ECOLOGY OF
FRESHWATER FISH

Large-scale, seasonal habitat use and movements of yellow American eels in the St. Lawrence River revealed by acoustic telemetry

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Accepted for publication January 18, 2014

Abstract – Large-scale habitat use and movements of yellow American eels (*Anguilla rostrata*) from the St. Lawrence River were examined using acoustic telemetry from early summer to late fall in 2010 and 2011. Sixty-seven eels were tagged, and their passage or presence was recorded using fixed acoustic arrays covering a 400 km distance along the St. Lawrence River and Estuary. Sixty-four per cent of the 67 tagged eels were detected. Most eels were detected at only one array; the closest to their release location and at several occasions during the tracking period, suggesting a high proportion of freshwater residency in the upstream part of the St. Lawrence River. Downstream movements towards the brackish estuary (63–418 km distance) were demonstrated for 16.4% of the eels, particularly for those caught at the most downstream site that is close to the brackish estuary. Our results strongly suggest a lower activity of freshwater resident yellow eels during summer, a behaviour that may be related to day length, which defines time available for their nocturnal foraging. Indeed, yellow eels were detected primarily at night; no effect of moon phase was revealed. Movements in the vicinity of arrays (up to 116 km in the fluvial estuary) were suggested and smaller-scale movements within Lac St. Louis were demonstrated, highlighting a yellow-eel home range far more extensive than previously reported in smaller systems. Evidence for within-season homing and site fidelity is also reported.

Key words: Anguilla; juveniles; behaviour; ecology; telemetry

Introduction

The American eel (*Anguilla rostrata*) has recently been designated as a threatened species in Canada (COSEWIC 2012). Dramatic declines of the recruits (young, yellow-stage eels) and maturing adults (silver-stage) were particularly observed in Lake Ontario and in upper St. Lawrence River areas. American eel recruitment to Ontario waters has declined by approximately 97% since the early 1980s, and yellow eel abundance indices show similar declines over the same timeframe in Lake Ontario (Mathers & Pratt 2011). In the upper St. Lawrence, both bottom trawling and quantitative electrofishing survey suggested that yellow eels currently are at a very low abundance in this area (Mathers & Pratt 2011). Commercial landings for yellow eels in Québec (from Lac St. François to the St. Lawrence estuary) were around 30 t per year on average for the period 1990–2006 (Cairns et al. 2008). In addition to fishing, eels face

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Ecology of FRESHWATER FISH

doi: 10.1111/eff.12129

many important threats across their range: dams (habitat fragmentation, turbine mortality), habitat degradation, chemical and biological contamination, and very recently an introduced parasite (COSEWIC 2012). To determine the relative importance of each threat requires an understanding of habitat use and movements between habitats. However, the American eel is a facultative catadromous species characterised by a relatively complex life cycle (Daverat et al. 2006; Jessop 2010). Several parts of its life cycle remain largely unknown, particularly the growth-phase stage in continental waters. Yellow eels reside in fresh and brackish water of the St. Lawrence system for up to 32 years (Tremblay 2009) before leaving the system to reproduce at sea. Habitat use and the seasonal and diel patterns of activity of yellow eels in the St. Lawrence River and estuary are poorly documented. Yet, the St. Lawrence River and Estuary system represents the largest system (>1200 km in length from Lake Ontario to the Maritime estuary) where eels are found in its entire range and is the principal source of old, large and fecund spawners (Jessop 2010). Such lack of knowledge represents a serious impediment to any meaningful management efforts directed at conserving the species.

The purpose of this study is to clarify two aspects of the ecology of yellow-stage American eels inhabiting the St. Lawrence system. These include large-scale activity patterns and habitat switching and diel and seasonal patterns of activity. Concerning the first aspect, several patterns of activity and habitat switching consisting of either residency in one habitat (fresh, brackish or marine) or movements between habitats have been demonstrated for yellow-stage anguillid eels (Daverat et al. 2006; Thibault et al. 2007b; Jessop et al. 2008). These patterns have consequences for several important processes, including growth that appears greater in estuarine habitats than in fresh waters (Helfman et al. 1987; Morrison et al. 2003; Cairns et al. 2004, 2009; Jessop et al. 2004, 2008; Daverat et al. 2012). Habitat use and movements between habitats were mainly inferred by Sr:Ca analysis in otoliths (e.g. Jessop et al. 2008). However, a limitation of otolith analysis is that seasonal migration between habitats can be difficult to detect (Morrison & Secor 2003; Thibault et al. 2007b). Fixed array acoustic telemetry has been shown to be an effective method for determining patterns of American eel movements (Thibault et al. 2007a; Hedger et al. 2010). Thibault et al. (2007a) provided the first direct observation of yellow eels leaving fresh water to exploit the brackish-water environment (St. Jean River watershed, Gaspé, QC, Canada). In an adjacent river-estuary (York River and Gaspé Bay), Hedger et al. (2010) found that approximately half of the eels caught and tagged in the river swam to the estuary, 15 km downstream, with some fish returning to the river before the end of the survey. These movements were very rapid: eels used tidal currents to move several kilometers per night. In their review, Jessop et al. (2008) found a positive relationship between the percentage of freshwater-resident American eels and the distance of sampling site upstream from the river mouth in Canada, with more than 90% of exclusively freshwater residence beyond 80 km upstream. The daily and seasonal patterns of activity of yellow eels are principally characterised by nocturnal activity. Such activity has been observed for American eels (Dutil et al. 1988; Thibault et al. 2007a; Hedger et al. 2010) as was previously observed for other anguillid eel species (e.g. Aoyama et al. 2002).

The first objective of this study was thus to document the large-scale habitat use of yellow-stage eels inhabiting the fresh waters of the St. Lawrence system during the ice-free season and thus to verify whether habitat-switching varies along the longitudinal axis of the river, as proposed by Jessop et al. (2008). A second objective was to examine the diel and seasonal pattern of yellow eel's activity. We particularly searched for evidence that activity increased with declining day length during the ice-free season. Small scale movements were also documented and, although not an initial goal of the study, we analysed these movements for any evidence of site fidelity or in season homing.

