NRC Research Press

ARTICLE

Large-scale migration patterns of silver American eels from the St. Lawrence River to the Gulf of St. Lawrence using acoustic telemetry

Mélanie Béguer-Pon, Martin Castonguay, José Benchetrit, Daniel Hatin, Guy Verreault, Yves Mailhot, Valérie Tremblay, Denis Lefaivre, Michel Legault, David Stanley, and Julian J. Dodson

Abstract: Downstream migration of silver American eels (*Anguilla rostrata*) from the St. Lawrence system was examined using acoustic telemetry. One hundred and thirty six silver American eels were tagged, and their passage was recorded using fixed acoustic arrays covering a 420 km distance along the St. Lawrence River and Estuary. Eighty-nine percent of the tagged eels were detected. All migrant eels (111) exhibited unidirectional and downstream movements, but the migration was not completed in one continuous direct movement. High individual variability in migratory longitudinal profiles was documented as well as in individual speed with no apparent relation to river discharge or morphological traits. Migration speed increased over the season. Our observations demonstrated that migrating silver American eels are largely nocturnal and demonstrated the use of nocturnal, ebb tide transport to leave the estuary. With 44 additional eels tagged and released in the maritime estuary, escapement of 180 silver American eels from the Gulf of St. Lawrence system was monitored along a 125 km acoustic line that entirely covered Cabot Strait in 2011. Surprisingly, only four of the tagged eels were recorded escaping the Gulf of St. Lawrence.

Résumé : La migration de dévalaison de l'anguille d'Amérique argentée (*Anguilla rostrata*) a été étudiée grâce à un système de télémétrie acoustique. Cent trente-six anguilles argentées ont été marquées et leur passage ou présence a été enregistré grâce à des lignes acoustiques fixes couvrant une distance de 420 km le long du fleuve et de l'estuaire du St-Laurent. Quatre-vingt neuf pourcent des anguilles marquées ont été détectées. Toutes les anguilles migrantes (111) montrent des mouvements unidirectionnels vers l'aval mais la migration n'est pas menée d'une seule traite. Une très grande variabilité individuelle au niveau des profils de migration a été démontrée, ainsi qu'au niveau des vitesses de migration sans que ces dernières ne puissent être reliées ni au débit du fleuve ni à des traits morphologiques. La vitesse de migration augmente au cours de la saison. Nos observations suggèrent l'utilisation du transport de jusant nocturne pour quitter l'estuaire. Avec 44 anguilles supplémentaires marquées et relâchées en estuaire maritime, l'échappement de 180 anguilles argentées du système St-Laurent a été suivi grâce à une ligne acoustique couvrant les 125 km du détroit de Cabot en 2011. Étonnamment, seulement quatre des anguilles marquées sortant du Golfe du St-Laurent ont été détectées.

Introduction

The American eel (*Anguilla rostrata*) and the European eel (*Anguilla anguilla*) are facultative catadromous fishes inhabiting continental waters in fresh, brackish, or saltwater environments (e.g., Daverat et al. 2006), and migrate long distances for spawning in the Sargasso Sea. Their individual migration patterns from continental waters to the Atlantic Ocean are not well known, and oceanic migration routes to the spawning site are also unknown (Aarestrup et al. 2009).

The American eel is an important fisheries resource (COSEWIC 2012; Tesch 2003). However, the status of the species in Canada has been of major concern for over 20 years (Caron et al. 2007; Castonguay et al. 1994*a*; COSEWIC 2012). The long-term abundance index of eel at the Saunders eel ladder in the upper St. Lawrence River is currently about 8% of the abundance observed in the mid-1980s (COSEWIC 2012). Causes for this decline probably involve multiple factors such as mortality at hydroelectric generation stations, over harvest, habitat modification, oceanic conditions, and contaminants (Castonguay et al. 1994*b*; Haro et al. 2000; Knights 2003), but the causes of decline are difficult to rank because of the unique and complex ecology of this species. The eel decline is much more pronounced in the upper St. Lawrence River and Lake

Received 17 April 2013. Accepted 30 May 2014.

Paper handled by Associate Editor Marie-Joëlle Rochet.

M. Béguer-Pon,* J. Benchetrit, and J.J. Dodson. Université Laval, Département de Biologie, Pavillon Vachon, 1045 av. de la Médecine, Québec, QC G1V 0A6, Canada.
M. Castonguay and D. Lefaivre. Institut Maurice-Lamontagne, Pêches et Océans Canada, 850 route de la Mer, C.P. 1000, Mont-Joli, QC G5H 3Z4, Canada.
D. Hatin. Direction régionale de l'estrie, de Montréal et de la montérégie secteur de la faune, Ministère des Forêts, de la Faune et des Parcs, 201 Place Charles Le Moyne, 4e étage, Longueuil, QC J4K 2T5, Canada.
G. Verreault. Direction régionale de la faune du Bas-Saint-Laurent, Ministère des Forêts, de la Faune et des Parcs, 186 rue Fraser, Rivière-du-Loup, QC G5R 1C8, Canada.
Y. Mailhot. Direction de la protection de la faune de la Mauricie–Centre-du-Québec, 100 rue Laviolette, bureau 102, Trois-Rivières, QC G9A 5S9, Canada.
V. Tremblay. AECOM, 2 rue Fusey, Trois-Rivières, QC G8T 2T1, Canada.
M. Legault. Direction de la faune aquatique, Ministère des Forêts, de la Faune et des Parcs, 880 chemin Sainte-Foy, Québec, QC G1S 4X4, Canada.
D. Stanley. Ontario Power Generation, 14000 Niagara Parkway, Niagara on the Lake, ON L0S 1J0, Canada.
Corresponding author: Mélanie Béguer-Pon (e-mail: melanie.beguer.1@ulaval.ca).
*Present address: Dalhousie University, Department of Oceanography, 1355 Oxford Street, P.O. Box 1500, Halifax, NS B3H 4R2, Canada.

Ontario than documented elsewhere in the species' range, which is difficult to understand considering the panmictic population structure of the species (Castonguay et al. 1994*a*; Côté et al. 2013).

Investigations of the migration pattern of eels in the St. Lawrence River and Estuary have been restricted to analyses of commercial fisheries data and capture–tag–recapture experiments (de Lafontaine et al. 2009; Dumont et al. 1997; Verreault et al. 2003). Silver American eels from the St. Lawrence River start their downstream migration in early May through to September (Dumont et al. 1997), and a synchronization of their passage in the brackish estuary in autumn has been demonstrated (Verreault et al. 2003; de Lafontaine et al. 2009). Significant changes in both the timing and duration of the silver American eel downstream migration since the late 19th century were recently documented and related to hydroclimatic conditions (Verreault et al. 2012). The migration started earlier than in pristine times (1843–1872) but ended at the same time in the brackish estuary, leading to a longer migration duration relative to changes in both temperature and river flow (Verreault et al. 2012). Nevertheless, the individual migration patterns of American eels are poorly documented. The use of selective tidal stream transport during some life-history stages has been reported, but it appears equivocal and has never been clearly demonstrated for the silver stage of the American eel (Bradford et al. 2009; Parker and McCleave 1997). Furthermore, although the number of silver American eels leaving the freshwaters of the St. Lawrence have been estimated (Caron et al. 2003; G. Verreault, Ministère des Ressources Naturelles et de la Faune, personal communication), no estimates of the silver American eel numbers leaving the St. Lawrence system, i.e., from the freshwater and estuarine sections to the exit of the Gulf of St. Lawrence, have been attempted.

The recent introduction of low-cost, moored data-logging acoustic receivers has provided opportunities for tracking aquatic organisms over small and large scales (Heupel et al. 2006). The objective of this study was to determine the patterns and behaviour of silver American eels during their downstream migration in the St. Lawrence River and Estuary, and at Cabot Strait, the southern connection of the Gulf of St. Lawrence to the Atlantic Ocean, using fixed array acoustic telemetry. Environmental influences (diel and tidal periodicity, and river discharge) and effects of individual morphological traits were investigated to establish their impact on migratory behaviour. Another important objective of this study was to obtain a first estimate of the escapement rate of eels from the St. Lawrence system.

Materials and methods

Study area

The St. Lawrence River is one of the largest rivers in North America. The river system extends 1600 km from the outlet of Lake Ontario to the Atlantic Ocean and comprises three fluvial lakes connected to lotic sections, a freshwater estuary, a brackish estuary, and a lower (maritime) estuary flowing into the Gulf of St. Lawrence (Therriault 1991) (Fig. 1). The Gulf of St. Lawrence is a semi-enclosed sea with an estuarine-type circulation dominated by the St. Lawrence River. The Gulf of St. Lawrence has a total area of 168 000 km^2 and extends roughly 900 km along its widest axis from southwest to northeast. It has two main outlets to the Atlantic Ocean, the Strait of Belle Isle to the northeast and the Cabot Strait to the southeast (Fig. 1). The Gulf of St. Lawrence is also characterized by the Laurentian Channel, with depths as great as 500 m, which extends for over 800 km from the St. Lawrence Estuary to the Atlantic Ocean through Cabot Strait.

