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River and estuary movements of yellow-stage American eels *Anguilla rostrata*, using a hydrophone array

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Patterns of summertime movement and habitat use of yellow-stage American eels *Anguilla rostrata* within York River and estuary and Gaspé Bay (Gaspesia, Québec, Canada) were examined using acoustic telemetry. Fifty fish were tagged with acoustic transmitters and released, either in the river or in the upper estuary, and their patterns of movement and habitat use were monitored at short spatial and temporal scales during the summer months using a dense hydrophone array. Approximately half of the fish released in the river swam to the estuary; two-thirds of the fish released within the estuary did not move out of the estuary. *Anguilla rostrata* were detected more frequently and had a greater areal range of detections during night, suggesting greater nocturnal activity. Longitudinal movements within the estuary tended to occur nocturnally, with upstream movements from early to late evening, and downstream movements from late evening to early morning. Approximately one-third of fish showed a regular pattern of movement, tending to reside in the deeper, downstream part of the estuary during day and in the shallower, more upstream part of the estuary during night. Approximately a quarter of fish, located in the upper estuary, remained upstream during both night and day. The remaining fish showed patterns intermediate between these two. © 2010 The Authors

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Key words: *Anguilla rostrata*; habitat selection; nocturnal longitudinal movements; sedentary behaviour.

INTRODUCTION

The American eel *Anguilla rostrata* (LeSueur) is a facultatively catadromous fish found in estuaries, rivers and lakes of the east coast of North America, ranging from the Yucatan Peninsula to the Labrador Coast. They may reside in fresh and brackish waters as juveniles (yellow-stage) for up to *c.* 25 years, and on reaching maturity (silver-stage) migrate to the Sargasso Sea. Worldwide populations of anguillid eels

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are declining, possibly as a result of climatic oscillations experienced at sea such as the North Atlantic Oscillation (Friedland *et al.*, 2007), fishing pressure, obstructions to migration, hydroturbine mortality, pollution, competition from non-native species and parasites (Haro *et al.*, 2000; Feunteun, 2002). Given that many of the threats to anguillid eels living in freshwater or brackish habitats are anthropogenic in origin, there is potential for implementing mitigation measures to help sustain eel populations during these parts of the life cycle. For such measures to be effective, however, it is necessary to have detailed information on how anguillid eels use these habitats.

Yellow-stage *A. rostrata* exhibit sedentary rather than migratory behaviour (Aoyama *et al.*, 2002), although they may move from rivers to estuaries for summer feeding before returning for overwintering in cold temperate climates (Thibault *et al.*, 2007). A bias towards nocturnal activity is the most consistently observed characteristic across the range of species: *A. rostrata* (Lamothe *et al.*, 2000; Thibault *et al.*, 2007); European eel *Anguilla anguilla* (L.) (Baras *et al.*, 1998; Barbin, 1998; van Ginneken *et al.*, 2005); Japanese eel *Anguilla japonica* Temminck & Schlegel (Aoyama *et al.*, 2002) and Australian shortfinned eel *Anguilla australis australis* Richardson and longfinned eel *Anguilla dieffenbachia* Gray (Jellyman & Sykes, 2003). This activity may be related to foraging at night, with anguillid eels using olfaction to identify prey (Barbin, 1998). During daytime, anguillid eels may bury themselves in the substratum for sheltering and feeding (Glova & Jellyman, 2000). Tidal influences may also be apparent. Anguillid eels have been observed to move in the direction of tidal flow (Helfman *et al.*, 1983) and may use tidal currents to move around their home range (Parker, 1995). Selective tidal stream transport (STST) is often evident, with fishes ascending towards the surface when tidal flow is in the migratory direction and descending towards the bottom when tidal flow is in a non-migratory direction (Parker & McCleave, 1997; Barbin, 1998; McCleave & Arnold, 1999).

Yellow-stage anguillid eels may also show evidence of homing to specific areas (Parker, 1995), fidelity to specific habitats (Jellyman & Sykes, 2003) or the occupancy of distinct locations according to diel period (Helfman *et al.*, 1983; Thibault *et al.*, 2007). Reported areal ranges of anguillid eels in tidal creeks, estuaries and salt marshes have varied over several orders of magnitude: for example, mean home ranges of *c.* 0.01 km² (Helfman *et al.*, 1983; Bozeman *et al.*, 1985), *c.* 0.02 km² (Ford & Mercer, 1986), 0.16 km² (Thibault *et al.*, 2007) and 3.25 km² (Parker, 1995) have been reported. These variations will have resulted from variation in the anguillid eel characteristics, habitat type and methods used to determine locations.

Acoustic and radio-telemetry, which involve tagging fishes with ultrasonic or radio transmitters and monitoring emitted signals, are commonly used for determining patterns of anguillid eel movement and habitat use. The dominant method for detecting anguillid eels is through the use of mobile tracking, which involves moving boat-mounted or hand-held receivers through the area of study and estimating the position of the fish from the position of the receiver when signals are detected (Helfman *et al.*, 1983; LaBar *et al.*, 1987; Parker, 1995; Baras *et al.*, 1998; Barbin, 1998; McCleave & Arnold, 1999; Aoyama *et al.*, 2002; Behrmann-Godel & Eckmann, 2003; Jellyman & Sykes, 2003; Thibault *et al.*, 2007). In comparison to using a fixed array of receivers (Hedger *et al.*, 2008a, 2009; Martin *et al.*, 2009), mobile tracking is limited in the amount of information that is provided, both spatially and temporally, because

it is not possible to cover the whole study area simultaneously. Study of anguillid eel movements by fixed array telemetry is therefore warranted.

The objective of this study was to robustly determine summer patterns of movement (and influences on these patterns) of yellow-stage *A. rostrata* within York River and estuary and Gaspé Bay, Québec, Canada, using fixed array acoustic telemetry. Environmental influences that were studied were diel period (night *v.* day), tidal phase, river discharge, water temperature, cloud cover and lunar illumination. The effect of total length (L_T) was also investigated. It was hypothesized that fish would move from the river to the estuary [the movement for feeding hypothesis of Thibault *et al.* (2007)] but that movements out of the estuary would be limited (the yellow-stage being non-migratory). It was also hypothesized that there would be strong environmental influences on fish activity: in particular, that fish would move further under conditions of low illumination (during night, and particularly under new moon, and during cloudy conditions), that tidal effects would be apparent, and that smaller fish would have lower nocturnal detection rates due to an ability to feed within interstitial spaces.