Materials and methods

Study location

The St. Lawrence River is one of the largest rivers in North America with a drainage area of 1.6 million km². The river system extends 1600 km from the outlet of Lake Ontario (the most downstream of the five Great Lakes) to the Atlantic Ocean and comprises three fluvial lakes (Lacs St. François, St. Louis, and St. Pierre) connected to lotic sections, a freshwater estuary (Fluvial), a brackish estuary (Upper, also referred to as the middle, estuary) and a maritime estuary (Lower) flowing into the Gulf of St. Lawrence (Fig. 1) (Therriault 1991). The fluvial section between Lac St. Louis and Lac St. Pierre includes over 100 islands, Montreal Island being the largest. The water is <6 m deep in most parts of the lakes of this river section, depths declining to 10–12 m in the primary channel. Flow is unidirectional (downstream) and waters from tributaries do not mix. The fluvial section is the most urbanised and industrial region. In particular, many dams were built between 1912 and 1971 to harness the hydroelectric potential of the 26-m drop between Lac

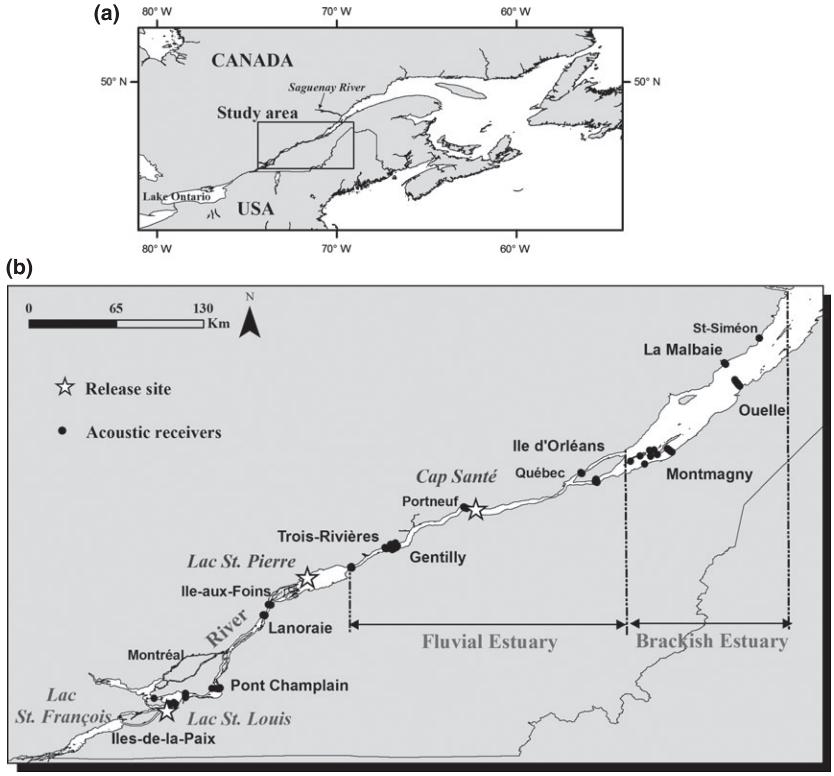


Fig. 1. Study area: (a) Location within Canada, (b) Acoustic arrays deployed in the St. Lawrence River and Estuary and release sites of tagged eels.

St. François and Lac St. Louis. The St. Lawrence Fluvial Estuary is 160 km long, 870 m–5 km wide and its main channel is generally 13–40 m deep. For the first 100 km (i.e. until Portneuf), freshwater flows downstream without current reversal. Between Portneuf and Québec, tidal influence increases gradually, causing current reversal at flood tide and mixing. The St. Lawrence brackish estuary begins at the eastern tip of Île d'Orléans and runs 150 km to the mouth of the Saguenay River. It is on average 17 km wide and harbors some 50 islands. There are three flow channels generally more than 10 m deep but depths >100 m occur in a trough about 50 km long at St. Siméon. Wetlands are a very important component of the St. Lawrence River fluvial ecosystem, comprising almost 30% of a 1-km-wide shoreline strip in the Fluvial Section and Fluvial Estuary (St. Lawrence Centre 1996). Macrophyte beds, which compose more than half of the wetlands are not evenly distributed along the St. Lawrence but are concentrated in lake areas with slower current. The surface area of marshes and swamps between Lac St. François and the beginning of the maritime estuary at approximately the Saguenay River (i.e. total distance of approximately 580 km) was estimated at 28,992 ha for 2000–2002 (Martin & Létourneau 2011). This is considered as preferred habitat for juvenile eels (Jellyman & Sykes 2003).

Eel tagging

During summers 2010 and 2011, a total of 67 yellow-phase eels were captured, tagged and released in the St. Lawrence (Fig. 1 and Table 1). In 2010, eels from Lac St. François and Lac St-Pierre/Gentilly (respectively 32 km upstream and 131/178 km downstream from the most upstream release site – Ile-de-la-Paix, see below, thereafter noted Fluvial lake – Km-32 and Fluvial Estuary – Km 131, Km 178) were caught by commercial fishermen with fyke nets. Eels caught in Lac St. François were displaced 32 km downstream to Lac St. Louis (Fluvial lake – Km 0) to avoid the Beauharnois Hydroelectric Power Station and the subsequent mortality due to potential passage through the turbines (Verreault & Dumont 2003). Eels caught at Lac St.Pierre and at Gentilly (Km 131–Km 178) were obtained from commercial fishermen fishing in both Gentilly and Lac St. Pierre, thus their exact origin (i.e. either Lac St. Pierre or Gentilly) could not be established. Therefore, eels from both locations were released at Lac St. Pierre (Fluvial Lake, Km 131). In 2011, eels from Lac St. Louis (Fluvial lake – Km 0) were caught by electrofishing, whereas eels from Cap Santé (Fluvial estuary – Km 232) were caught by traditional tidal weirs. Eels from Cap Santé were released at the same location, whereas most eels caught in Lac St. Louis where

Table 1. Tagging effort and acoustic recapture (detections) of yellow eels in the St. Lawrence River and Fluvial Estuary.

				Number of detected eels			
Period of tagging	Capture location	Release location	*N*	During 2010	During 2011	Total	Proportion of detected eels
26-Aug-10	Fluvial Lake -Km -32 - Lac St. François	Fluvial Lake - Km 0 - Lac St. Louis	14	0	4	4	28.6%
27-Aug-10	Fluvial Estuary - Km 131 & Km178 Lac St.Pierre/Gentilly	Fluvial Lake - Km 131 Lac St. Pierre	11	5	2†	6	54.5%
15-Jul-7-Sep 2011	Fluvial Estuary - Km 232 Cap Santé	Fluvial Estuary- Km 232 - Cap Santé	19		17	17	89.5%
21-22-Jun 2011	Fluvial Lake - Km 0 - Lac St. Louis (Iles de la Paix)	Fluvial Lake - Km 2 - Lac St. Louis	23		16	16	69.6%
Total			67	5	39	43	64.2%

N is the total number of tagged eels.
†One eel was detected both in 2010 and 2011.