Eel capture and tagging

During the summers of 2010 and 2011 and the fall of 2011, a total of 180 silver American eels were captured by commercial fishermen using hoop nets in the freshwater section of the St. Lawrence River and tidal weirs set in the brackish water estuary (Fig. 1; Table 1). To retain eels that were potentially ready to migrate, only the largest eels (total length greater than 800 mm, all females: Table 1) characterized by diagnostic coloration criteria were selected for tagging. The coloration criteria used to identify silver American eels were based on studies on European eel (Acou et al. 2005; Okamura et al. 2007) and on personal observations. These included a visible lateral line, fully or partially melanized pectoral fins, black or dark dorsal coloration, and white, silver, or dark/black ventral coloration. Several morphometric measurements were also made to insure that eels were in the silver stage in 2011: total length (TL), fresh body mass (Wf), left eye diameter (Dv: vertical and Dh: horizontal, to calculate an ocular index (OI) = π/TL × ((Dv + Dh)/4)^2 (Pankhurst 1982)), and length of left pectoral fin (PF) (to calculate the pectoral fin index (PFI) = 100 × PF/TL). All eels were weighed before release. Fulton's condition factor (*K*) was calculated: K = Wf/TL^3 (Ricker 1975). All selected eels had phenotypic traits that were consistent with the silver stage (TL = 710–1150 mm; Wf = 709–3340 g; OI = 4.0–9.3; PFI = 3.3–6.2; V. Tremblay 2001 and 2002, unpublished data; G. Verreault, 2010, unpublished data). Vemco acoustic transmitters (frequency of 69 Hz) (http://www.vemco.com) were used in this study: 143 tags were V13-1x (13 mm in diameter, 36 mm in total length, 6 g in water, 153 dB in output power) with a nominal delay of 60 s (life time of 195 days) and 37 tags were V9-2x (9 mm in diameter, 29 mm in total length, 2.9 g in water, 147 dB in output power) with a nominal delay of 120 s or 90 s (life time of 193 and 143 days, respectively). The transmitter mass was <2% of body mass and did not exceed the maximum threshold recommended by Lucas and Baras (2000) and Thorstad et al. (2009). Eels were anaesthetized in a 40 mg·L^{-1} metomidate solution (Aquacalm) for approximately 4 min following the procedures of Aarestrup et al. (2009). 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 two or three synthetic suture points. A recent 6-month experiment with a similar acoustic tag demonstrated that this kind of surgery did not affect survival or behaviour, and tags were not expelled from the eel body (Thorstad et al. 2013). All acoustically tagged eels were released near their capture site within approximately 7 h following surgery (Fig. 1; Table 1).

In addition to acoustic transmitters, all eels were marked with individual passive integrated transponder (PIT) tags injected at the same time and location as the acoustic tags. This micro tagging allowed identification of tagged eels in case of recapture by commercial fishermen along the St. Lawrence system. All fisherman were equipped with a PIT tag detector, and a reward was given for tagged live eels that were detected and released.

Acoustic lines

Acoustically tagged eels were recorded using fixed receiver lines composed of Vemco VR2 and VR2W receivers deployed along the St. Lawrence River and Estuary, covering a distance of 420 km. In addition, a receiver line was deployed at Cabot Strait, 900 km downstream of the Ouelle – La Malbaie line (Fig. 1). In 2010, 39 receivers distributed along six lines were deployed about 2 m off the bottom across the St. Lawrence River and Estuary from mid-August to early November (Table 2; Fig. 1). Twenty-seven percent of the width of the brackish estuary at La Malbaie – Ouelle (418 km from the most upstream release site — Ile-de-la-Paix, see below, thereafter noted 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–June to November (Table 2; Fig. 1). The length of the Ouelle line was doubled, covering 44% of the width of the St. Lawrence Estuary. The mean distance between neighboring receivers was 433 m in the river and 602 m in the estuary. The Montmagny line included 10 receivers installed perpendicular to the shore. Seven additional receivers

Fig. 1. Study area: (*a*) Location within Canada. SBI, Strait of Belle Isle; (*b*) Acoustic arrays deployed in the St. Lawrence River and Estuary and release sites of tagged eels; (*c*) Acoustics receivers deployed at Cabot Strait and Canso Strait. Isobaths are in metres. L1, L2, L3, L4, and L5 correspond to sections for which individual migration speed was calculated. See Table S1 and Fig. 5.

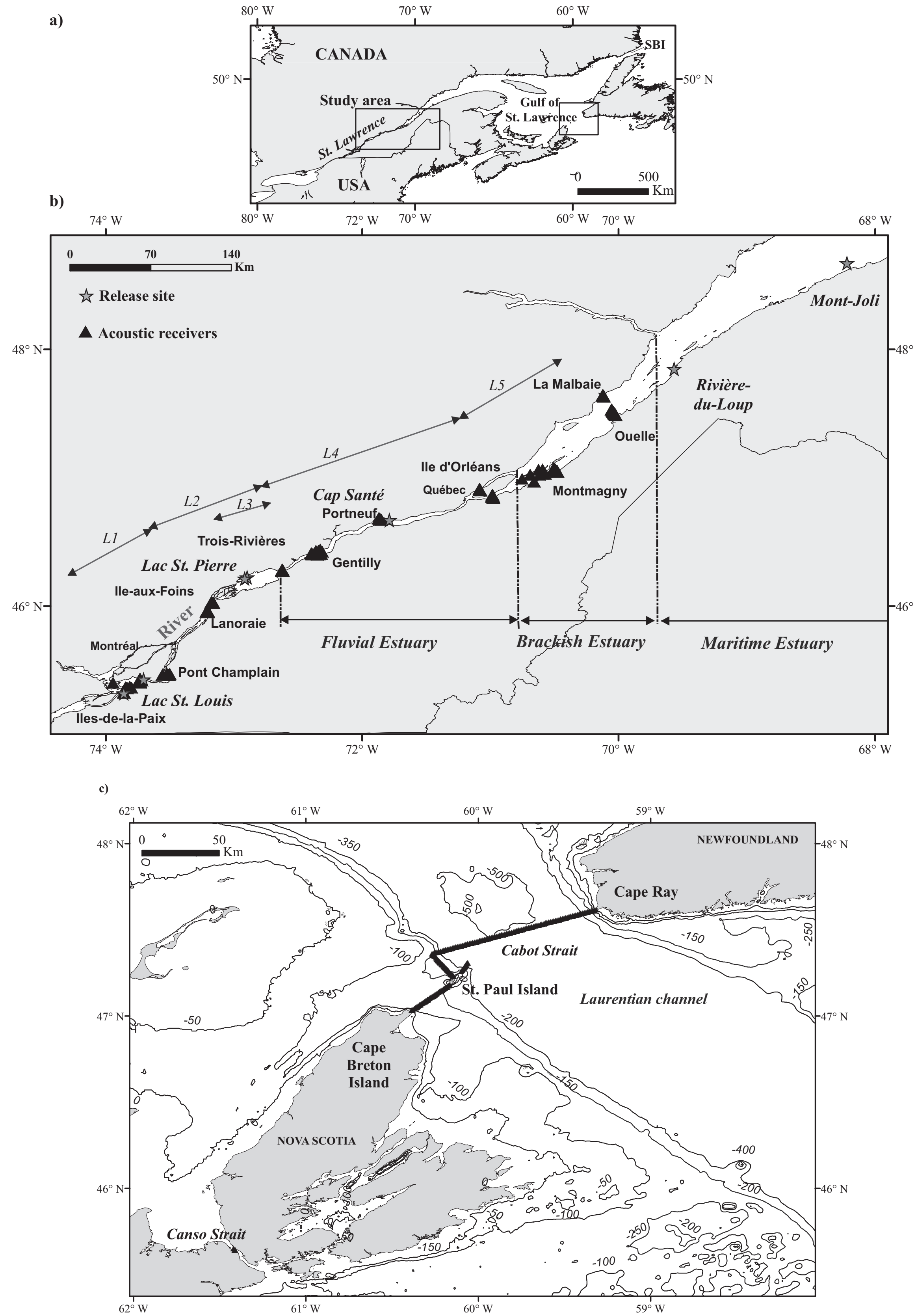


Table 1. Characteristics of the 180 silver American eels tagged in 2010 and 2011 with an acoustic transmitter and released in the St. Lawrence system for monitoring their downstream migration.

			Release location		Total length (mm)		Body mass (g)		Ocular index		Pectoral fin index	
Year	Period	No. of eels	Section, River km	Local name	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range
2010	24 Aug. to 16 Sept.	49	Fluvial lake, km 131	Lac Saint-Pierre	990±74	806–1145	2251±510	950–3400	—	—	—	—
2010	19 Aug. to 09 Sept.	18	Fluvial lake, km 11	Lac St-Louis	985±43	893–1068	2242±373	1400–2850	—	—	—	—
2011	21 June and 22 June	3	Fluvial lake, km 0	Lac St-Louis	882±60	815–931	1900±87	1850–2000	8.5±2.8	6.3–11.7	5.1±0.7	4.4–5.8
2011	03 Oct. and 10 Oct.	8	Maritime estuary, km 610	Mont-Joli	1051±38	980–1090	2665±327	2120–3060	9.6±1.9	6.4–12.5	5.1±0.6	4.3–5.9
2011	04 July and 05 July	50	Fluvial lake, km 131	Lac Saint-Pierre	1007±50	920–1140	2292±187	2000–2650	6.9±1.8	3.7–10.8	4.6±0.5	3.4–5.5
2011	28 July to 15 Aug.	16	Fluvial estuary, km 232	Cap Santé	949±77	815–1120	1975±365	1200–2650	6.5±1.3	4.3–8.5	5.1±0.3	4.4–5.5
2011	07 Oct. to 19 Oct.	36	Maritime estuary, km 470	Rivière-du-Loup	985±76	880–1183	1961±468	1377–3207	7.0±1.7	3.8–10.8	4.5±0.4	3.6–5.4
Total		180			990±68	806–1183	2192±425	950–3400	7.1±1.8	3.7–12.5	4.7±0.5	3.4–5.9

Note: All eels were females. River km is the distance from the most upstream release site (in kilometres).