MATERIALS AND METHODS

STUDY AREA

The study area was a watercourse consisting of the York River, York Estuary and Gaspé Bay, located on the north-eastern coast of Gaspesia, Québec, Canada (48.85° N; 64.45° W; Fig. 1). The York River discharges into the estuary in the form of a delta. This delta stretches for several kilometres, and its flow and water quality characteristics are dominated by the discharge from the river, *i.e.* tidal effects are minimal, water is fresh water and temperature varies on a diel basis. The York Estuary is a coastal plain estuary. It is shallow, with a mean depth of *c.* 3 m, but depth increases to >10 m in a narrow channel separating the estuary from Gaspé Bay. Salinity and temperature within the estuary are controlled by the balance between freshwater input from the York River and the intrusion of water of greater salinity into the lower estuary from Gaspé Bay. Surface waters in the estuary–bay system change from cold and relatively fresh in early May (from the massive input of cold fresh water from melting snow) to warmer and more saline from late May onwards (from both solar heating and decreased freshwater inflow after spring). The water column is generally mixed or weakly stratified throughout the shallow upper estuary, but within the deeper, downstream part of the estuary, point measurements have shown a temperature and salinity stratification in the water column, with a thermocline and pycnocline at a depth of between 2 and 3 m (Martin *et al.*, 2009). Within this area, temperatures near the bottom (water column depth >10 m) may be *c.* 5° C less than those at the surface and salinities near to the bottom may be *c.* 15 greater than those at the surface in early July, although stratification may break down by early August. The coastal embayment, Gaspé Bay, is composed of two 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 (*c.* 10 km). It is separated from the outer bay by a sand wedge that is submerged at high tide.

ACOUSTIC TELEMETRY AND ENVIRONMENTAL CHARACTERIZATION

Acoustic telemetry was conducted in 2006 and 2007. In 2006, 20 *A. rostrata* were captured in the river by a rotary screw trap, and were tagged and then released near the point of capture in the river from 20 to 30 May (Fig. 1 and Table I). In 2007, two groups were captured and released: (1) 15 fish were captured within the river with the rotary screw trap, tagged and

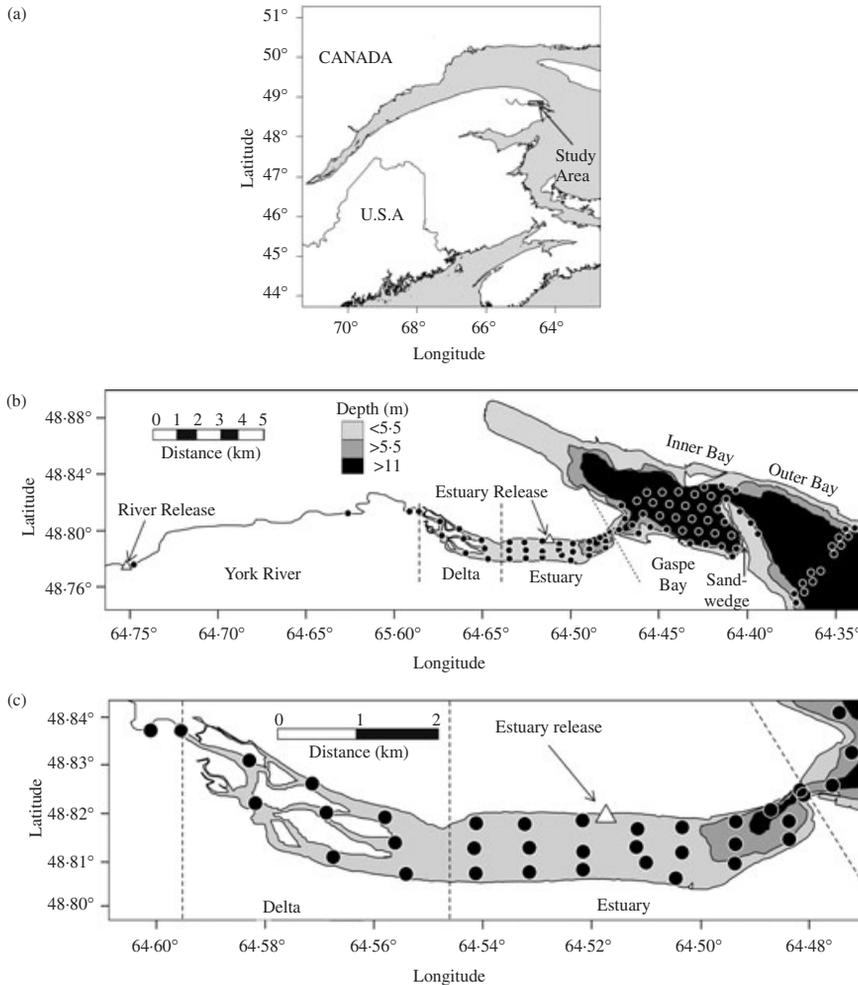


FIG. 1. Study area: (a) location within Canada, (b) York River, York Estuary and Gaspé Bay and (c) York Estuary. Hydrophones are shown (●). *Anguilla rostrata* were released at point of capture.

then released near the point of capture in the river from 4 to 6 June and (2) 15 fish were captured in the estuary with a Pennsylvania trap net, tagged and then released near the point of capture in the estuary from 28 to 30 July (Fig. 1 and Table I). The total length (L_T) and mass (M) were measured before release: fish released in the river were of a similar L_T to those released in the estuary (Mann–Whitney U -test, $W = 200$, $n = 50$, $P > 0.05$); however, fish released in the river were of significantly lower M than those released in the estuary (Mann–Whitney U -test, $W = 384$, $n = 47$, $P < 0.001$; three fish were not weighed due to logistical problems). A standard surgery procedure was used (Summerfelt & Smith, 1990) to insert the acoustic transmitter in each fish. The transmitter was the V9-1L model (Vemco Ltd; www.vemco.com): random burst rate = 20–50 s, estimated longevity = 100 days, length = 24 mm, mass = 2.2 g. The transmitter mass was <2% of M and so did not exceed the maximum threshold suggested by Lucas & Baras (2000) and Thorstad *et al.* (2009).