Table 2. Morphological characteristic of yellow eels collected in the St. Lawrence and acoustically tagged.

	TL (mm)	Wf (g)	IC	OI	G (mm)	PF (mm)	PFI
Mean	811	1128	0.20	5.6	161	39	4.7
SD	72	371	0.04	1.0	16	5	0.5
Min	587	250	0.11	3.7	125	26	3.6
Max	940	1950	0.38	8.2	202	46	5.8
N	67	67	67	42	41	41	41

N is the total number of individuals, TL is the total length, Wf is the fresh weight, IC is the condition index, OI is the ocular index, G is the girth length, PF is the pectoral fin length, PFI is the pectoral fin index.

released 14 km upstream from their capture site (2 km upstream from the Lac St. Louis acoustic line), to record possible movements back to their capture site. We chose eels larger than 580 mm in total length for tagging (Table 2). Eels were determined as yellow eels according to coloration criteria of various body parts (Okamura et al. 2007 and personal observations), that is, with pectoral fins completely transparent or with a metallic hue at the base but without melanisation at the tip, green or gray dorsal coloration, yellow ventral coloration and no visible lateral line. Several morphometric measurements were also recorded to insure that eels were in the yellow stage: total length (TL), fresh body mass (Wf), left eye diameter (Dv: vertical and Dh: horizontal, to calculate an ocular index $OI = \pi \ /TL \times ((Dv + Dh)/4)\ ^2$ (Pankhurst 1982)), length of left pectoral fin (PF) (to calculate the pectoral fin index (PFI) = 100 × PF/TL). Fulton's condition factor (K) was calculated: $K = Wf/TL^3$ (Ricker 1975). All selected eels had phenotypic traits that were consistent with the two first immature stages described in the study described by McGrath et al. (2003) (TL: 537–1098 mm; Wf: 237–2833 g; G: 89–224 mm; OI: 2.8–11.2; PFI: 3.3–6.0, see Table 2 for morphological characteristic of the tagged eels).

Coded acoustic transmitters (frequency of 69 Hz) from Vemco (http://www.vemco.com) were used in this study: V9-2x (9 mm in diameter, 29 mm in total length, 2.9 g in water) with a nominal delay of 90s, 120s or 240s (life time of 147, 193 and 369 days respectively). The transmitter mass was <2% of W and did not exceed the maximum threshold suggested by Lucas & Baras (2000) and Thorstad et al. (2009). Eels were anaesthetised in a 40 $mg \cdot l^{-1}$ metomidate solution (Aquacalm) during ca. 4 min. The tags were surgically implanted in the abdominal cavity: a 30 mm incision was made in the posterior part of the abdomen, 10 mm in front of the anus. Following insertion of the acoustic transmitters, the incision was stitched with 1 or 2 synthetic suture points. All tagged eels were released within approximately 7 h following surgery (Fig. 1 and Table 1). In addition to acoustic transmitters, all eels were marked with individual PIT tags injected at the same time and location as acoustic tags. This PIT tagging allowed identification of tagged eels in case of capture by commercial fishermen along the St. Lawrence.

Acoustic lines

The passage or presence of acoustically tagged eels was recorded using fixed receiver lines composed of Vemco VR2 and VR2W acoustic receivers deployed along the St. Lawrence River and estuary, covering a river distance of 400 km (Fig. 1 and Table S1). In 2010, 39 receivers distributed along six lines were deployed about 2 m off the bottom from mid-August to early November (Table S1 and Fig. 1). Twenty-seven per cent of the width of the brackish estuary at La Malbaie-Ouelle (Km 418) was covered by receivers. In 2011, a total of 103 receivers distributed among 12 lines were deployed in the St. Lawrence River and Estuary from April-May to November (Table S1 and

Fig. 1). The length of the Ouelle line was increased in 2011, covering 44% of the width of the St. Lawrence Estuary. The mean distance between neighbouring receivers of a same line was 433 m in the river and 602 m in the estuary. The Montmagny line (Brackish Estuary, Km 354) included 10 receivers installed perpendicular to the shore. Seven additional receivers were installed upstream of this line for another study. For the same reason, 11 receivers were deployed within a 5 km area downstream of the Gentilly line (Fluvial Estuary, Km 178) which comprised five receivers. The range of detection for V9-2x was tested periodically and varied between 200 and 1000 m in the freshwater section and up to 1240 m in the brackish section. Sentinel tags (V9-2x with a nominal delay of 30 min) were also moored at each line during the whole survey in 2011 and tests for acoustic breaches were performed for lines covering the entire cross section of the river (i.e. all lines except Ouelle and La Malbaie arrays, Table S1) with a V13-1x (nominal delay of 60 s) immersed at 1 m depth and trolled by a drifting boat (engine off) for ca. 1600 m. The daily detection probability of sentinel tags varied from 0.5 to 1.0 for distances between 0 and 200 m and no acoustic breaches were detected at closed arrays.

Data analysis

The movement patterns of yellow eels in the St. Lawrence River and Estuary at a large scale (mean distance between arrays of 50 ± 20 km (SD)) and at a finer scale in the Lac St. Louis area (Fluvial Lake Km 0) were examined. At a large-scale, eels were classified into two main categories: sedentary and vagrant. Sedentary eels were fish showing no movements between arrays but repeatedly detected at one location (always the closest array to their release site, that is, Lac St. Louis/Île-de-la Paix arrays (Fluvial Lake Km 0 and Km 11), or the Trois-Rivières array (Fluvial Estuary Km 155) or the Portneuf array (Fluvial Estuary Km 232)). As Île-de-la-Paix and Lac St. Louis arrays were very close to each other compared with other arrays (8–14 km, Fig. 1), eels detected uniquely at these arrays were considered as sedentary eels, even though small-scale movements between these arrays were detected. Vagrant eels were eels detected by at least two more distantly-spaced arrays and thus showing large-scale movements between arrays such as in Hedger et al. (2010). Individual profiles of movement at a large scale were represented by plots showing the number of detections per day across the receiver arrays for the duration of the tracking season. Statistical relationships between individual behaviour and morphological measurements were examined using a Wilcoxon test for non-normal data. The statistical differences in proportion of observed behaviours according to location and years were evaluated using Chi square tests (χ^2). Number of eels recorded per receiver and array and number of detections per eel were calculated. The residency of fish within the detection range of an acoustic line, that is, the elapsed time between the earliest detection date and the latest detection date at an array, was calculated for each eel. Differences in residency around arrays were compared using the Wilcoxon signed-rank test. To assess the seasonal pattern of yellow eel activity, the interval (in days) between daily detections per eel was calculated for each month. The frequency and the number of detections per eel and per day were also calculated. The respective trends over the season were examined using Pearson correlations.

