indicated a kelt depth of ≤1 m from the surface). The mean swimming depth of sonic-tagged kelts ranged from 0.22 to 3.80 m. Diving behavior was observed for short time periods (<1 to 6 min) for only 3 of the 13 kelts. Swimming depth during diving ranged from 4 to 15 m.
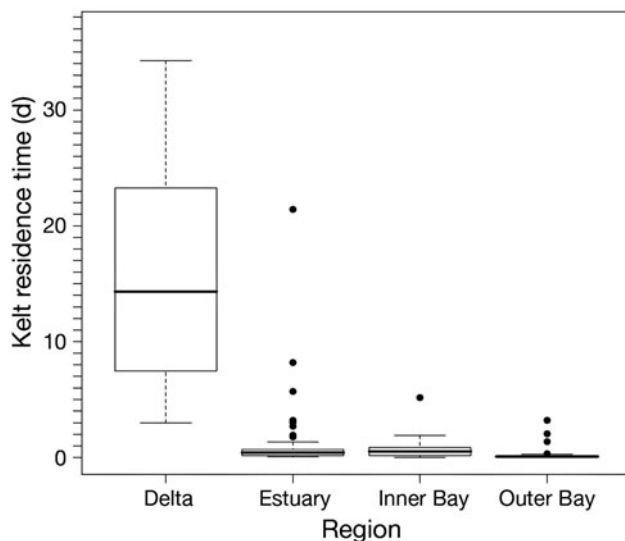

Fig. 6. *Salmo salar.* Atlantic salmon kelt residence time according to region. Thick horizontal line = median; the box bounds the first and third quartiles; whiskers = all values outside box within 1.5× interquartile range

Table 2. *Salmo salar.* Effect of discharge, mean temperature and fork length on kelt residence time within the delta, estuary and inner bay as determined using stepwise linear modeling

	Estimate	SE	*t*-value	p-value
Delta				
(Intercept)	−1.520	0.650	−2.338	0.024
Mean water temperature	0.574	0.121	4.723	<0.001
Fork length	0.015	0.004	3.631	<0.001
Adjusted R^2 = 0.53, $F_{3,37}$ = 23.06, p < 0.001				
Estuary				
(Intercept)	4.532	1.398	3.241	0.002
Mean discharge	−0.034	0.009	−3.567	<0.001
Mean water temperature	−0.405	0.110	3−3.671	<0.001
Adjusted R^2 = 0.24 $F_{2,39}$ = 7.43, p < 0.001				
Inner Bay				
(Intercept)	2.584	0.855	3.019	0.005
Mean discharge	−0.013	0.007	−1.807	<0.081
Mean water temperature	−0.271	0.072	−3.771	<0.001
Adjusted R^2 = 0.31, $F_{2,27}$ = 7.66, p = 0.002				

DISCUSSION

Factors controlling coastal zone migration

Kelts resided in the delta for relatively long periods (up to several weeks), followed in most cases by rapid seaward migration on reaching the estuary. The lack of a relationship with discharge in the delta indicates that kelts were actively maintaining station within the delta. We hypothesize that long-term residence in the delta resulted from a period of feeding in response to the requirement to improve somatic reserves for seaward migration. Atlantic salmon lose between 60 and 70% of their body reserves due to upstream migration and spawning (Jonsson et al. 1997). Rapid seaward migration of fish surviving to the spring following spawning thus requires the restoration of some minimum level of somatic reserves. This hypothesis is supported by the fact that residence time in the delta was positively related to fork length. Both absolute and relative energy losses in Atlantic salmon during migration and spawning increase with fish length (Jonsson et al. 1997), probably due to the relatively higher maintenance metabolism in larger fish (Jonsson et al. 1991). Larger post-spawning fish would then be expected to require more time to build their energy reserves prior to seaward migration. Although there is no information on food availability across the delta-estuary-embayment, the delta is characterized by shallow waters and extensive macrophyte beds: ideal settings for the development of an invertebrate fauna and the forage fish that prey upon them. The longer kelt residence within the delta with increasing temperatures (~4.5°C to 6.5°C) may reflect the increasing profitability of the delta for feeding and the accumulation of energy stores.