Transmitter-tagged fish were monitored using a fixed acoustic hydrophone array (VR2 model, Vemco Ltd), with hydrophones moored within *c.* 1 m of the surface. Hydrophones

TABLE I. *Anguilla rostrata* characteristics. Vagrancy is defined as any case where a river-released fish is detected in the estuary or bay, or an estuary-released fish is detected in the river, delta or bay. Movement pattern shows the temporal sequence of detections across the regions: river (R), delta (D), estuary (E) and bay (B). For example, a sequence of RDED indicates movement from the river, through the delta to the estuary, and then a return to the delta. Three fish released in the estuary in 2007 were not weighed due to operational errors. Detections from one fish released in the river in 2007 were discarded because the detection pattern suggested that the fish had died. Ranges are shown in parentheses

	River release		Estuary release
	2006 (<i>n</i> = 20)	2007 (<i>n</i> = 15)	2007 (<i>n</i> = 15)
Mean L_T (mm)	553 (492–633)	541 (483–625)	580 (516–779)
<i>M</i> (g)	288 (177–466)	254 (167–466)	436 (256–918)
% vagrant	55.0	40.0	33.3
Number of days from release to final detection	24.7 (7.5–55.8)	62.5 (2.4–107.6)	46.2 (10.4–69.5)
% non-vagrant	25.0	46.6	66.6
% not detected or discarded	20.0	13.3	0.0
% of fish with movement pattern			
R	0.0	40.0	NA
RD	25.0	6.7	NA
RDE	40.0	20.0	NA
RDEB	10.0	6.7	NA
RDED	5.0	6.7	NA
RDEDR	0.0	6.7	NA
E	NA	NA	66.6
EB	NA	NA	6.67
EBE	NA	NA	13.3
ED	NA	NA	13.3

L_T , total length; *M*, mass; NA, not applicable.

were placed within the river at the place of release, within the river delta, in a continuous grid within the estuary and inner bay, and in two rows crossing the outer bay (91 hydrophones in 2006; 90 hydrophones in 2007; Fig. 1). The mean distance between neighbouring hydrophones was 317 m in the estuary and 610 m in the inner bay. The range of detection of the hydrophones for V9-1L transmitters typically varies between *c.* 200 and *c.* 700 m, and is lower when background noise increases attenuation (Simpfendorfer *et al.*, 2008). There were some instances of hydrophones losing their mooring in 2007; data from these periods were removed. The hydrophone array was removed in mid-August in 2006 and in mid-October in 2007, except for the outer linear array in the embayment in 2007 which was removed in mid-June. Hydrophones had sufficient battery life to be operational throughout the study period. Detections from the day of release were removed because fish were released during daytime, which would have caused a slight initial bias towards daytime detection. Detections from one fish were removed because its detection pattern suggested it died soon after release.

Discharge within the York River was measured by a flow gauge. Tidal phase was predicted using the WTides package (www.wtides.com) (verified using measurements from a boat harbour in Gaspé Bay). Lunar illumination (the proportion of the moon that was illuminated)

was obtained from the Astronomical Applications Department of the U.S. Naval Observatory (<http://aa.usno.navy.mil/data/docs/MoonFraction.php>). Meteorological data were obtained from a weather station 5 km south of the York Estuary at Gaspé Airport (48°76' N; 64°46' W) through the National Climate Data Archive of Environment Canada (www.climate.weatheroffice.ec.gc.ca), from which a cloud cover index was derived: (1) clear sky, (2) mostly clear, (3) mostly cloudy and (4) overcast. Temperature experienced by each fish as a function of time was estimated as a weighted mean of thermograph measurements in the river delta and the inner bay (depth = 1 m), with the weights being proportional to the relative proximity of the fish to each of the thermographs.

ANALYSIS OF PATTERNS OF DETECTIONS

The diel pattern of detections (night *v.* day) was determined for each region (river, delta, estuary and bay). The diel pattern that would be expected if there was no preference for night or day was then predicted (dependent upon the relative proportion of nocturnal and daytime hours during the time that fish were present within each region), and Pearson's χ^2 tests were then used to determine whether there was a diel effect on detection rates within each region. The effect of L_T on the nocturnal detection rate within the estuary was determined using Spearman's rank correlation (r_s).

ANALYSIS OF MOVEMENTS WITHIN THE RIVER AND DELTA

Anguilla rostrata released in the river were classified into two categories: (1) non-vagrant (fish that were only detected within the river and delta) and (2) vagrant (fish that were subsequently detected within the estuary or bay). Stepwise generalized linear modelling (GLM) was then used to determine the effect of river discharge and L_T on: (1) the probability of fish being vagrant and (2) the residence time within the river and delta of those fish which were vagrant. For the former model, discharge at time of release was used, with the interaction between response and predictor variables modelled with a binomial family. For the latter model, mean discharge throughout the time that each fish was resident within the river and delta was used. Residence time was determined as the time difference between release in the river and first detection in the estuary. A \ln transformation was applied to normalize the distribution of the residence time, and the interaction between response and predictor variables was modelled with a Gaussian family. Interaction effects were allowed in both models. Finally, ANOVA was used to compare the mean L_T of groups of fish according to where they were detected last (river and delta, estuary or bay).

ANALYSIS OF MOVEMENTS WITHIN THE ESTUARY AND BAY

Anguilla rostrata released in the estuary were classified into two categories: (1) non-vagrant (fish released in the estuary that were only detected within the estuary) and (2) vagrant (fish released in the estuary that were subsequently detected within the river or bay). The L_T of the non-vagrant fish was compared with that of the vagrant fish using Mann-Whitney U -tests.

Anguilla rostrata positions were interpolated as a function of time from the hydrophone detections using kernel smoothing (Hedger *et al.*, 2008b). The function `ksmooth` (kernel distribution = normal, bandwidth = 60 min, estimation interval = 60 min) of the open source package R (Hornik, 2009) was used. It was not possible to interpolate fish positions for two of the 32 *A. rostrata* detected within the estuary because they were detected too infrequently. From the interpolated positions, two properties of the fish movements were derived at a 60 min interval: (1) absolute ground speed (the distance moved over time, which is the sum of swimming speed and passive displacement by currents) and (2) downstream ground speed (the x -component of the ground speed, which was positive when the movement was in a downstream direction, towards the sea). A further property, areal range was determined for each diel period (night *v.* day) from the total area encompassed by the interpolated positions using the minimum convex polygon method [R function `calc_mcp(aspace)`; <http://cran.r-project.org/packages/aspace/index.html>]. This method calculates the minimum area polygon

that will encompass a set of co-ordinates (Burgman & Fox, 2003) and has been frequently used to define areas occupied by fishes (Collins *et al.*, 2007; Thibault *et al.*, 2007; Abecasis & Erzini, 2008).