For vagrant eels, transit time and travel speed between arrays were calculated. The transit time corresponds to the time elapsed between the departure from an array, that is, the last detection at this array, and the arrival, that is, the first detection, at the successive downstream array. The travel speed was calculated from the transit time, considering a mean straight distance between mid-arrays and was expressed in km per day.

The diel pattern of detections (night vs. day) was determined for each eel. To determine whether there was a diel effect on detection rates within each array, the proportional composition was compared with the theoretical value expected if there was no preference for day or night (i.e. according to day length), using Chi-square tests. For arrays located in the tidal sections, the tidal pattern of vagrant eels was determined by matching acoustic detections with a tidal state or current direction determined from hourly water levels obtained from the Canadian Hydrological Service Environment website (www.wsc.ec.gc.ca) and from hourly current direction and speed predictions obtained from Fisheries and Oceans Canada models. The tidal cycle was divided in six periods of similar length for each location: beginning, mid and end of flood or ebb tide. The effect of moon phase on yellow-phase eel movement patterns was determined by matching detections with an index of lunar illumination (the proportion of the moon that was illuminated) obtained from the U.S. Naval Observatory (aa.usno.navy.mil/data/docs/MoonFraction.php).

Results

A total of 10,965 signals corresponding to codes of tagged yellow eels were recorded within the river and estuary (2586 signals in 2010 and 8379 signals in 2011). This corresponds to a total of 43 tagged yellow eels that were detected across the system, that is, 64.2% of the total number of tagged eels (25 eels in

2010 and 42 eels in 2011) (Table 1). A mean of 255 ± 476 detections per eel were recorded (range 2–2171), with no significant differences between the two years (W = 136, df = 13.3, $P > 0.1$). Significantly, more yellow eels tagged in 2011 were detected compared with eels tagged in 2010 (Table 1, 78.5% vs. 40.0%, $\chi^2 = 8.53$, df = 1, $P < 0.005$). For both years, the proportion of undetected eels did not differ according to the release location (2010: $\chi^2 = 0.82$, df = 1, $P > 0.1$, and 2011 $\chi^2 = 1.41$, df = 1, $P > 0.1$).

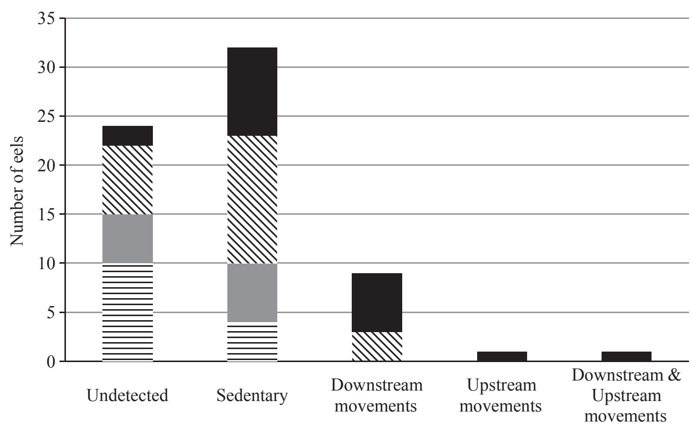
Large-scale movement patterns

The majority of detected eels were classified as sedentary, that is, exhibiting no large-scale movements (Fig. 2). Sedentary eels represented 74.4% of the detected eels (47.8% of the tagged eels), while vagrant eels (large-scale movements) represented 25.6% of the detected eels (16.4% of tagged eels) (Fig. 2 and Fig. 3). No significant differences in morphological traits were found between undetected eels, sedentary eels and vagrant eels (Table 3). Sedentary eels ($N = 32$) were recorded at Lac St. Louis (Fluvial Lake Km 0), Trois-Rivières (Fluvial Estuary Km 155) and Portneuf arrays (Fluvial Estuary Km 232) from early May to November 23 (end of the tracking period) (Fig. 4). Ninety-one per cent of the time, only one eel per day was recorded at each array (i.e. no peak of activity at any array). A maximum of 5 sedentary eels per array on one day was recorded at Portneuf (Fluvial Estuary Km 232), 3 at Lac St. Louis (Fluvial Lake Km 0) and 2 at Trois-Rivières (Fluvial Estuary Km 155). The proportion of sedentary eels among tagged eels was neither significantly different between years of the study ($\chi^2 = 1.09$, df = 1, $P > 0.1$) nor between release locations ($\chi^2 = 2.01$, df = 1, $P > 0.1$).

Vagrant eels ($N = 11$) travelled between approximately 63 and 418 km (ground distance, average of 200 km). Most of them showed unidirectional downstream movements to the brackish estuary ($N = 8$, Fig. 3, second panel) with no return observed during the tracking period. Most vagrant eels originated from the fluvial estuary (Cap Santé, Km 232) but 3 were from the Fluvial Lake Lac St. Louis (Km 0) and travelled to the estuary. Two eels moved from the Fluvial Lake Lac St. Louis (Km 0) to the Ouelle array (Brackish Estuary Km 418) in 116 days, representing a mean transit speed for both eels of 3.6 km·day^{-1}. The mean transit speed of eels that moved from Cap Santé (Fluvial Estuary Km 232) to Île d'Orléans array (Fluvial Estuary Km 307) was 9.5 ± 13.7 km·day^{-1} (range 1–39.2, $N = 7$). Six eels were recorded at the Île d'Orléans array (Fluvial Estuary Km 307) and at the Ouelle array (Brackish Estuary Km 418) a few weeks later. They travelled the 111 km between these two arrays at a mean transit speed of 4.1 ± 3.3 km·day^{-1} (range: 1.9–10.8). Two particular cases were observed: one eel showed a downstream movement to the brackish estuary followed by an upstream return to the fluvial estuary and one eel showed a unique upstream movement within the fluvial estuary after a residency of 41 days at the Portneuf array (Fluvial Estuary Km 232) (Fig. 3, lower panel).