Table 2. Characteristics of the acoustic lines deployed in 2010 and 2011 in the St. Lawrence system in order to monitor the downstream migration of silver American eels.

Location	Name of acoustic line	Latitude (°N)	Longitude (°W)	Total no. of receivers deployed	Mean section width (m)	Mean distance between hydrophones (m)	Mean depth (m)	Mean depth of receivers (m)	Date of deployment	Date of recovery
River	Lanoraie	45.9532	73.2025	14	1272	192	6.9	5.9	12 Aug. 2010	23 Nov. 2010
Fluvial estuary	Trois-Rivières	46.2776	72.6248	6	1520	511	10.6	3.5	17 Aug. 2010	8 Nov. 2010
Fluvial estuary	Île d'Orléans (N)	46.9090	71.0830	4	1540	324	5.4	5.1	12 Aug. 2010	12 Nov. 2010
Fluvial estuary	Île d'Orléans (S)	46.8540	70.9800	5	3167	610	14.8	5.7	17 Aug. 2010	12 Nov. 2010
Brackish estuary	La Malbaie (N)	47.6400	70.1200	4	19 967	723	22.1	14.8	17 Aug. 2010	9 Nov. 2010
Brackish estuary	Ouelle (S)	47.4970	70.0300	6	19 967	708	8.6	5.7	18 Aug. 2010	9 Nov. 2010
River	Îles-de-la-Paix (S)	45.3626	73.8411	8	4770	1162	6.6	6.0	12 July 2011	24 Nov. 2011
River	Lac St-Louis	45.4208	73.7337	9*	4105	605	5.8	5.0	7 Apr. 2011	21 Nov. 2011
River	Pont Champlain	45.4554	73.5230	9	2710	519	4.4	3.5	1 June 2011	22 Nov. 2011
River	Île-aux-foins	46.0267	73.1705	6	1751	417	9.7	8.9	14 Apr. 2011	25 Nov. 2011
Fluvial estuary	Trois-Rivières	46.2776	72.6248	6	1520	511	12.7	3.3	9 May 2011	21 Nov. 2011
Fluvial estuary	Gentilly	46.4065	72.3959	16	2098	603	8.0	3.6	26 Apr. 2011	22 Nov. 2011
Fluvial estuary	Portneuf	46.6772	71.8635	6	2592	637	12.3	4.2	20 May 2011	22 Nov. 2011
Fluvial estuary	Île d'Orléans (N)	46.9090	71.0830	5	1570	380	7.0	5.7	19 Apr. 2011	14 Nov. 2011
Fluvial estuary	Île d'Orléans (S)	46.8540	70.9800	8	3224	777	13.8	10.2	19 Apr. 2011	14 Nov. 2011
Brackish estuary	Montmagny	47.0617	70.4928	17	4968	610	10.9	6.1	26 Apr. 2011	15 Nov. 2011
Brackish estuary	La Malbaie (N)	47.6400	70.1200	4	19 967	723	23.3	16.3	16 June 2011	16 Nov. 2011
Brackish estuary	Ouelle (S)	47.5090	70.0380	12	19 967	708	19.0	13.9	16 June 2011	16 Nov. 2011
Gulf	Cabot Strait	47.3270	60.0010	40 (2010) and 151 (2011)	105 000	765	175.5 (2010) 327.5 (2011)	173 (2010) 325 (2011)	13 Oct. 2009	—
Gulf	Canso Strait	45.6430	61.4130	3	924	349	31	30.3	Fall 2010	—

Note: N is for north shore of the St. Lawrence River and S is for south shore of the St. Lawrence River.
*Three eels were removed on 11 July to place them at Îles-de-La-Paix.

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 which comprised 5 receivers. The range of detection for V9-2x transmitters 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 complete lines (shore to shore) with a V13-1x transmitter (nominal delay of 60 s) immerged at 1 m depth and trolled by a drifting boat (engine off) for approximately 1600 m. The daily detection probability of sentinel tags varied from 0.5 to 1.0 for distances between 0 and 200 m.

VR2W receivers were also deployed at Cabot Strait, the southern outlet of the Gulf of St. Lawrence, and also at Canso Strait, a narrow (~1 km) strait (blocked by a causeway but traversed by ship locks) that separates the Nova Scotia mainland from Cape Breton Island (Fig. 1; Table 2). In October 2010, 3 receivers were deployed at Canso Strait and 40 receivers across Cabot Strait, with 31 of these 40 receivers extending northeastward from Cape North (Cape Breton Island) to St. Paul Island and 9 receivers beyond St. Paul Island. This allowed coverage of approximately 40 km (28%) of Cabot Strait. In September 2011, this line was extended to Newfoundland, entirely covering Cabot Strait with a total of 151 receivers forming an approximate 125 km line. The mean depth of Cabot Strait is approximately 328 m, with bottom depths varying from 150 to 500 m, and receivers were moored close to bottom. The mean distance between neighboring receivers was 765 m for the Cabot Strait line. Sentinel tags were moored at the bottom of each line and showed high variability in detection efficiency. The daily detection probability of fixed sentinel tags varied between 0.6 and 1.0 for distances between 0 and 300 m. At a distance of 400 m, this probability was 0.5 on average but varied between 0.17 and 1.0. The Cabot Strait and Canso Strait lines were moored year-round and were downloaded twice a year in spring and fall.

Environmental data

Tidal state coinciding with each acoustic detection at estuarine arrays was 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 daily discharge of the St. Lawrence River was obtained from the Canadian Hydrological Service website, station Lasalle (02OA016) (in Montréal). Lunar illumination (the proportion of the moon that was illuminated) was obtained from the U.S. Naval Observatory (aa.usno.navy.mi/data/docs/MoonFraction.php). Five thermographs were moored in the fluvial and brackish estuarine areas during the tracking period in 2011. As recorded water temperature was highly correlated with air temperature obtained from Environment Canada (http://climate.weather.gc.ca/) for the station at Québec ($0.85 < r^2 < 0.89$, df = 101, all $p < 0.0001$), we used the air temperature as a proxy for the water temperature during the tracking period in 2010 and 2011.

Data analysis

Basic calculations were made to describe the frequency of detections across the system and over time: number of eels recorded per receiver and per array (line), proportion of receivers that had detected the same individual during the same day, time elapsed between the earliest and the latest detection at an array per eel, and number of different days a fish was recorded at an array per eel. For each year, the general migration pattern, i.e., the total number of eels detected per array over time, was summarized in violin graphs, which are a combination of a box plot and kernel density plot (Hintze and Nelson 1998).

We then examined large-scale migratory behaviour of individual eels within the St. Lawrence. Individual profiles 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 (Hollander and Wolfe 1973).

The transit time and migration speed between arrays were calculated for each individual eel. The transit time corresponds to the time elapsed between the departure from an array, i.e., the last detection at this array, and the arrival, i.e., the first detection at the successive downstream array. The migration speed (km·day^{-1}) was calculated from the transit time, considering a mean straight-line distance between mid-arrays. The influence of the location of the array, the date (as Julian day), lunar illumination, release site, and morphometric measurements on migration speed were examined with a generalized linear mixed model (GLMM) (Bolker et al. 2009, function glmmPQL (MASS), R Core Team 2013). The Julian day was alternatively replaced by day length and temperature in the best model. Individuals were considered as a random variable, whereas all other variables were considered as fixed effects. To evaluate the best model, the dataset was randomly divided into two subsets. The first subset (75% of the dataset) was used to calibrate the model, whereas the second subset (25% of the dataset) was used to evaluate model predictions. A linear regression model was then used to compare the predicted and observed data. This procedure was repeated 1000 times.

To determine if diel and tidal patterns of migration occurred, each acoustic detection was associated with a period of the day and a tidal state or current direction. The proportions of detections per eel and per day according to each category were calculated. The tidal effect was examined at estuarine arrays where there was significant tidal variations, i.e., Orléans north and south (km 304 and km 307), Montmagny array (km 354), and Ouelle array (km 418). Only the first and last detections per eel at each array, i.e., arrival and departure, were considered. Statistical differences between years and arrays were detected using chi-square tests. The diel and tidal pattern that would be expected if there was no preference for either night or day or for any tidal phase was then predicted (dependent upon the relative proportion of nocturnal and daytime hours and tidal phases during the time that eels were recorded at arrays). Pearson's χ^2 tests were then used to determine whether there was a diel and tidal effect on detection rates for estuarine arrays. Observed values (number of detections per tidal and diel periods) from sentinel tags moored at these arrays in 2011 were also calculated at various distances from where the sentinel tag was located to detect any loss of signal due to tidal currents that may have influenced detection patterns of migrating eels.