The effect of environmental characteristics and L_T on (1) absolute groundspeed, (2) downstream ground speed and (3) areal range was determined using generalized linear mixed-effects modelling (Hedger *et al.*, 2009; Martin *et al.*, 2009). The R function `glmmPQL(MASS)` (<http://cran.r-project.org/packages/MASS/index.html>) was used. A Poisson family was used for absolute ground speed and areal range; a Gaussian family was used for downstream ground speed. The individual fish was used as a random effect. Fixed effects for ground speed models were: (1) diel period (night *v.* day), (2) tidal phase (ebb *v.* flood); (3) water temperature, (4) cloud cover index and (5) L_T . Fixed effects for the areal range model were identical except that tidal phase was omitted (tidal phase was at a finer temporal scale than that of areal range). Given that nocturnal effects were shown to be dominant, mixed models were also fitted using data from night-time alone. Fixed effects in these models were the same as those in the models incorporating diel period, with two differences. First, diel period was replaced by nocturnal period: early to late evening (sunset to <2300 hours) *v.* late evening and morning (≥ 2300 hours to sunrise). This delineation was determined from preliminary analysis of the data. Second, lunar illumination was added as a fixed effect.

Finally, the effect of diel period on habitat use for all fish detected within the estuary ($n = 32$) was established. Two-dimensional kernel density estimation was used to predict patterns of habitat use within the estuary from the detections received at the hydrophones [R function, `kde2d(MASS)` (<http://cran.r-project.org/packages/MASS/index.html>) bandwidth = 1000 m], separately for night and day, with the detections from each fish weighted so that each fish had equal weight on the estimate. The mean water column depth of each fish per diel period was then determined, and the means of these for each diel period were compared using a Mann–Whitney U -test.

RESULTS

PATTERNS OF DETECTIONS

The mean time range that each fish was detected in 2006 (mean = 24.7 days; range = 7.5–55.5 days) was less than that of 2007 (mean = 53.7 days; range = 2.4–107.6 days). Given that the estimated life span of the transmitters was in the order of 100 days, and that there was no indication of the fish leaving the study area, it is probable that transmitters in 2006 were failing prematurely.

Fish were detected across the system: river ($n = 12$), delta ($n = 25$), estuary ($n = 32$) and bay ($n = 7$). Ignoring the first day of detection, a total of 154 626 signals were detected (mean = 3514, range = 2–3086). There were more nocturnal than daytime detections throughout the system: in total, 75.7% of all detections occurred during night. For every part of the system, the diel distribution of detections was significantly different to that which would have been expected if there had been no diel effect (χ^2 test, d.f. = 1, $P < 0.001$; Fig. 2). Highest detection frequencies occurred at 2200–2300 hours, and lowest detection frequencies occurred at 1400–1500 hours.

Although diel period was the most evident influence on detection frequency within the estuary (one-third of the 32 fish detected within the estuary were not detected during daytime), variation in detection frequency occurred over time-scales of greater than a day. Periods of extended absence of detection existed: for example, five fish went for periods of greater than a week without being detected. The L_T had no effect on the nocturnal detection rate ($r_s = -0.02$, $n = 32$, $P > 0.05$).

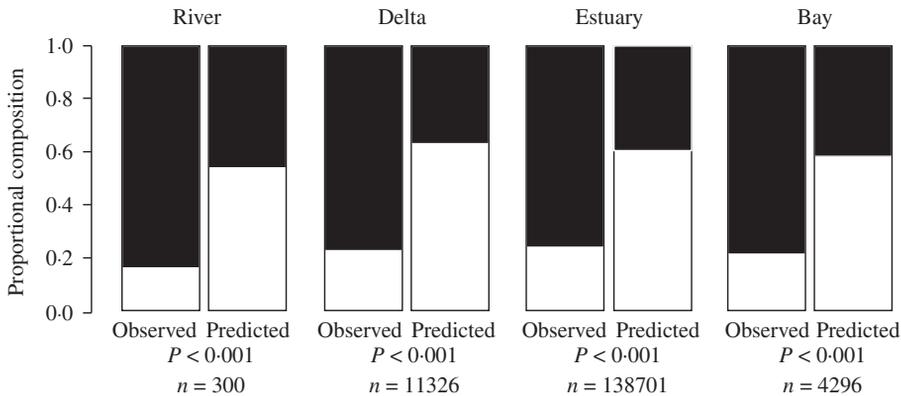


FIG. 2. Detection rate according to diel period. Detections in each region are compartmentalized into proportion of detections occurring during night (■) and during day (□). Predicted proportions have been determined by compartmentalizing the observed number of detections in each region according to the proportional composition of night and day when each *Anguilla rostrata* was present in each region. The number of detections in each region is shown below each bar. Detections occurring on the day of release have been removed.

MOVEMENTS WITHIN THE RIVER AND DELTA

Of the 35 *A. rostrata* released in the river, five were not detected by the hydrophone array (suggesting transmitter failure, death of the fish within the river at a location distant from a hydrophone or upstream movement within the river) and one fish showed a detection pattern suggesting it had died (Table I). Of the 29 remaining fish, 17 were detected in the estuary with three of these being detected in the bay. Three fish reaching the estuary later returned to the river or river delta. The non-vagrant fish remaining in the river or delta showed a variety of detection patterns. Some fish were only detected at the hydrophone moored at the release site in 2007, but there were periods of non-detection lasting for several days, which may have been caused by fish temporarily migrating upstream or downstream from the release point. Other *A. rostrata* were detected further downstream within the river or within the delta, sometimes returning to the release point in the upper river. The vagrant fish varied greatly in the time they took to reach the estuary, with a mean river and delta residence time of 14.6 days (range = 0.6–93.5 days) representing a mean downstream ground speed of 5.5 cm s^{-1} (range = $0.2\text{--}38.0 \text{ cm s}^{-1}$).