Diel and seasonal pattern of activity

Sedentary eels were recorded at an array for up to 132 days (maximum observed at the Lac St. Louis array (Fluvial Lake Km 0). A high variability was



	Undetected	Sedentary	Downstream movements	Upstream movements	Downstream & Upstream movements
2011 Fluvial Estuary Km 232- Cap Santé	2	9	6	1	1
2011 Fluvial Lake Km 0- Lac St. Louis	7	13	3		
2010 Fluvial Lake Km 131 -Lac St. Pierre	5	6			
2010 Fluvial Lake Km 0- Lac St. Louis	10	4			

Fig. 2. Detection patterns of yellow eels determined by acoustic tracking in the St. Lawrence River and Estuary during summer and fall 2010 and 2011, according to their release site.

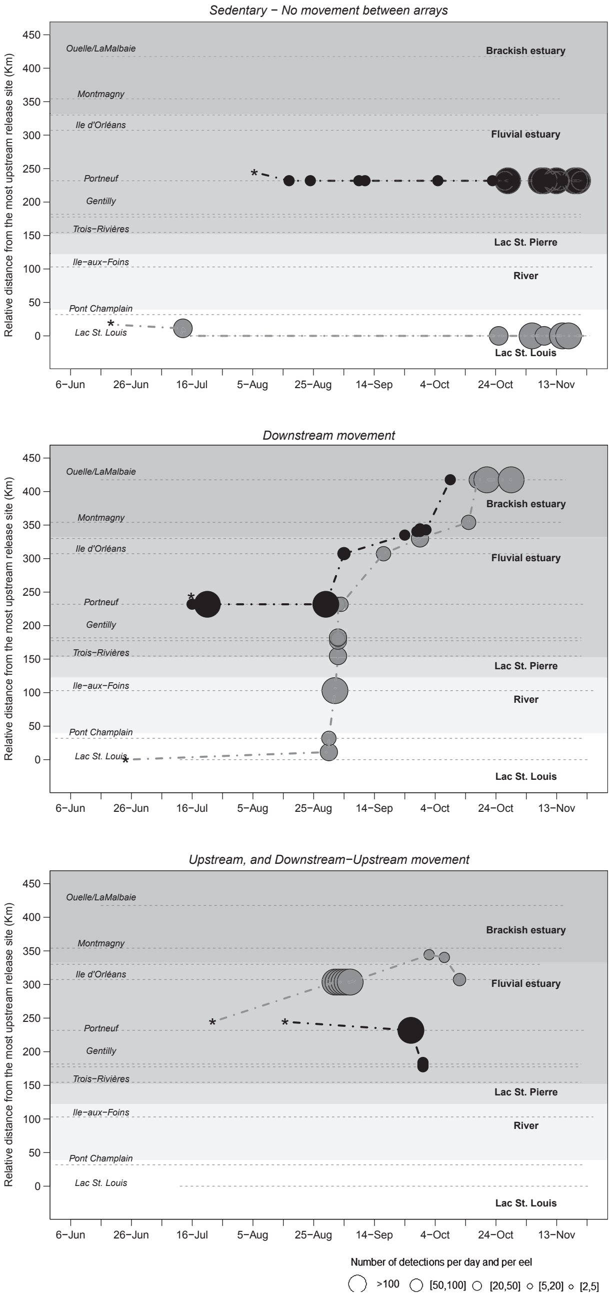


Fig. 3. Illustration of behavioural patterns of yellow-phase American eels, revealed by acoustic telemetry within the freshwater and brackish sections of the St. Lawrence estuary. Date and location of release are represented by an asterisk. Dotted lines represent acoustic arrays. Large-scale movements between arrays are reported for only 16.4% of the tagged eels (middle and bottom panels).

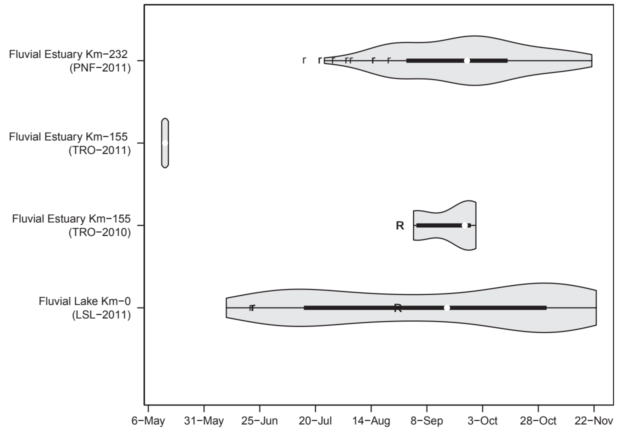


Fig. 4. Spatio-temporal distribution of detected sedentary yellow eels at acoustic arrays deployed in 2010 and 2011 in the St. Lawrence River and Estuary. LSL is Lac St. Louis array, PNF is Portneuf array and TRO is Trois-Rivières array. The letter 'R' indicates the date of release of the detected eels, capital letters are for eels tagged and released in 2010 and lowercases are for eels tagged and released in 2011. The plots include a marker for the median of the data and a box indicating the interquartile range. The shape of the violins shows the distributional characteristics of batches of data.

observed in individual residency. The median value of residency was 20.4 days, with 40% of the eels exhibiting a residency shorter than 1 day. The duration of residency around the Portneuf array (Fluvial Estuary Km 232) (median of 41.3 days) was significantly greater than that around the Trois-Rivières (Fluvial Estuary Km 155) and Lac St-Louis arrays (Fluvial Lake Km 0) (median of respectively 0.4 and 1.0 days) (Pairwise comparisons; Wilcoxon rank sum test, both $P < 0.05$) (Fig. 5). There was no significant relationship between residency recorded at an array and any of the morphological traits of eels (Pearson correlation, all $P > 0.05$). Eels were not recorded continuously at an array, but at a mean interval of 7.3 days (range: 1–119). A strong seasonal effect on the pattern of detection of sedentary eels at arrays was observed. The interval between detections per eel and per day decreased significantly over the season ($r^2 = -0.42$, $P < 0.001$), both at Portneuf (Fluvial Estuary Km 232) and Lac St. Louis array (Fluvial Lake Km 0) (Fig. 6, upper panel). Conversely, the number of detection per eel increased at the end of the season (Fig. 6, lower panel). This seasonal effect can also be seen in individual eel patterns (Fig. 3, first panel). Furthermore, sedentary eels were detected mainly at night. On average, 75.8% of the detections per eel were recorded at night (Fig. 7), which is significantly different from the expected value if there had been no diel effect (44.5% on average, $\chi^2 = 1475.2$, df = 1, $P < 0.0001$); location had no effect on this relationship (Pairwise comparisons; Wilcoxon rank sum test, both $P = 1$). It should be noted that there seems to be a large individual variability in the diel detection pattern of sedentary eels: some eels were mostly detected in daytime while others were exclusively detected at night (Fig. 7). No effect of moon phase on detection pattern was detected for sedentary eels (mean fraction value of 0.48 ± 0.27, ranging from 0.05 to 0.98, normal distribution).