Results

Migration patterns from the St. Lawrence River to the brackish estuary

Frequency of detections across the system and over time

Proportionally, 79.1% of the eels tagged in 2010 and 98.5% of the eels tagged in 2011 were detected within the river and estuary (Tables 3 and 4). This corresponds to a total of 121 silver American eels. A total of 105 436 detections were recorded with a mean of 837 detections per eel (median = 143 detections per eel, range = 4 – 19 620; number of significant differences between years: W = 17635, $p > 0.5$). For both years, more silver American eels were detected on the south shore of the St. Lawrence than on the north shore. Indeed, 69% of the eels detected at Île d'Orléans (fluvial estuary, km 304) were detected at the southern array, and only two eels were detected at the La Malbaie array (brackish estuary,

Table 3. Detection rate of silver American eels at arrays deployed during the ice-free season in 2010 and 2011 in the fluvial and estuarine parts of the St. Lawrence system.

Year	Location	Name of acoustic line	River km	No. of detected eels	Proportion of detected eels
2010	River	Lanoraie	93	5	27.8%
2010	Fluvial estuary	Trois-Rivières	155	51	76.1%
2010	Fluvial estuary	Ile d'Orléans North	304	15	22.4%
2010	Fluvial estuary	Ile d'Orléans South	307	31	46.3%
2010	Brackish estuary	La Malbaie	418	2	3.0%
2010	Brackish estuary	Ouelle	418	28	41.8%
Total 2010				53	79.1%
2011	River	Iles-de-la-Paix	0	0	
2011	River	Lac St-Louis	11	1	33.3%
2011	River	Pont Champlain	32	3	100.0%
2011	River	Ile-aux-foins	103	3	100.0%
2011	Fluvial estuary	Trois-Rivières	155	53	100.0%
2011	Fluvial estuary	Gentilly	178	50	94.3%
2011	Fluvial estuary	Portneuf	232	42	79.2%
2011	Fluvial estuary	Ile d'Orléans North	304	13	18.8%
2011	Fluvial estuary	Ile d'Orléans South	307	31	44.9%
2011	Brackish estuary	Montmagny	354	26	37.7%
2011	Brackish estuary	La Malbaie	418	0	0.0%
2011	Brackish estuary	Ouelle	418	27	39.1%
Total 2011				68	98.6%

Note: The proportion of detected eels at each array is the number of detected eels divided by the number of eels tagged and released upstream of this array. River km is the distance of the array from the most upstream release site (Ile-de-la-Paix in Lac St. Louis), in kilometres.

Table 4. Detection patterns of silver American eels across the fluvial and estuarine parts of the St. Lawrence system, according to their release location.

Year	No. of released eels	Release location	Non-migrants	Migrants	Proportion Migrant: Of detected eel	Proportion Migrant: Of total tagged eel
2010	49	Fluvial lake, km 131, Lac St-Pierre	4	44	91.7%	89.8%
2010	18	Fluvial lake, km 11, Lac St-Louis	0	5	100.0%	27.8%
2011	3	Fluvial lake, km 0, Lac St-Louis	0	3	100.0%	100.0%
2011	50	Fluvial lake, km 131, Lac St-Pierre	4	46	92.0%	92.0%
2011	16	Fluvial estuary, km 232, Cap Santé	2	13	86.7%	81.3%
Total	136		10	111	91.7%	81.6%

Note: Non-migrants were eels detected at only one acoustic array (the closest to their release site), whereas Migrants were eels detected between two and six successive acoustic arrays.

km 418) compared with 56 individuals at the Ouelle array (Table 3). On average, when an eel was detected at an array, it was detected by 47.3% of the receivers for a given day (±29.0%, range = 8.3%–100%), indicating a wide lateral range of detection as fish approached a line. Eels equipped with V13 tags (nominal delay of 60 s) were recorded by 25.2% more receivers on average than eels equipped with V9 tags (nominal delay of 90 or 120 s).

The frequency of detections varied widely across the system and over time, although general migration patterns can be visualized from the river section to the brackish estuary (Fig. 2). On average, fish downstream were detected on fewer dates and later for both years. During fall, eels were detected for 40 days within the brackish estuary during both years. During summer, eels were detected for 62 and 123 days in 2010 and 2011, respectively, within the fluvial estuary. Peaks of detections at arrays close to release sites were recorded several days after their release (Fig. 2). Despite a more restricted tagging period in 2011 (2 days at Lac St-Pierre in 2011 vs. 3 weeks in 2010), the temporal frequency of detections within the fluvial estuary was more widespread in 2011 than in 2010. At Île d'Orléans (fluvial estuary, km 304), eels were detected during 59 days in 2010 and during 112 days in 2011. However, in the brackish estuary, at the Ouelle – La Malbaie arrays (km 418), the temporal distribution of detections was very similar between both years, i.e., approximately 40 days, from late September to early November.

Individual escapement behaviour within the estuary

Individual profiles

Of the tagged eels, 81.6% (111 individuals) were recorded by at least two successive acoustic arrays (Table 4). Of these migrants, 57% were detected at more than three successive downstream arrays (maximum detection at six arrays). No eel was ever recorded continuously at any one array, suggesting that no individuals died and remained in the vicinity of an array.

Except for four eels that moved back and forth between nearby arrays once during their downstream migration, all migrant eels exhibited unidirectional and downstream movements with no detected upstream movements (Figs. 3 and 4). Variability in individual migration profiles was observed, with some eels spending extended periods of time in various sections of the estuary (Fig. 3). Three eels were detected on both sides of Île d'Orléans (north and south, km 304) a few days apart, indicating possible movements around this island. At each array, most eels were recorded on only one or two different dates with a time elapsed between the earliest and the latest detection of between 11.4 min and 7.9 h (1st and 3rd quartiles, respectively). In 13.3% of the cases, eels were detected on more than three dates (up to 54 dates), and the time elapsed between the earliest and the latest detection was greater than 5 days, reaching a maximum of 92 days.

Fig. 2. Spatio-temporal distribution of detected silver American eels at acoustic arrays deployed in 2010 and 2011 within the St. Lawrence River and Estuary. Vertical expansion of the violins are relative to the number of detected individuals for each year (see Table S1 for details). Black violins represent the distribution frequency of the released eels at three locations: R-Km 0-LSL (Lac St. Louis), R-Km 131-LSP (Lac St. Pierre), and R-Km 231-CS (Cap Santé). Acoustic arrays are ordered on the *y* axis according to their distance from the most upstream release site (Ile-de-La-Paix, Lac St. Louis), noted Km (in kilometres; LAN, Lanoraie array; PCH, Pont Champlain array; IAF, Ile-aux-Foins array; TRO, Trois-Rivières array; GEN, Gentilly array; PNF, Portneuf array; IOL, Ile d'Orléans array; MNG, Montmagny array; OUE, Ouelle – La Malbaie arrays). The plots include a marker for the median of the data and a box indicating the interquartile range. The shape of the violins show the distributional characteristics of batches of data.

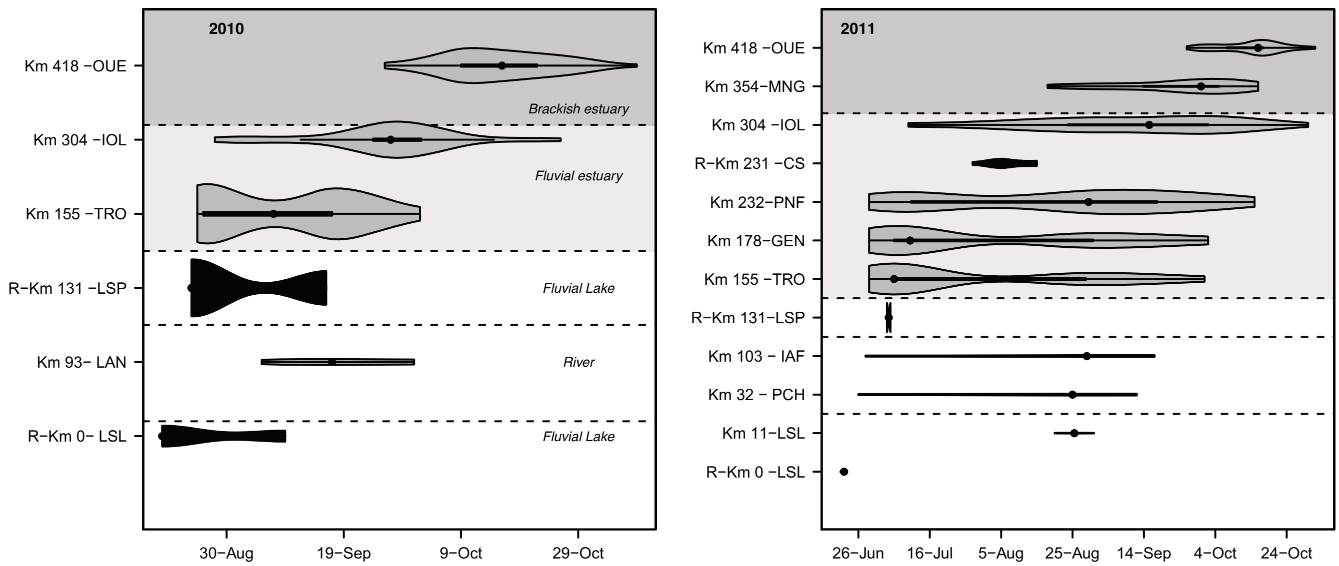
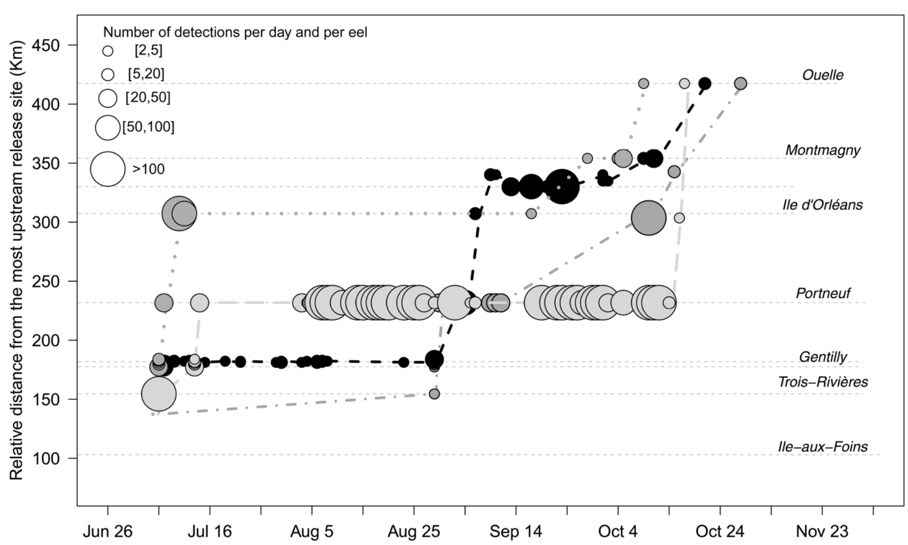