Discharge at the time of release and L_T had no significant effect on the probability of fish being vagrants in the logistic regression model. For the vagrant fish, discharge and L_T had no effect on the residence time within the river and delta in the stepwise logistic regression model when allowing for interaction between the predictors. A purely additive model, however, showed that residence time decreased with an increase in discharge (F -test, d.f. = 1,15, $P < 0.05$; Fig. 3). Fish with final detections in the bay were longer than those with final detections in the estuary, which in turn were longer than those with final detections in the river (Fig. 3), but the difference in L_T was not statistically significant (F -test, d.f. = 2,27, $P > 0.05$).

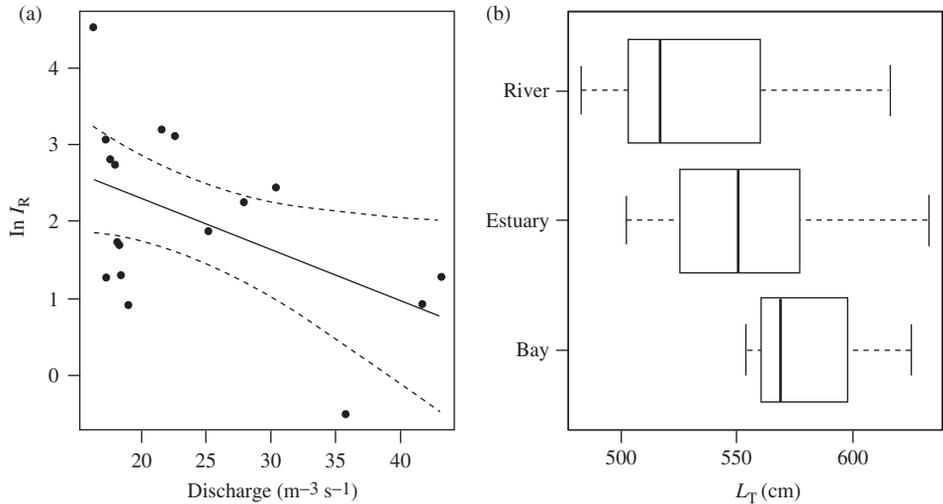


FIG. 3. River release: (a) effect of discharge on residence time (I_R) within the river and delta and (b) effect of total length (L_T) on final destination (I, median; whiskers, all observations within $1.5 \times$ the interquartile range). (a) The curve was fitted by: $\ln y = 3.63 - 0.066 \times x$ ($n = 17$, $r^2 = 0.24$, $P < 0.05$).

MOVEMENTS WITHIN THE ESTUARY AND BAY

No significant difference was found in the mean interpolated fish ground speeds between the first week of release (mean = 4.3 cm s^{-1}) and subsequent weeks (mean = 3.5 cm s^{-1} ; Mann–Whitney U -test, $n = 14$, $P > 0.05$; one fish was not detected in the first week), suggesting that fish had recovered rapidly from their tagging and that results were not biased by the presence of a long period of recovery.

Of the 15 *A. rostrata* released in the estuary, 10 were non-vagrant, remaining within the estuary, two were detected within the delta and three were detected within the bay (Table I). No significant difference existed in L_T between non-vagrant and vagrant fish (Mann–Whitney U -test, $n = 15$, $P > 0.05$). A wide range of behaviour was apparent. Fish released at the same time, and thus experiencing the same set of initial environmental conditions, moved in different directions. For example, of the 10 fish released in the lower estuary on 30 July 2006, six moved downstream (two entering the inner bay) and four moved upstream. Despite this variation, clear patterns of detections, movements and environmental influences on these patterns were evident.

The generalized linear mixed-effects model showed clear influences on movements within the estuary (Table II). Ground speed was faster during the night (mean = 6.3 cm s^{-1}) than during the day (mean = 1.3 cm s^{-1}), and was positively related to water temperature. Most longitudinal movements occurred during nocturnal hours. Fish tended to move upstream in the evening from 1700 to 2300 hours (mean = 1.8 cm s^{-1} in an upstream direction) and downstream in the late evening and early morning from 2300 to 0700 hours (mean = 2.8 cm s^{-1} in a downstream direction; Fig. 4). Relatively little upstream or downstream movement was detected from 0700 to 1700 hours. Tidal effects were also apparent, with fish tending to move upstream during flood tides and downstream during ebb tides, but these effects were weaker

TABLE II. Final mixed-effects models for movements within the estuary. Categorical variables are: diel period (night *v.* day); tidal phase (ebb *v.* flood); nocturnal period [early to late evening (sunset to <2300 hours) *v.* late evening and morning (≥ 2300 hours to sunrise)] and cloud cover index

Response variable	Initial predictor variables	Retained predictor variables (type or relationship) (<i>P</i> -values)
Movements during day and night		
Absolute ground speed	Diel period Tidal phase Water temperature Cloud cover index L_T	Diel period (night; +ve) (<0.001) Water temperature (+ve) (<0.001)
Downstream ground speed	Diel period Tidal phase Water temperature Cloud cover index L_T	Night (+ve) (<0.001) Ebb (+ve) (<0.001)
Areal range	Diel period Water temperature Cloud cover index L_T	Night (+ve) (<0.001) Water temperature (+ve) (<0.001)
Movements during night		
Absolute ground speed	Nocturnal period Tidal phase Water temperature Cloud cover index Lunar illumination L_T	Nocturnal period (evening; +ve) (<0.001) Water temperature
Downstream ground speed	Nocturnal period Tidal phase Water temperature Cloud cover index Lunar illumination L_T	Nocturnal period (late evening and morning; +ve) (<0.001) Tidal phase (ebb; +ve) (<0.001) L_T (+ve) (<0.01)
Areal range	Water temperature Cloud cover index Lunar illumination L_T	Lunar illumination (-ve) (<0.01) Water temperature (+ve) (<0.01)

L_T , total length.

than those for the effect of evening *v.* morning. Fish occupied a greater areal range during the night (mean = 817 m²) than during day (mean = 80 m²), and the areal range increased with an increase in water temperature. L_T had no effect other than a significantly positive effect for downstream ground speed during the night. Lunar illumination had no effect other than for areal range during the night.