Table 3. Comparison of morphological trait of yellow eels according to their status determined by acoustic telemetry.

	Undetected (U)	Sedentary (S)	Vagrant (V)	P (from pairwise comparisons between group levels with Bonferroni correction)		
				U-S	U-V	S-V
Total length (mm)	805 ± 89	811 ± 64	823 ± 58	>0.5	>0.5	>0.5
N	*24*	*32*	*11*			
Fresh body mass (g)	1082 ± 440	1140 ± 325	1195 ± 355	>0.5	>0.5	>0.1
N	*24*	*32*	*11*			
Condition index	0.19 ± 0.04	0.21 ± 0.05	0.21 ± 0.04	>0.5	>0.5	>0.5
N	*24*	*32*	*11*			
Ocular index	5.0 ± 0.5	5.8 ± 1.1	5.7 ± 1.1	>0.05	>0.1	>0.5
N	*9*	*23*	*10*			
Pectoral fin index	4.5 ± 0.4	4.7 ± 0.6	4.8 ± 0.3	>0.5	>0.1	>0.5
N	*8*	*23*	*10*			
Body girth (mm)	167 ± 22	156 ± 12	166 ± 10	>0.1	>0.5	>0.1
N	*9*	*23*	*10*			

N is the total number of eels. Mean ± SD are indicated for each morphological trait.

Vagrant eels started to move downstream (i.e. were detected at the first downstream array) either immediately (min 7 h) or a few days after their release (25 days on average, 67 days maximum). They were detected in the brackish estuary (at Ouelle array, Km 418) during a restricted period between October 10 and October 29. The median value of their residency within the acoustic detection range of arrays was significantly lower than residency values for sedentary eels (16.8 min, range 0–44.5 days, W = 1201, df = 44.1, $P < 0.0001$). Vagrant eels concentrated their movements at night during the ebb tide. Upon arrival at arrays, 73% of detections were recorded at night and 92.3% were recorded during the ebbing tide at estuarine arrays. Diel cycle and tidal cycle combined indicated that most detections of vagrant eels upon arrival at estuarine arrays were recorded at night during ebb tide (61.5%), while no eels were detected in daytime during the flood tide.

Small-scale movements and evidence for site fidelity and homing

Small-scale movements (<19 km) were observed in Lac St. Louis. Of the 17 tagged sedentary yellow eels from Lac St. Louis, 8 showed movements between the Lac St. Louis array and receivers of Îles-de-la-Paix (Fig. 5, upper panel) while six moved between receivers of Îles-de-la-Paix (Fig. 5 middle panel). The minimal distance between the two furthest locations (or between the release site and the farthest receiver) where each eel was detected varied between 2.4 and 19 km (mean of 11.1 km, $N = 14$). For eels detected at more than three distant receivers (in Lac St. Louis), the area of the minimal polygon comprising all receivers that had detected each eel varied between 790 and 1300 ha ($N = 6$).

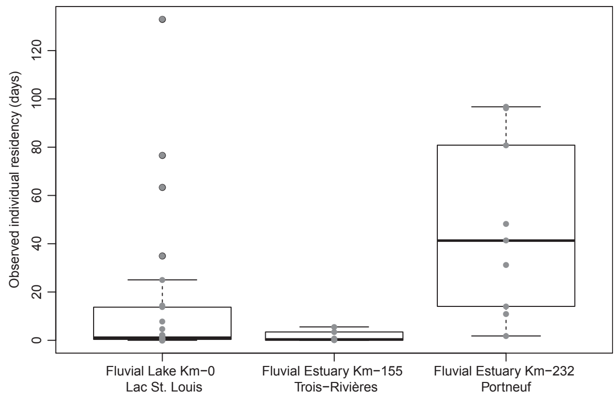


Fig. 5. Residency around arrays of sedentary yellow-stage eels tagged in the St. Lawrence River during the ice-free season in 2010 and 2011 (in days, $N = 32$). Raw data are superimposed on Boxplot (grey dots).

None of the eels that had been released in Lac St. Louis in 2010 were detected in 2010, but four of these eels were detected in the same area from June to September in 2011 (Table 1, Fig. 5, lower panel) suggesting a certain degree of site fidelity. Of the 15 yellow eels that were displaced in Lac St. Louis in 2011 (i.e. caught in Iles-de-la-Paix (Fluvial Lake Km 0) and released approximately 12 km downstream, 2 km beyond Lac St Louis acoustic array) nine eels showed evidence for homing, i.e. they were detected several days later at Lac St. Louis array and six even at Iles-de-la-Paix receivers, up to 19 km upstream from the release site. These eels came back to their capture site where they were recorded on several occasions during the tracking period (sedentary eels) and nowhere else (Fig. S1, upper panel). Similarly, but at a larger scale, in 2010, of the 11 eels released in Lac St. Pierre (Fluvial Lake Km 131) 5 were detected several days