Fig. 3. Examples of four migration patterns of silvering American eels, shown by acoustic telemetry within the freshwater and brackish sections of the St. Lawrence Estuary and demonstrating the variability of the profiles. The four eels were caught, tagged, and released in Lac St-Pierre in 2011.



Transit time and migration speed

Migration speeds were highly variable, ranging between 0.27 and 88.7 km·day^{-1} (or 0.0028 and 1.12 BL·s^{-1}) (Poisson distribution, mean of 20.0 km·day^{-1} (0.23 BL·s^{-1}) and median of 9.4 km·day^{-1} (0.11 BL·s^{-1}), Table S1[1] and Fig. 5). The best GLMM includes only the location and the Julian day or day length or temperature alternatively as significant fixed effects. Neither the year, release site (fluvial lakes, tidal freshwater), moon phase nor any of the individual morphological characteristics were significant (all $p > 0.05$) and thus were not retained in the model. The best model performed well, i.e., predicted well the migration speed values when considering the whole dataset, although the predictability performance was lower when using the calibration and test dataset (Table 5). The individual was a very important factor as the null

[1]Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2013-0217.

Fig. 4. Example of two unusual migration patterns of silver American eels showing upstream movements in the freshwater and brackish sections of the St. Lawrence Estuary in 2011.

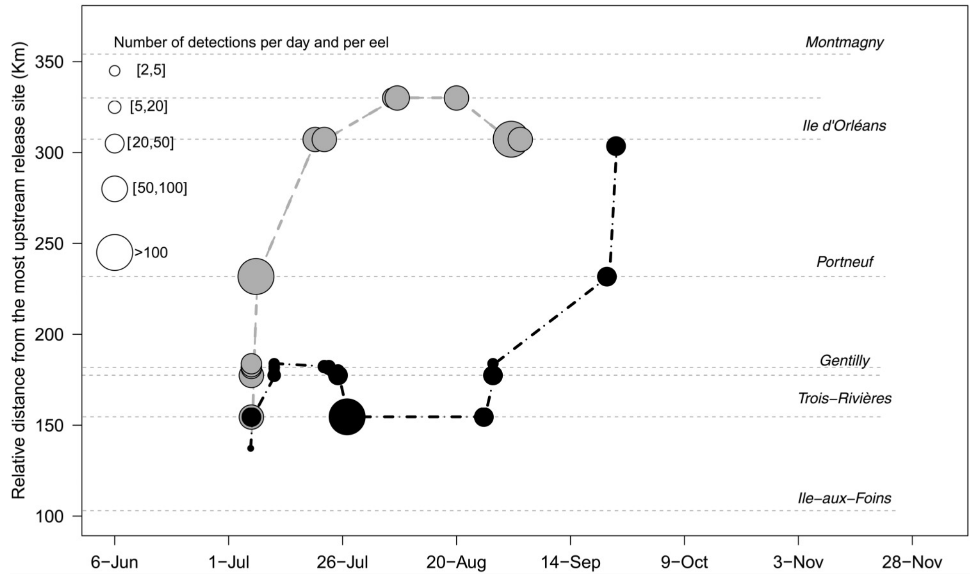
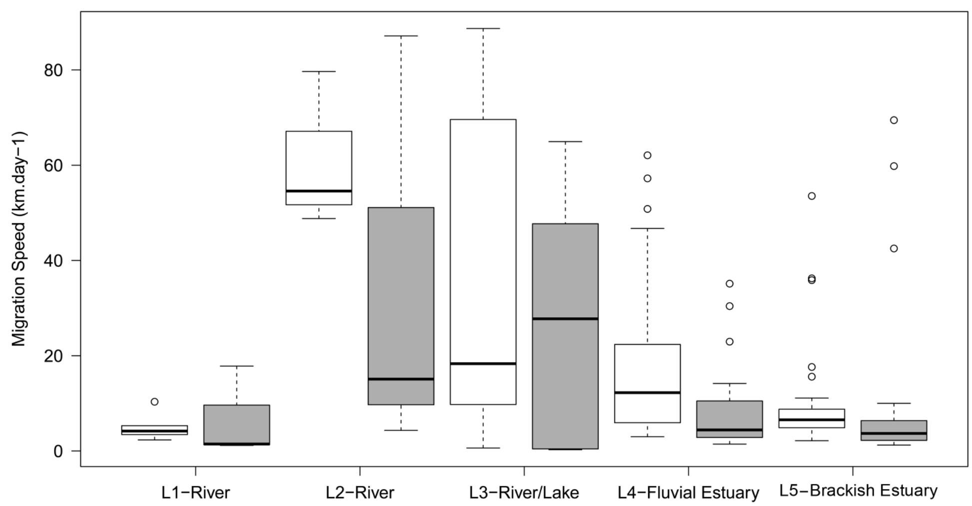


Fig. 5. Individual migration speed of silvering American eels calculated between arrays over the season and across the St. Lawrence system (see Table S2 for details). Open boxplots are data from 2010 and shaded boxplots are data from 2011. L1 is from the release site Lac St-Louis (km 11) to the first upstream acoustic array, i.e., Lanoraie in 2010 (km 93) or Ile-aux-Foins in 2011 (km 103); L2 is from Lanoraie or Ile-aux-Foins arrays to Trois-Rivières array (km 155); L3 is from the release site in Lac St. Pierre (km 131) to the first downstream array Trois-Rivières (km 155); L4 is within the fluvial estuary, i.e., between Trois-Rivières (km 155) and Orléans Island (km 304) arrays; L5 is within the brackish estuary, i.e., between Orléans Island (km 304) and Ouelle – La Malbaie arrays (km 418), see Table S1 for details.



model that includes only this random variable as a covariate already explained 64% of the variability. The migration speed was also significantly affected by the section of the St. Lawrence (Table 5): it decreased downstream for both years (Fig. 5; post-hoc test on GLMM (pairwise comparisons using Wilcoxon rank sum test), $p < 0.0001$). This was confirmed at a finer scale in 2011 within the fluvial estuary section (Table S1). The Julian day, day length, and temperature were all highly correlated variables during the tracking season (Pearson correlation coefficient greater than –0.86, df = 216, $p < 0.001$). Either of these covariables explained a significant part of the variability in migration speed (Table 5). The later the movement through an array was in the season (the lower was the day length and the temperature), the higher the eel migration speed was (or the lower the transit time was, Fig. 6).

No relationship between migration speed and freshwater discharge was observed. Indeed, the migration speed increased over the season for both years, whereas the trends of freshwater discharge were reversed between the two years during the tracking season: while the discharge increased between June and November in 2010 ($r = 0.81$, $p < 0.05$), it decreased for the same period in 2011 ($r = -0.92$, $p < 0.05$) (Fig. 7).