Anguilla rostrata were detected throughout the estuary during night, particularly along the northern shore (Fig. 5). Greatest detection rates during day occurred in the

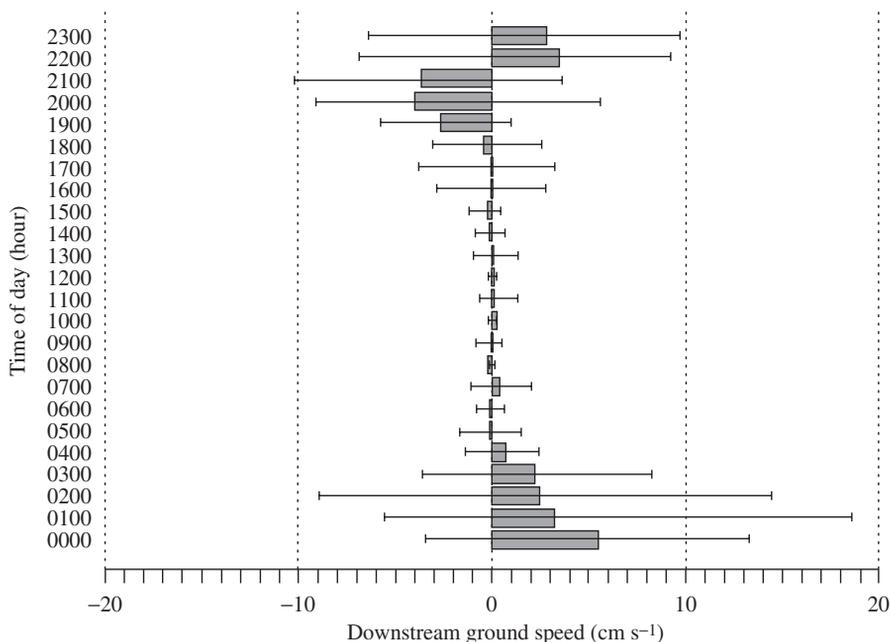


FIG. 4. Mean \pm s.d. downstream ground speed within the estuary.

more downstream part of the estuary, particularly at the trench on the northern shore separating the estuary from the inner bay. The mean depth of the part of the estuary occupied during night-time (mean = 4.33 m) was significantly less than that occupied during daytime (mean = 7.37 m; Mann-Whitney U -test, $n = 32$, $P < 0.01$). Fish showed a range of longitudinal movements (Fig. 6). Of the 32 fish detected in the estuary, 12 were mostly maintaining positions in distinct home ranges in the east during the day, to move longitudinally upstream and then downstream within the estuary during night [Fig. 6(a)–(f)]. The average distance travelled longitudinally along the estuary between night and daytime was 456 m. Eight fish were only detected within the upper estuary (mostly at night) and were not detected migrating to the deeper lower estuary [Fig. 6(g), (h)]. The remainder showed a variety of patterns intermediate between these two.

In total, six fish were detected within the bay (three from the river release and three from the estuary release). All movements between the estuary and the inner bay occurred at night. Four of the fish entering the inner bay were only observed in the south-western inner bay, near to the mouth of the estuary (mean distance into the bay = 976 m, range = 696–1364 m). Detections from two of these ceased almost immediately on entering; the other two returned to the estuary after a short time (*c.* 1 h and *c.* 1 day). In contrast, two fish moved far into the bay. One of these migrated slowly to the south-west of the sand wedge (maximum distance into the bay = 7642 m). The other was detected on the eastern side of the sand wedge, suggesting that it had migrated into the outer bay at high tide (maximum distance into the bay = 8940 m). Neither of these was detected in the linear array in the outer bay and final detections occurred in the inner bay. Mean ground speeds were

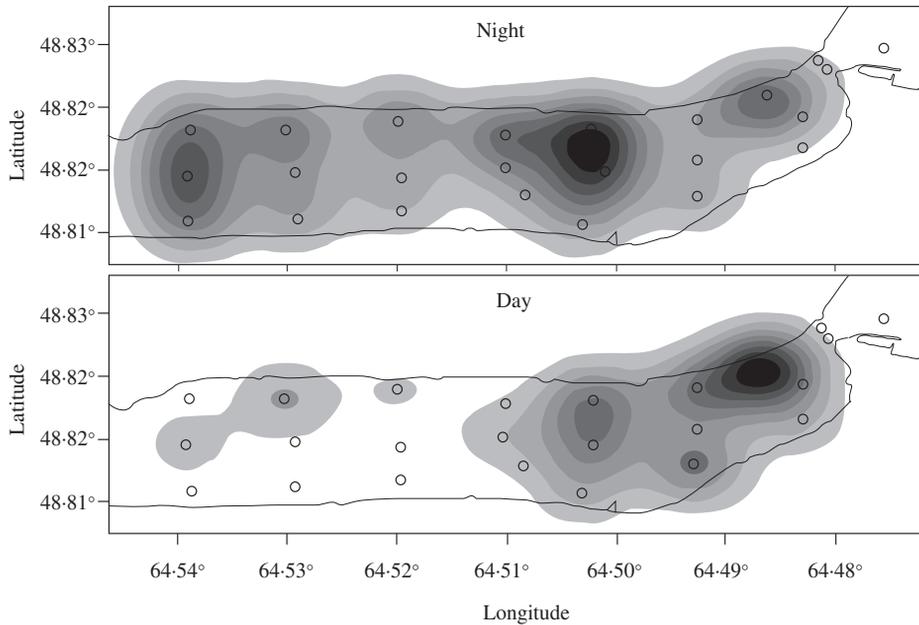


FIG. 5. Spatial distributions of detections within the estuary estimated through two-dimensional kernel estimation. The grey-scale varies from □ (lowest density) to ■ (highest density). Kernel estimation was not used for the inner bay because there were too few detections.

faster in the bay (mean = 17.0 cm s^{-1} , range = $3.9\text{--}25.1 \text{ cm s}^{-1}$, $n = 6$) than in the estuary (mean = 7.0 cm s^{-1} , range = $3.6\text{--}13.1 \text{ cm s}^{-1}$, $n = 6$; Mann–Whitney U -test, $n = 6$, $P < 0.05$). Only one fish had a slower ground speed in the bay than in the estuary. This fish, which migrated to the south-west of the sand wedge, had an initial ground speed within the bay comparable to that within the estuary, but dramatically slowed as it approached its destination.