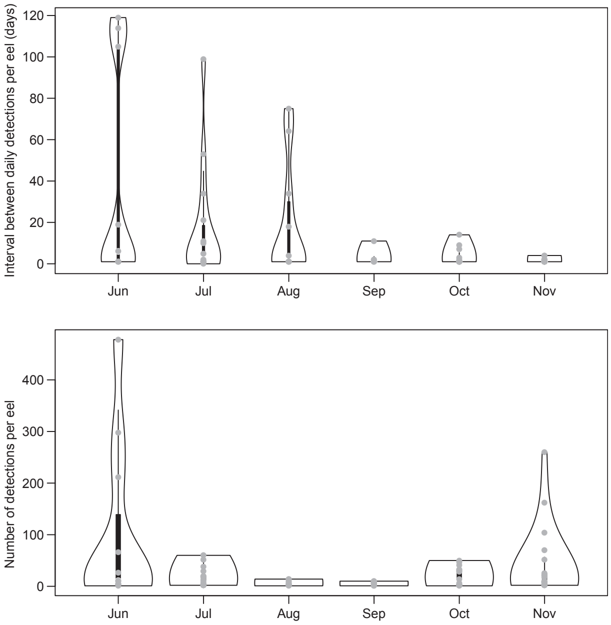


Fig. 6. Seasonal activity of freshwater resident yellow eels recorded in Lac St. Louis in 2011. Upper panel: Time elapsed between detections per day and per eel according to the month of first daily detection, violin plot and raw data (grey dots) ($N_{Jun\text{-}Interval}$ = 367, $N_{Jun\text{-}Eels}$ = 11, $N_{Jul\text{—}Interval}$ = 240, $N_{Jul\text{-}Eels}$ = 17, $N_{Aug\text{-}Interval}$ = 200, $N_{Aug\text{-}Eels}$ = 10, $N_{Sep\text{-}Interval}$ = 19, $N_{Sep\text{-}Eels}$ = 10, $N_{Oct\text{-}Interval}$ = 44, $N_{Oct\text{-}Eels}$ = 16, $N_{Nov\text{-}Interval}$ = 26, $N_{Nov\text{-}Eelsl}$ = 22); Lower panel: Total number of detections per eel according to the month, violin plot and raw data (grey dots), (N_{Eels} are the same as in upper panel, $N_{June\text{-}Detections}$ = 1115, $N_{Jul\text{-}Detections}$ = 227, $N_{Aug\text{-}Detections}$ = 64, $N_{Sep\text{-}Detections}$ = 60, $N_{Oct\text{-}Detections}$ = 293, $N_{Nov\text{-}Detections}$ = 805). The shape of the violins shows the distributional characteristics of batches of data.

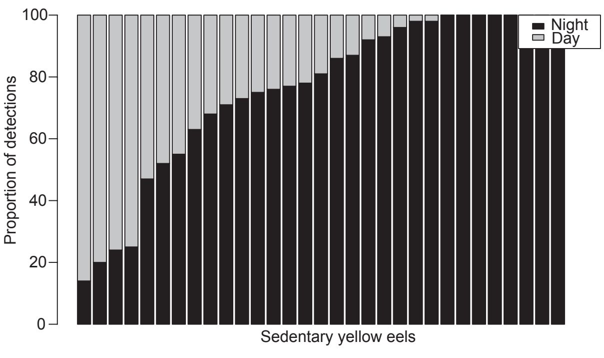


Fig. 7. Composition of detections according to diel period for each of the 32 nonvagrant yellow eels tracked in both 2010 and 2011 in the St. Lawrence River.

later downstream at the Trois-Rivières array (Fluvial Estuary Km 155) only and during a 28-day period, in September (Fig. 4), suggesting a downstream movement to their capture site (Gentilly, Km 178) that was not covered by acoustic receivers during the first year of tracking.

Discussion

Our study showed that most yellow eels caught in fresh waters of the St. Lawrence are sedentary and do not undertake large-scale movements (i.e. greater than about 32 km in the upper St. Lawrence) within freshwater or to the estuary during summer and autumn. Indeed, around 75% of the detected eels were recorded repeatedly during long periods within the vicinity of only one acoustic array, usually the one closest to their release site after tagging. In their review, Jessop et al. (2008) reported that exclusively freshwater residence increases with distance upstream and beyond 80 km freshwater residency exceeds 90%. In our study area, eels were released at either Lac St. Louis, Lac St. Pierre or Cap Santé; three locations that respectively lie 310 km, 185 km and 85 km upstream from the brackish estuary. With 88.4% of sedentary eels caught and released at Lac St. Louis and Lac St. Pierre (92% when considering the undetected fish as sedentary eels) and 65% of sedentary eels caught at Cap Santé (68.4% when considering the undetected fish as sedentary eels), our results support the trend revealed by Jessop et al. (2008). No eels were recorded continuously at arrays, that is, within the detection radius of about 500 m, indicating that eels were moving around arrays and were not dead. These movements could potentially encompass a maximum distance of 116 km within the fluvial estuary (46 km upstream of the Portneuf array plus 70 km downstream to the Orleans arrays) and <32 km distance in the upper fluvial lake (Lac St. Louis). Smaller-scale movements (<19 km) were thus demonstrated in Lac St. Louis. Our observations suggest that home range of freshwater resident yellow eels could be much greater than values reported in other systems. Minimum values of 2.4–19 km or 790–1300 ha were highlighted for eels living in Lac St. Louis in our study vs. 65.4 ha in Lake Champlain (Labar & Facey 1983), <325 ha in estuaries (Parker 1995; Thibault et al. 2007a), 4.7 km in rivers (Oliveira 1997; Morrison & Secor 2003), about 1 ha in an estuarine stream (Helfman et al. 1983), 0.4–4.1 km in a tidal river and open estuary system (Walker et al. 2013) and <5 ha in a tidal river (Dutil et al. 1988). Estimates of home range proved to be extremely variable depending on location, eel size (increase with total length, Thibault et al. 2007a) and methods used to determine location (mark-recapture, telemetry). Such a great home range estimate needs to be further investigated as it has serious consequences for habitat management.

Evidence for site fidelity of eels living in fluvial lakes was highlighted in our study. With an area of 148 km² and 353 km² respectively, Lac St. Louis and Lac St. Pierre represent large areas and thus provide many potential habitats for eels. These fluvial lakes are rich in wetlands, with respectively 685 ha and 16,098 ha, that is, approximately 10 times higher than for the lower estuary (Martin & Létourneau 2011). Wetlands are very rich ecosystems that are essential to fish populations providing food, shelter and clean water (Burton & Tiner 2009). The distribution of yellow eels in fluvial lakes of the St. Lawrence, and the ecological importance of these lakes for eels, have never been investigated but they may represent an important habitat for yellow-stage eels (e.g. Glova et al. 1998; Laffaille et al. 2004). We also found evidence for homing in Lac St. Louis with eels going back to their capture site in Iles-de-la-Paix several days after their release and detected on several occasions over a long period of time. Homing to specific areas at various scales was demonstrated for yellow-stage American eels living in a river of New Brunswick (Canada) (Vladykov 1971), in small freshwater ponds in Maine (USA) (Lamothe et al. 2000), in a lake in Vermont (Labar & Facey 1983) and in a tidal estuary in Maine (Parker 1995). Pronounced homing capacities were also largely demonstrated for European eel with displaced eels able to find their way back at distances of over 200 km from the home location (e.g. Rossi et al. 1987; Tesch 2003).