The pattern of rapid seaward migration of Atlantic salmon kelts after a period of extended river residence is similar to that identified by Halttunen et al. (2009) in Alta Fjord (Norway), where kelts initiated their migration an average of 18 d after tagging, but differs somewhat to the pattern identified by Hubley et al. (2008) in the LaHave River and Estuary (Nova Scotia, Canada) where no initial long-term residence in the river was found. Kelt migration speeds across the estuary-embayment in our study (~12 km d^{−1}) were less than those of kelts in the fjord studied by Halttunen et al. (2009) (~40 km d^{−1}) but were greater than those of kelts in the estuary studied by Hubley et al. (2008) (~2 km d^{−1}).

The faster migration within the Alta Fjord may have been related to its greater salinities that have generally been associated with rapid seaward migration of salmon. The increase in seaward migration speed with an increase in proximity to the sea that was found in our study concurred with that found in the studies of Halttunen et al. (2009) and that of Hubley et al. (2008). This increase occurred across all monitored parts of the fjord in Halttunen's study, but was only consistently found in the outer-most part of the coastal area in Hubley's study. The shorter residence times observed in the estuary and embayment in the present study when temperatures were warm and discharges were high is suggestive of an orthokinetic increase in seaward swimming speed in response to an increase in temperature (see Bendall et al. 2005) and the use of the seaward residual current to aid seaward migration.

The mixed-effects model showed that kelt seaward movement was controlled by tidal phase (faster seaward migration on the ebb tide). Tidal phase has consistently been identified throughout the literature as being a control of migration of Atlantic salmon within the coastal zone, and seaward migration on the ebb tide has been proposed as being the most energetically efficient form of seaward migration (Bendall et al. 2005). No diel control was apparent. The pattern of diel control on kelt seaward migration had been less consistent throughout the literature (Bendall et al. 2005 and Scruton et al. 2007 identifying nocturnal migration; Östergren & Rivinoja 2008 identifying daytime migration). We hypothesize that the lack of a tendency for nocturnal migration is suggestive of low predation pressure on the kelts from piscivorous fish and birds: avoidance of predation should cause a preference for movement under the cover of darkness (Bendall et al. 2005). Swimming depth however was greatest during daytime. Diving during daytime could be associated with either feeding behavior or the identification of bed features to aid in orientation out of the estuary-coastal embayment system, light being required for either of these processes.

Seaward orientation and swimming depth

Several behavioral mechanisms may have been exploited by kelts to achieve active seaward migration out of the estuary and bay. The most probable mechanism would involve a response to properties of the body of water. Temperature and salinity gradients and current directions may have played a role in kelt orientation, as has been identified for smolts in both the estuary (Martin et al. 2009) and the inner bay (Hedger et al. 2008b). Within the inner bay, more kelts migrated towards the deep channel separating this bay from the outer bay than towards the sand-wedge. Stronger salinity gradients across the inner bay and more temporally consistent current directions were identified towards the deep channel than towards the sand-wedge, so this may have been a mechanism by which kelts oriented themselves. Additionally, we speculate that swimming at depth may have been associated with the requirement for detecting temporally consistent terrestrial-marine gradients in temperature and salinity and/or temporally consistent current flow directions for establishing orientation. Surface eddying in the inner bay has been seen to temporarily destroy temperature and salinity gradients (or reverse them) on a non-periodic basis, and superimpose a seemingly chaotic current flow direction and speed on the more predictable tidal-induced flow (Hedger et al. 2008b). The data from the inner bay thermograph and ADCP showed that short-term heterogeneity in temperature and currents decreased with increasing depth (and by inference, salinity will have become less variable), so kelts may have been diving to experience these more temporally consistent temperature and salinity gradients and current flows. These observations of kelt migration are also consistent with the hypothesis that kelts exploit an innate compass to maintain a preferred bearing (reviewed in Dodson 1988), as suggested for smolts in this area by Hedger et al. (2008b) and Martin et al. (2009). Finally, the preferred eastward bearing may have been a conditioned response (Dodson 1988, Smith & Smith 1998). Throughout the time when kelts were within the York River, they were swimming in an eastward direction against a gradient of increasing salinity. It is possible that they associated an increase in salinity with swimming in an eastward direction and that this eastward bias continued on their transition into the inner bay.