DISCUSSION

Acoustic telemetry was able to resolve patterns of *A. rostrata* movement at both large and small spatial and temporal scales. Approximately half of the fish released in the river swam to the estuary. In contrast, relatively few fish swam from the estuary to the river or bay. Fish activity was predominantly nocturnal. Within the estuary, fish swam faster and occupied a greater areal range at night and when waters were warm, and fish swam upstream during evening and downstream during morning. *Anguilla rostrata* also appeared to be utilizing the tides, with fish tending to move upstream on flood tides and downstream on ebb tides. A range of patterns of habitat use within the estuary was found: some fish occupied deeper downstream parts of the estuary during day and the shallower upper estuary during night, and others remained in the upper estuary during both night and day, while other fish showed patterns intermediate between these two.

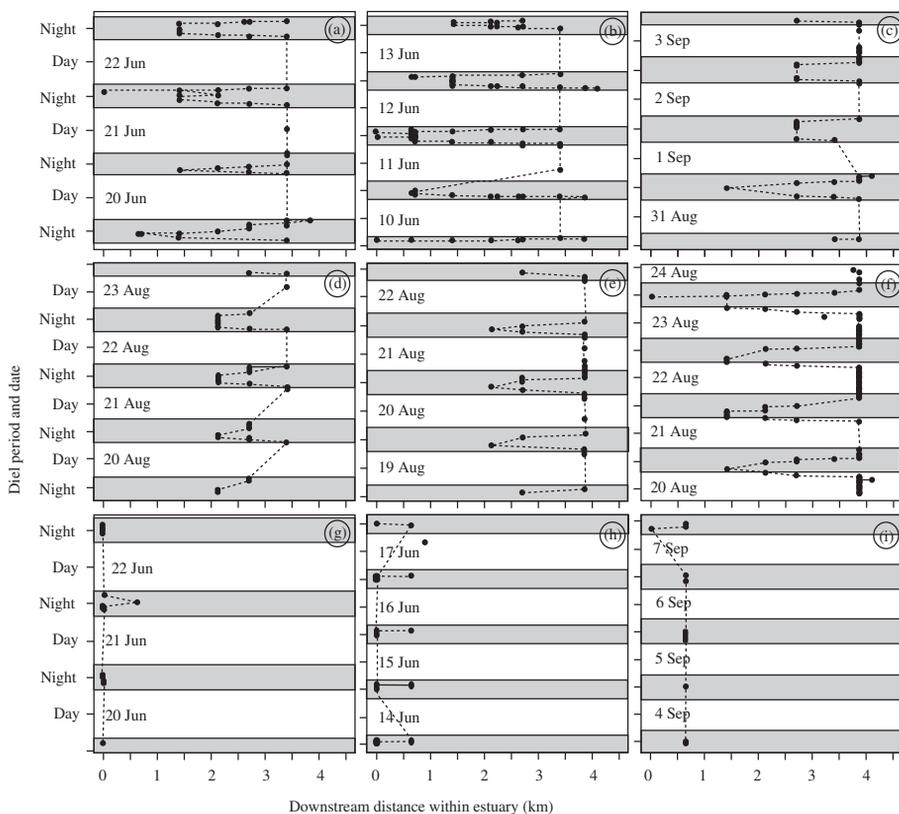


FIG. 6. Estuarine diel longitudinal movement of (a)–(i) selected *Anguilla rostrata*. Detections as a function of distance from the most upstream row of hydrophones positioned within the estuary are shown (●). Dashed lines joining the detections have been added for clarity. Time periods coloured (□) correspond to night.

PRINCIPAL CHARACTERISTICS OF MOVEMENTS

Large-scale detection patterns suggested that the estuary was the optimal summer habitat. Half the river-released *A. rostrata* swam to the estuary, and most estuary-released fish remained there throughout the summer. Movements to and residence within the estuary were probably for the purpose of feeding: in an adjacent river-estuary system (St Jean River and Estuary), Thibault *et al.* (2007) found that 87% of estuarine resident yellow *A. rostrata* contained prey items, in comparison with 6% in the river and 27% in a connected fluvial lake, which suggests that the estuarine environment may be relatively food-rich. Not all river-released fish migrated to the estuary, suggesting that although the estuary may have been optimal summer habitat, the river was still a viable habitat for summer survival. The decision for vacating the river or remaining there was not influenced by L_T ; hence, it is suggested that future studies should ideally include data on physiology of the fish rather than simple morphological measurements to ascertain if this may explain the reason for vacating or residing in riverine habitats. The present study terminated in the autumn; hence, it was not possible to test the hypothesis that fish return from estuaries to upstream

river habitats for overwintering in cold temperate climates [*e.g.* studies based in Nova Scotia, Canada, by Medcof (1969) and Jessop (1987)].

The large-scale movement of river-released *A. rostrata* from the river to the estuary appeared to be influenced by river discharge. Several studies have shown discharge effects on migrating silver *A. anguilla* (Vøllestad *et al.*, 1986; Behrmann-Godel & Eckmann, 2003; Cullen & McCarthy, 2003; Durif & Elie, 2008). The present study shows that this pattern may also exist at an earlier non-migrating life stage (yellow-stage) within *A. rostrata*. In the present study, discharge may have affected the speed of fish movement to the estuary either (1) by directly affecting the fish through drag or (2) through decreasing the salinity in the upper estuary, aiding acclimation to the estuarine environment [as suggested by Thibault *et al.* (2007) for an adjacent river–estuary system].

Diel patterns of detection showed that *A. rostrata* activity within the water column was predominantly nocturnal, similar to the pattern identified by Thibault *et al.* (2007) for an adjacent river–estuary system. The diel pattern observed in the present study is indicative of fish hiding in the substratum during the day and moving into the water column during the night for feeding. Glova & Jellyman (2000) found a positive size-effect on nocturnal detection rates, and hypothesized that small anguillid eels would spend more time in the substratum at night because their small size would enable them to feed in interstitial spaces in the substratum. The L_T , however, did not affect nocturnal detection rates in the present study; that is, smaller fish also moved from the substratum into the water column at night. Fish detected in the estuary were large (mean = 567 mm, range = 502–779 mm) in comparison with those in the study of Glova & Jellyman (2000) (range = <100–299 mm); hence, it is possible that all fish within the study were too large to feed within the interstitial spaces during night. Proving this assertion, however, would require visual observation of the fish activity, which is better suited to laboratory study. Although activity was predominantly nocturnal, some fish within the estuary remained undetected for periods of several days. Given the high level of coverage by the hydrophones, this suggests that some fish were not emerging from the substratum every night; hence, it is possible that fish were not feeding every night, concurring with the inferences of Jellyman (1989) and Jellyman & Sykes (2003).