Our study highlighted a seasonal variability in activity of freshwater resident yellow eels: a low activity was observed during summer while an increase in activity was recorded in the autumn. This pattern may be related to day length which defines the time available for nocturnal foraging. In our study area, approximately 7 h of darkness were available in mid-June versus 14 h in mid-November while our study confirmed that yellow eels were active mainly at night. A bias towards nocturnal activity is the most consistently observed characteristic across the range in *Anguillidae* (e.g. Baras et al. 1998; Lamothe et al. 2000; Aoyama et al. 2002; Jellyman & Sykes 2003; Thibault et al. 2007a; Hedger et al. 2010). This activity may be related to foraging at night, with anguillid eels using olfaction to identify prey (Barbin 1998). During daytime, eels may bury themselves in the substrate for sheltering and feeding (Glova & Jellyman, 2000). It was recently demonstrated that yellow-stage American eels in the southern Gulf of the St. Lawrence spend approximately 74% of their time in the substrate (Tomie 2011). The duration of substrate occupancy by eels is linked to nonwinter daytime duration which varies with latitude (Tomie 2011). Jessop (2010) hypothesised that lower growth rates observed in northern areas could be partly explained by confinement to the substrate during long summer days which reduces time available for nocturnal foraging during the warmest months. Seasonal and diel movements of yellow eels could also be explained by temperature variations and the observed increase in activity during fall could reflect an exploratory phase, that is, eels searching for wintering sites (Feunteun et al. 2003).

Of the 67 tagged eels, 11 exhibited a vagrant behaviour, that is, large-scale movements from 63 to 418 km. Except for two eels, these movements were unidirectional and downstream. They moved to the brackish estuary and no return movement was ever observed during the tracking season that ended mid-November for both years. A parallel otolith Sr:Ca study, conducted on 59 eels collected in the same area at the same periods, showed that four eels living in freshwater made an incursion during their life into the estuary before returning to freshwater until capture (Benchetrit 2013). Like most of our vagrant eels, these eels were all caught at the sites closest to the Brackish Estuary (50–185 km). Eels collected in the upper St. Lawrence did not show any evidence of estuarine habitat use during their life. Two studies conducted in smaller systems in the Gaspé Peninsula (Québec, Canada) demonstrated that between 11 and 40% of yellow eels moved seasonally from river to estuary (Thibault et al. 2007a; Hedger et al. 2010). Such behaviour was related to summer feeding, the estuarine brackish environment being more productive than fresh waters (Thibault et al. 2007a,b). Eels then might return very late in autumn for overwintering in fresh waters. In our study, none of the vagrant eels was tracked back to the river before winter despite an acoustic coverage until mid-November. One eel caught in the fluvial estuary in mid-August showed an upstream movement and could have been an eel returning to fresh waters after having spent some time in the estuary. Vagrant eels observed in our study could stay several years in the estuary before returning to fresh waters as was demonstrated by otolith Sr:Ca analysis (Benchetrit 2013). We detected vagrant eels upon arrival at estuarine acoustic arrays mainly during ebb tides (and at night), suggesting that vagrant eels use tidal currents to move downstream as was observed by Hedger et al. (2010) for yellow-phase eels in the Gaspé estuary in Canada and for silver-phase eels migrating down the St. Lawrence Estuary (Béguer-Pon et al. unpublished data).

In their review, Feunteun et al. (2003) proposed that movements of eels in inland habitats at the scale of entire river systems could be governed by age-related, density-dependent behaviour. Neither the densities of yellow eels in the St. Lawrence River system nor the carrying capacity of this system have ever been estimated, preventing us from discussing possible density-dependent movement behaviour. Nevertheless, it remains a plausible hypothesis that highlights the need for obtaining eel density estimates in the St. Lawrence system.

Some of the vagrant eels may have initiated maturity and the silver developmental stage after having been tagged, although no morphological differences between vagrant and sedentary eels were observed. Furthermore, vagrant eels were significantly smaller and had a lower ocular index, on average, than migrant silver eels tracked in a parallel study (Béguer-Pon et al. submitted). Nevertheless, coloration criteria and morphological measures cannot be considered as definitive indicators of sexual maturity or migratory status (Cottrill et al. 2002; McGrath et al. 2003). An increase in maturation as the season progresses could also have occurred for some eels. Dutil et al. (1987) showed that in a two-month period, from mid-August to mid-October, the diameter of oocytes increased by 42%. In our study, four vagrant eels were recorded downstream of their release site only after several weeks (7–10).

The individual variation in spatial behaviour found in this study (sedentary behaviour and downstream migratory behaviour) is a common feature among species that exhibit a migratory life cycle, including anguillids. A number of recent studies carried out on anguillids have demonstrated that the typical catadromous life cycle is not obligatory (e.g. Tsukamoto & Arai 2001; Tzeng et al. 2002; Daverat & Tomas 2006). Some individuals switch between freshwater and brackish or marine habitats on one or multiple occasions during the yellow phase (Daverat et al. 2006). Such observations together with our findings illustrate the extent of plasticity that characterises habitat use among anguillids.

Conclusion

Our study demonstrated that most yellow-stage American eels living in fresh waters of the St. Lawrence system were sedentary during summer and autumn, but that a fraction of yellow eels seem to exploit the brackish estuary, probably at the scale of several years. Yellow eels could move for several tens of kilometres within fresh waters as was demonstrated at a smaller scale in Lac St. Louis. They were less active during summer, which might be related to their nocturnal foraging. The importance of fluvial lakes for yellow eels should be further investigated, and exploitation of wetlands deserves particular attention. Possible movements during spring and for smaller (thus younger) eels should also be explored. There is evidence that young yellow-phase American eels accomplish a protracted summer upstream migration for several years before becoming sedentary (Dutil et al. 1989; Castonguay et al. 1994) but such a migration has never been thoroughly examined.

Acknowledgements

Funding for this project was provided to Julian J. Dodson and Martin Castonguay as part of the Ocean Tracking Strategic Network funded by the Natural Science and Engineering Research Council of Canada and the Canadian Foundation for Innovation. The authors would like to thank Yannick Bergeron, Florent Archambault, Guillaume Lemieux, David Leblanc, Nicolas Harnois, Jean-Guy Frenette, Hacène Tamdrari, Simon Bernatchez, Yanick Soulard, David Paez for their technical support during this study. The authors also acknowledge Québec-Océan (www.quebec-ocean.ulaval.ca) for its material support. This manuscript is a contribution to the scientific program of the Ocean Tracking Network (oceantrackingnetwork.org).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Characteristics of the acoustic lines deployed in 2010 and 2011 in the St. Lawrence River and Estuary for eel tracking.

Figure S1. Illustration of small-scale movements in Lac St. Louis (eels never detected further downstream).