Tidal transport and nocturnal activity

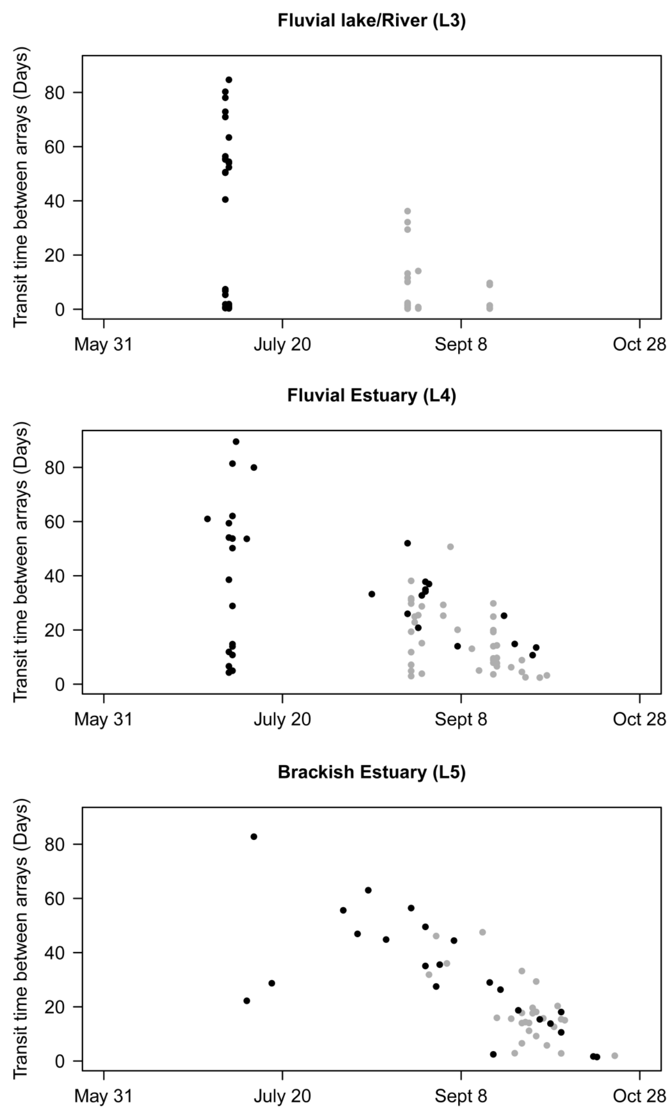
Diel and tidal cycle combined indicated that most eels were detected for the first time and the last time at arrays at night during ebb tide (54.6%), while few eels were detected in daytime during flood tide (4.1%) (Fig. 8, upper panel). There was no significant differences between years or between lines (see Table S2). For every array, the diel and tidal distribution of detections was significantly different from that which would have been expected if there had been no diel and tidal effect (χ^2 test, df = 3, $p < 0$ .001; Fig. 8, upper panel; Table S2). Also, for each array, the predicted

Table 5. Results of GLMM explaining individual migration speed variability of silver American eels in the St. Lawrence River and Estuary.

	Whole data set				Calibration data set (75%)			Test data set (25%)		
	AIC	BIC	Δ deviance (%)	Corr. fitted/ observed data	Sl.	Int.	Corr. fitted/ observed data	Sl.	Int.	Corr. fitted/ observed data
Speed ~ Day length × Location + (1|Individual)	20321	20348	68.9	0.91	1.03 (0.80; 1.09)	−2.23 (−4.33; 1.61)	0.85 (0.58; 0.92)	0.54 (0.10; 1.12)	8.02 (−0.74; 17.64)	0.41 (0.11–0.65)
Speed ~ Temperature × Location + (1|Individual)	20354	20381	68.8	0.90						
Speed ~ Julian day × Location + (1|Individual)	21890	21917	66.5	0.90						
Speed ~ Location + (1|Individual)	30749	30766	52.9	0.86						
Speed ~ Julian day + (1|Individual)	64845	64859	0.6	0.65						
Speed ~ Day length + (1|Individual)	64685	64698	0.8	0.65						
Speed ~ Temperature + (1|Individual)	59320	59333	9.0	0.66						
Speed ~ (1|Individual)	65217	65227	0	0.64						

Note: The table shows the dependent variable (Speed is the individual migration speed calculated between each array) and the covariates for each model, where (1|Individual) designates the random variable acoustically tagged individual. Also shown are the Akaike's information criterion (AIC), the Bayesian information criterion (BIC), the percent change in deviance (Δ deviance) from the designated null model which includes the random variable as a covariate and the evaluation of the predictive power of the best model. Sl. is for slope of the linear regression between observed and fitted data; Int. is for estimate of intercept; the mean values from the 1000 iterations are reported as well as the 2.5% and 97.5% quantiles in parentheses.

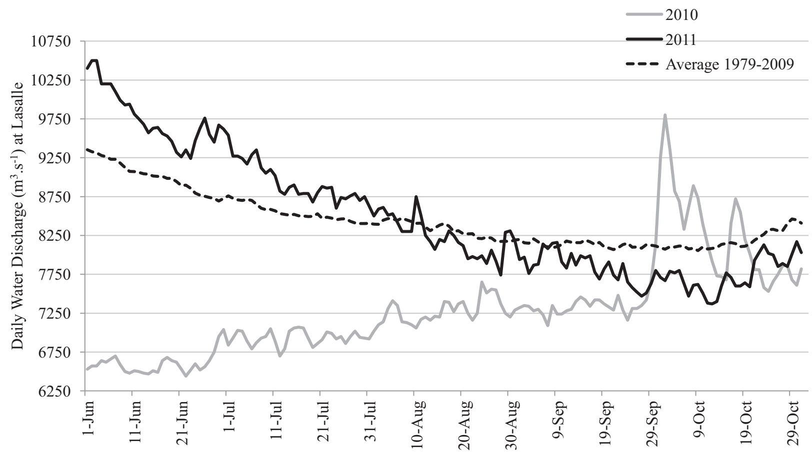
Fig. 6. Transit time of silver American eels calculated between acoustic arrays deployed in the St. Lawrence system over the season in 2010 and 2011. L3 is from the release site in Lac St.Pierre to the first downstream Trois-Rivières array; L4 is within the fluvial estuary, i.e., between Trois-Rivières and Île d'Orléans arrays; L5 is within the brackish estuary, i.e., between Île d'Orléans and Ouelle – La Malbaie arrays, see Table S2 for details. Filled dots are data from 2011 and shaded dots are data from 2010 (NL3 2010 = 44, NL3 2011 = 46; NL4 2010 = 44, NL4 2011 = 34; NL5 2010 = 27, NL5 2011 = 23).



diel and tidal distribution of detections were not different from those recorded by the sentinel tags at any distance (χ^2 test, df = 3, $p > 0.05$; Table S2), indicating that the detection pattern of tagged eels was not affected by environmental conditions in the vicinity of the arrays.

Most eels were first and last recorded during the middle and the end of ebb tide (59.6% at arrival and 58.9% at departure; Fig. 8, middle panel; Table S3). For all arrays and both years, the detailed tidal phase distribution of detections was significantly different to that which would have been expected if there had been no tidal phase effect (χ^2 test, df = 5, $p < 0.001$; Fig. 8, middle panel; Table S3). Also, the predicted distributions were not different from those observed with the sentinel tags for all distances (χ^2 test, df = 5, $p > 0.05$; Table S3). The middle and end of ebb tide at estuarine arrays corresponded to periods when current speeds were the greatest (Fig. 8, lower panel). Finally, 71.4% of the eels detected at tidally influenced

Fig. 7. St. Lawrence River discharge at Lasalle (near Montréal, QC) during the acoustic tracking period in 2010 and 2011. From daily data obtained at http://www.cehq.gouv.qc.ca.



lines were recorded during less than 20 min, indicating a relatively short period of time when eels were present within the detection range of the receivers.

Escapement from the Gulf of St. Lawrence

No eels were detected at the Canso Strait line (km 1360) in either year. In 2010, no eels were detected at the Cabot Strait line (km 1300), keeping in mind that only 28% of the strait was covered by receivers. In 2011, 83 signals corresponding to four eels were detected at Cabot Strait when the acoustic array extended across the strait. All detected eels were released in the maritime estuary (Rivière-du-Loup, km 470) in October 2011. Thus, the detection rate at Cabot Strait array was only 4.0% when taking into account the total number of eels that were detected migrating down the St. Lawrence brackish estuary plus the eels released in the maritime estuary (n = 98). Four eels were detected at Cabot Strait between 1 November 2011 and 28 November 2011, i.e., between 18.5 and 39.4 days after their release date. Considering a straight-line distance between Cabot Strait array and the release site or the last estuarine array where the eels were detected, this represented a mean migration speed of 33.5 km·day^{-1} (Table S1). Three of the tagged eels were detected by receivers moored between Cape Breton and St. Paul Island (mean depth of 162 m, see Fig. 1). Each of these three tags was detected at an interval of 0 (only one detection), 2, 4, and 43 min between the first and last detection. The fourth tag was recorded a first time during 2.2 h at five stations moored between 12 and 18 km from the northern tip of St. Paul Island (mean depth of 232 m) and 23 h later at a station moored at 4 km from the southern tip of St. Paul Island (mean depth of 174 m; see Fig. 1). All tagged eels were detected at night and during mid-flood tide, traversing the line with no back and forth movements.

Discussion

Our study documented individual silver American eel movement patterns within the St. Lawrence system and provided a detailed description of their escapement from the system. With the measurement of the 121 individual migration patterns of silver American eels obtained from the two years of the survey, silver American eel migration in the river and estuary appeared to be highly variable in both longitudinal migratory profiles and speed. This variability in migration speed did not appear to be related to river discharge or any phenotypic characteristic. Rather, behavioral differences among individuals appear to be a major source of variation in migration speed. The downstream migration was not completed in one continuous directed movement. Rather, eels paused at various locations within the estuary with clear preference for any place in particular. Most eels were recorded during several hours at arrays before continuing their downstream migration, and even for several days and weeks (up to 92 days) for some eels. Furthermore, four eels moved back and forth between nearby arrays during their migration and three eels were detected on both sides of Île d'Orléans (fluvial estuary, km 304) a few days apart.