Movements within the estuary suggest nocturnal foraging, with utilization of the tides to aid movements, and with an increase in swimming speed when waters were warm. Fish moved further and occupied a greater areal range at night, agreeing with the literature on yellow-stage *A. anguilla* (Aoyama *et al.*, 2002) and yellow-stage *A. rostrata* (Thibault *et al.*, 2007). There was some evidence of anguillid eels exploiting tides, with a propensity to upstream and downstream movement on the respective flood and ebb tides. This is consistent with selective tidal-stream transport (STST) but this cannot be proven in the absence of knowledge of fish depth within the water column. Alternatively, there may have been some passive displacement of fish in the direction of the tidal flow. Fish swam faster and covered a larger area when waters were warm, a pattern that concurs with that of Baras *et al.* (1998) who found an increase in activity in yellow-stage *A. anguilla* at temperatures $>16^\circ\text{C}$. Inconsistent results were found for lunar effects with reduced areal ranges under high lunar illumination, but no effect identified on absolute ground speed. The literature has shown a mixed pattern with Lamothe *et al.* (2000) identifying homing during the new moon and Baras *et al.* (1998) finding higher activity under full moon. In the

present study, the effect of lunar illumination on areal range was bordering on being only marginally significant, and it is possible that this was a spurious result. Cloud cover also had no effect, suggesting that it is the large fluctuation in light intensity between night and day, rather than small variations, that determines the choice of swimming within the water column or remaining within the substratum.

The *A. rostrata* population utilized the entire estuary, but different foraging patterns were evident. First, *c.* 33% of the fish showed a consistent pattern of daily longitudinal movements, being detected in the deeper, more downstream part of the estuary during day, swimming towards the upper estuary during evening and exploiting shallower upstream waters at night, before returning to the downstream part of the estuary during morning. These fish moved several kilometres per night. It is hypothesized that these fish selected the downstream waters during day because they offered a greater ability for sheltering, being deeper and therefore darker, and migrated upstream at night for nocturnal feeding. More information on the relative food supply in the upstream and downstream parts of the estuary is required to confirm this hypothesis. Second, *c.* 25% of fish remained in the upper estuary; hence, it is inferred that they burrowed into the substratum rather than moved downstream. Finally, the other fish showed patterns intermediate between these two. It thus appears that fish within the same population may individually show a range of foraging behaviours. The L_T may determine the extent of downstream movement within the water body and hence foraging tactic, but greater sample sizes are required to test this hypothesis.

FIXED ARRAY ACOUSTIC TELEMETRY AND IMPLICATIONS FOR MANAGEMENT

Fixed array acoustic telemetry was shown to be an effective method for determining patterns of *A. rostrata* movement. The advantage of using a fixed array over using mobile tracking was that the continuous coverage provided by the array meant that even the absence of detections at hydrophones in the array provided useful information. The absence of detections at a hydrophone at any given time showed that the fish was definitively not in the water column near to that location at that time. In contrast, with mobile tracking, it is only practicable to continuously cover relatively small areas; hence, there would be relatively little information on where the fish was present, and much less information on where the fish was specifically absent. The fixed array, for example, showed that there were occasions when fish remained within the substratum for several days (being detected nowhere). It would have been very difficult to identify this using mobile tracking, where an absence of detection could be attributed to the limited coverage provided by the sampling. An additional advantage of using a fixed array was that the lack of change in the spatial and temporal configuration of the fixed array minimized bias. With mobile tracking, unless the tracking is done in a grid format, there may be a spatial or temporal bias in detection rates, which may cause respective biases in estimates of areal ranges (Thibault *et al.*, 2007). Finally, fixed arrays may be less prone to bias caused by differences in fish ground speed. Mobile tracking has been shown to be less effective than fixed arrays for monitoring a rapidly moving fish species (Grothues & Able, 2007). Thus, a bias may exist within a population for decreased effectiveness of mobile tracking for individuals that are moving rapidly.

The acoustic telemetry configuration used in this study did have two limitations for application to anguillid eels. First, the extinction coefficient of transmitted signals may be greater than that under optimal conditions if fish is moving along the bottom of the water body, potentially reducing coverage. It is therefore suggested that the density of the array may need to be greater for successful use with anguillid eels than with fishes that spend more time near to the surface. Second, for anguillid eels, which have a tendency to move to the bottom of the water column during the day, use of a tag that detects depth and the actual temperature experienced by the fish is advised. A tidal effect was seen, but it was not possible to confirm if STST was occurring, rather than passive displacement or negative rheotaxis, because there was no information on the depth of the fish. That is, there was no way to determine whether fish were descending to the bottom of the water column when tides were in a non-favourable direction. Similarly, although the long-term trend in spatially integrated estuarine temperatures may have been predicted with reasonable accuracy, the lower estuary was thermally stratified; hence, a small vertical movement of fish could have caused a relatively large variation in the temperatures experienced by that fish. It is therefore suggested that future acoustic telemetry studies of anguillid eels should have dense fixed arrays and should use transmitters equipped with depth and temperature gauges.

It appears evident that although the entire estuary may be considered as critical foraging habitat for the yellow-stage *A. rostrata*, those areas that serve to congregate fish in daytime refuges merit particular conservation efforts. In the present study, a major daytime congregation area occurred in the deeper waters of a channel located towards the mouth of the estuary. In many systems, such channels are periodically dredged for the purpose of navigation. Such activities during summer could have a major effect on *A. rostrata* populations by disrupting the strong diel behaviour patterns associated with foraging. Anguillid eel stocks are collapsing, but there is a tendency to only monitor populations within riverine environments, whereas it may be necessary to monitor what is happening in estuaries [as proposed by Thibault *et al.* (2007)]. Increasingly, freshwater and marine protected areas (FPA and MPA) are being used for conservation of anguillid eel stocks (Cucherousset *et al.*, 2007), and knowledge of the distribution patterns of anguillid eels would be useful when implementing these. Fixed array acoustic telemetry is the optimal technique for doing this.

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