Behavioral consistency across life-stages of Atlantic salmon within the coastal zone

Two characteristics of kelt migration patterns have also been observed in salmon smolts within York Estuary and Gaspé Bay (Hedger et al. 2008b; Martin et al. 2009): (1) increased seaward ground speed as the individual passed from the estuary into the bay, and (2) increased rates of seaward migration on the ebb tide. Some differences also existed. Firstly, Martin et al. (2009) showed that most smolt movements in the estuary were in an upstream direction during the flood tide (i.e. positive rheotaxis regardless of current direction), whereas our study of kelts showed that, although the seaward ground speed decreased during the flood tide, the net movement on the flood tide was still in a seaward direction. Secondly, kelt migration across the

system was faster (with the exception of the delta) and a greater proportion exited the system than in the smolt study of Hedger et al. (2008b): kelts were more strongly and actively migrating offshore. Finally, diel effects on kelt seaward migration speed appeared to be minimal. The overall pattern of behavior, however, appeared to be retained from the smolt to the kelt life-stage, although kelt seaward migration appeared to be more pronounced.

Marine migration

The fact that high detection rates occurred in the Strait of Belle Isle is unique evidence that salmon spawning in rivers in the south-western part of the Gulf of St. Lawrence migrate to offshore areas through the Strait of Belle Isle. Assuming that the ~50% detection rate observed in 2007 in the Strait of Belle Isle is a minimum estimate of the proportion of potential repeat spawners that opt for alternative-year spawning rather than consecutive year spawning, it may be hypothesized that the increase in reproductive success afforded by increased growth at sea requires that kelts leave the Gulf of St. Lawrence, possibly because of cold winter temperatures along the coast. Further analysis of the life-histories and physiological characteristics of kelts migrating from rivers within the Gulf of St. Lawrence is warranted to further explore the proximate control and fitness benefits of these 2 alternative repeat spawning strategies.

The speed of migration between Gaspé Bay and the Strait of Belle Isle was positively related to the date of departure from Gaspé Bay. Two non-exclusive hypotheses can be proposed. On one hand, the relationship with date of departure may have been an artifact of a relationship between date of departure and the physical condition of kelts. The main influence on the date of departure from Gaspé Bay was the length of time that the kelts remained within the delta. That is, those kelts which resided within the delta for a long period of time showed rapid migration during the marine phase. It is therefore possible that the kelts which were rapidly migrating had remained within the delta long enough for them to have achieved sufficient physical condition to enable rapid migration. On the other hand, the speed of migration may have been related to a temporally dependent characteristic of the marine habitat (for example, an increase in sea surface temperature). Warmer temperatures are associated with higher metabolic rates and faster sustained swimming speeds. In either case, the non-significant relationship between marine migration rate and fish length was unexpected and may be explained by the small sample size of fish that were detected in the Strait of Belle Isle.

CONCLUSIONS

Three main controls on coastal zone migratory behavior were apparent: (1) a geographical control, with kelts showing extended residence in the river delta section of the upper estuary, followed by rapid seaward migration through the estuary and coastal embayment; (2) a diel control, with diving behavior during daytime (hypothesized to be a mechanism to exploit more stable physical gradients); and (3) a tidal control, with faster seaward migration on the ebb tide. There was strong evidence of active migration, with resistance to displacement in the river delta and rapid seaward migration on reaching the estuary and bay. The patterns of migration within the coastal zone were broadly similar to those previously identified for smolts in the same location, suggesting that there are universal patterns of migratory behavior in both life-history stages within the coastal zone. Kelts within the marine environment were detected in the Strait of Belle Isle: the only time that kelt migration from a river in Gaspésie to this area has been detected. Speed of migration within the marine environment was dependent on date of departure from Gaspé Bay, which in turn was dependent on residence time within the delta. It was hypothesized that extended residence within the delta enabled kelts to improve their physical condition to ensure rapid migration within the marine environment.

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