We observed that migration speed increased over the season (June to November) in both years. Day length and temperature both decreased over the season, and thus either could act as a cue in the downstream migration of silver American eels, as has been observed for European eels in Norway (Vollestad et al. 1994). Eels that left the river and fluvial estuary late in the season had a higher migration speed than those travelling earlier in the season. This resulted in a synchrony in the time of passage in the brackish estuary during the fall (40 days from late September to early November) for both years. This period of 40 days was previously identified by Verreault et al. (2003) and de Lafontaine et al. (2009) based on fishery statistics for several years. Finally, we found no evidence of a relationship between migration speed and river discharge for American eel migrating in the St. Lawrence, as has been reported for European eel in the Rhine (Breukelaar et al. 2009).

The migration speed calculated for eels migrating within the brackish section of the estuary was highly variable, ranging from 1.2 to 69.5 km·day^{-1}. The observed values are in accordance with those reported for American eel in New Brunswick (0.8–74.3 km·day^{-1}) (Bradford et al. 2009) and with those reported for European eel in Europe (9–36.3 km·day^{-1}) (Westerberg et al. 2007; Westerberg and Sjöberg 2011). The migration speed between the estuary (Rivière-du-Loup, km 470) and Cabot Strait (km 1300) was between 20.6 and 43.7 km·day^{-1}. However, few fish were detected, making comparisons of travel speeds in the Gulf of St. Lawrence with estuarine travel speeds tenuous at best. Similar values were also reported for silver eels of several anguillid species during their seaward migration (12–48 km·day^{-1}) (Jellyman and Tsukamoto 2002; Tesch 1978, 1989).

Our study indicated that silver American eels may exploit currents for migrating down the estuary. First, we demonstrated that eel detections were concentrated in the area where currents are strongest. In the fluvial and brackish estuary, eels were mainly detected along the south shore compared to the north for both years of the study. Two thirds of the tagged eels were recorded south of Île d'Orléans (km 304) compared to the north. The St. Lawrence River south of Île d'Orléans is approximately three times deeper and the currents are approximately three times stronger relative to the north side of the island. Furthermore, the

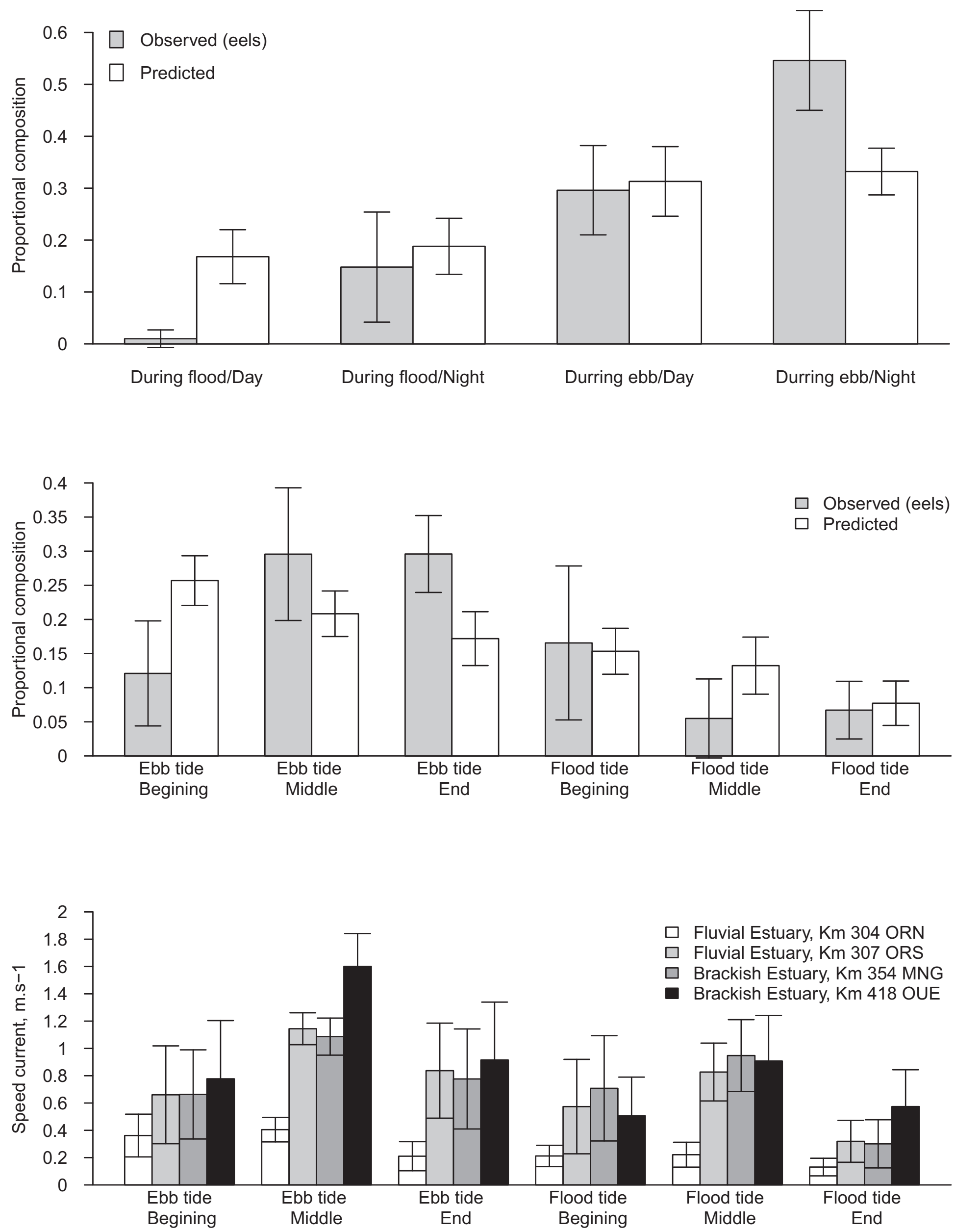


Fig. 8. Diel and tidal patterns of migrating silver American eels observed at estuarine arrays (first detection at Orléans North, Orléans South, Montmagny, and Ouelle arrays). Barplots represent the means of values calculated for each estuarine array and both years, and error bars represent the standard deviation associated with each mean (see Tables S2 and S3 for details). Predicted proportions were determined by compartmentalizing the observed number of detections according to the proportional composition of night and day and tidal phases when eels were recorded at arrays. Proportion for sentinel tags are not plotted here but are not statistically different from the predicted ones (see Tables S2 and S3 for details). The lower panel represents the values of current speed at arrays according to tidal phases (hourly predicted values obtained from Fisheries and Oceans Canada models for periods when eels were recorded).

few silver American eels detected at Cabot Strait appeared to follow the dominant current to exit the Gulf of St. Lawrence. Indeed, most detected eels were recorded at the western part of the Cabot Strait between Cape Breton and St. Paul Island. This area corresponds to the main surface outflow from the Gulf of St. Lawrence (Han et al. 1999). Most silver American eels exiting Passamaquoddy Bay (New Brunswick, Canada) also take the route that follows the dominant currents (Bradford et al. 2009; Carr and Whoriskey 2008). These observations may be influenced by passive movements, as the probability of detection of tagged eels will be greatest where the rate of transport of water is greatest.

Second, migrating silver American eels were detected upon arrival and departure from estuarine receiver arrays principally during ebb tide. More specifically, they were detected mostly at mid-ebb tide, when outflowing current speeds were at a maximum. In contrast, a small fraction of detections were recorded at mid-flood tide, when inflowing currents were at a maximum. The observed diel and tidal distribution of eels' detections were significantly different to that which would have been expected if detection patterns were uniquely a function of the relative proportion of nocturnal and daytime hours and tidal phases during the time that eels were recorded at arrays. Furthermore, examination of sentinel tag data showed that the patterns of acoustic detections were not affected by the current speed, direction, or diel period. This indicates that eels use nocturnal ebb-tide transport to migrate out of the estuary. This behaviour corresponds to the definition of selective tidal stream transport (STST) (Forward and Tankersley 2001; Gibson 2003), although the absence of knowledge of eel depth within the water column prevents us from categorically concluding that eels use STST. Furthermore, since most eels were detected at tidal arrays for only several minutes, it seems likely that the eels were actively swimming or drifting while traversing the acoustic arrays rather than residing on or near the bottom. Interestingly, all detections at Cabot Strait were made during flood tide, suggesting a major behavioral change from the behaviour observed in the estuary (although sample size was small). STST is a transport mechanism and also a means of orienting and moving in an appropriate direction (Forward and Tankersley 2001). The behaviour also offers significant savings in the energy required for migration (Weihs 1978). However, the extent and importance of STST among anguillid eels is still debated. No strong evidence for STST has been reported for American eels (Bradford et al. 2009; Parker and McCleave 1997). In the case of European eels, STST was demonstrated in the western North Sea (McCleave and Arnold 1999), whereas other studies did not detect such behaviour among yellow- or silver-stage eels (e.g., Tesch 1992).

At both estuarine and Cabot Strait arrays, migrating silver American eels were more frequently detected during night, indicating that the migration was predominantly nocturnal. This nocturnal activity has already been reported for silver American eels (Bradford et al. 2009; Parker and McCleave 1997) and also for the yellow stage of this species (e.g., Helfman et al. 1983). This is also in accordance with the behaviour of silver European eel (e.g., Aarestrup et al. 2010; Westerberg et al. 2007). In our study, the observed transit time of a silver American eel in the brackish section, from Ile d'Orléans array to Ouelle array, was 24.5 days on average (median of 18.1 days, range = 1.5–83 days). For the same section in September 2011, the transit time of a passive particle travelling only at night is around 14 days, and 11 days when travelling during both night and day (D. Lefaivre, unpublished data). This strongly suggests that transit time of most eels is greater than that of a passive particle and travelling only at night does not substantially increase the transit time at this time of the year in this area.

Only four silver American eels leaving the St. Lawrence system at the exit of the Gulf of St. Lawrence were detected, indicating a surprisingly low detection rate. At fluvial and estuarine arrays, 88.9% of tagged eels were detected compared with only 4.0% at the Cabot Strait. The low detection rate at Cabot Strait could be due to low detection efficiency and (or) to a true escapement rate. Low detection efficiency at the acoustic array could be explained by receiver performance and (or) tag life. Receiver performance was evaluated with sentinel tags and suggested high detection efficiency. Indeed, the daily detection rate of sentinel tags (V9-2x), moored close to the bottom between receivers half-way between Cape Breton and St. Paul Island during 2011, was between 60% and 100% at a distance of 383 m (mid-distance between neighboring receivers, keeping in mind receivers are close to bottom, with bottom depths varying from 150 to 500 m) (I. Jonsen, Dalhousie University, unpublished data). Thus, any eels swimming close to the bottom would most likely have been detected by the Cabot Strait receivers. For eels swimming close to the surface, the detection efficiency is less certain as no sentinel tags were deployed near the surface in 2011. However, in a parallel study tracking small silver American eels (resulting from stocking in the Richelieu River and the Upper St. Lawrence River and Lake Ontario) tagged with V9 tags (G. Verreault, unpublished data), detection rate at Cabot Strait array was 2.5 times greater, suggesting that acoustic range could not in itself be responsible for the low detection rate of wild silver American eels. Short tag life is a possible but unlikely reason for the low detection rate. All eels tagged at Rivière-du-Loup and Mont-Joli could have been detected at Cabot Strait until mid- to late April, whereas most eels tagged further upstream could have been detected only until mid-January (some until mid-February). Considering that silver American eels must arrive at the spawning grounds between January and July (Tesch 2003) and considering the great distance from Cabot Strait to the Sargasso Sea (>2000 km), it seems unlikely that eels had crossed the Cabot Strait after mid-April (assuming that they do not suspend their migration in the Gulf of St. Lawrence; see below). Although it is possible that some eels crossed the Cabot Strait after mid-January (making the assumption of a too-short a tag life plausible for some eels tagged in the upper St. Lawrence River in July), the detected eels were all recorded at Cabot Strait much earlier in November. In the absence of observations of swimming depth and the detection of acoustic tags as a function of depth, we are unable to quantify to what extent the low escapement rate observed at Cabot Strait was due to low detection probabilities of moored hydrophones.

The low detection rate may also reflect the true escapement rate because of (*i*) high mortality rate of migrating eels, and (or) (*ii*) cessation of migration before entering the open ocean. A high mortality rate, possibly due to predation, could be responsible for a low escapement rate. Indeed, in 2011, six of the eight eels equipped with archival pop-up tags were probably eaten by porbeagle sharks (*Lamna nasus*) while they were tracked in the Gulf of St. Lawrence (Béguer-Pon et al. 2012). Although tagging itself may contribute to increasing the eel's susceptibility to predation, porbeagle sharks are known eel predators, with American eels having been reported in their stomachs (Joyce et al. 2002; D. Cairns, Fisheries and Oceans Canada, personal communication), and predation during the spawning migration could represent an important source of mortality.

Finally, low escapement rate may reflect a decision by fish to suspend their migration in the Gulf of St. Lawrence for a period of time before continuing the following season. Hain (1975) suggested that American eel make several trial runs before leaving for the Sargasso Sea. Eel maturation could be more flexible than previously recognized, and the transition from the growth phase to the migration and maturation phases may be temporarily suspended and feeding resumed during the first part of the migratory phase in relation to the energetic status and feeding opportunities in different habitats (Svedäng and Wickström 1997). Considering the tag life of 195 days we used (and hence possible detections at Cabot Strait until at most mid-April 2012 for eels tagged during October 2011), this hypothesis of a two-step migration could not be verified. Escapement of eels at the Strait of Belle Isle (a 17.5 km wide strait located in the northeast Gulf of St. Lawrence, Fig. 1) seems very unlikely, as inflow largely predominates (Petrie et al. 1988) and it would add a distance of 1400 km for eels to reach the edge of the continental shelf at the exit of the Laurentian Channel.

Our study documented the migration patterns of silver American eels from the St. Lawrence River to the Gulf of St. Lawrence. However, further studies, involving acoustic tags equipped with depth sensors and also arrays separated by shorter distances, are needed to rigorously test the STST hypothesis for migrating silver American eels in the St. Lawrence River and the depth distributions of eels during out-migration from the Gulf of St. Lawrence. Longer life-time tags are also needed to test the two-step migration hypothesis. Further experiments are needed to test the efficiency of the Cabot Strait acoustic line to detect tags as a function of depth and the behavior of migrating eels. Finally, the great variability in individual behavior observed here could be related to anthropomorphic impacts on eels such as the heavy chemical contamination of these eels that could affect physiological performance (Castonguay et al. 1994*a*; Couillard et al. 1997). A comparison of the individual variability we have revealed in our study with that of eels inhabiting less-contaminated locations represents an interesting avenue for future research.

Acknowledgements

Funding for this project was provided to Julian J. Dodson and Martin Castonguay as part of the Ocean Tracking Network, a Strategic Network Grant of the Natural Science and Engineering Research Council of Canada and the Canada Foundation for Innovation. The authors would like to thank Yannick Bergeron, Florent Archambault, Guillaume Lemieux, David Leblanc, Nicolas Harnois, Jean-Guy Frenette, Simon Bernatchez, Yanick Soulard, Johanne Dussureault, Martine Tremblay, Kim Belzile, Hacène Tamdrari, Duncan Bates, Ian Beveridge, and David Paez for their technical support during this study. Ian Jonsen (Dalhousie University) and Dale Webber (Vemco) are acknowledged for their analysis of Cabot Strait sentinel tag and receiver data, respectively. The authors also acknowledge Québec-Océan (http://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).

References

Aarestrup, K., Økland, F., Hansen, M.M., Righton, D., Gargan, P., Castonguay, M., Bernatchez, L., Howey, P., Sparholt, H., Pedersen, M., and McKinley, R.S. 2009. Oceanic spawning migration of the European eel (*Anguilla anguilla*). Science, **325**(5948): 1660. doi:10.1126/science.1178120. PMID:19779192.

Aarestrup, K., Thorstad, E.B., Koed, A., Svendsen, J.C., Jepsen, N., Pedersen, M.I., and Økland, F. 2010. Survival and progression rates of large European silver eel *Anguilla anguilla* in late freshwater and early marine phases. Aquat. Biol. **9**: 263–270. doi:10.3354/ab00260.

Acou, A., Boury, P., Laffaille, P., Crivelli, A.J., and Feunteun, E. 2005. Towards a standardized characterization of the potentially migrating silver European eel (*Anguilla anguilla*, L.). Arch. Hydrobiol. **164**(2): 237–255. doi:10.1127/0003-9136/2005/0164-0237.

Béguer-Pon, M., Benchetrit, J., Castonguay, M., Aarestrup, K., Campana, S.E., Stokesbury, M.J.W., and Dodson, J.J. 2012. Shark predation on migrating adult American eels (*Anguilla rostrata*) in the Gulf of St. Lawrence. PloS ONE, **7**(10): e46830. doi:10.1371/journal.pone.0046830. PMID:23082131.

Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H., and White, J.-S.S. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends Ecol Evol **24**(3): 127–135. doi:10.1016/j.tree.2008.10.008.

Bradford, R.G., Carr, J.W., Page, F.H., and Whoriskey, F. 2009. Migration of silver American eels through a macrotidal estuary and bay. *In* Challenges for diadromous fishes in a dynamic global environment. *Edited by* A. Haro, K.L. Smith, R.A. Rulifson, C.M. Moffitt, R.J. Klauda, M.J. Dadswell, R.A. Cunjak, J.E. Cooper, K.L. Beal, and T.S. Avery. American Fisheries Society Symposium, Bethesda, Md. pp. 275–292.

Breukelaar, A.W., Ingendahl, D., Vriese, F.T., de Laak, G., Staas, S., and Klein Breteler, J.G.P. 2009. Route choices, migration speeds and daily migration activity of European silver eels *Anguilla anguilla* in the River Rhine, north-west Europe. J. Fish Biol. **74**(9): 2139–2157. doi:10.1111/j.1095-8649.2009.02293.x. PMID:20735693.

Caron, F., Verreault, G., and Rochard, E. 2003. Estimation of the population size, exploitation rate, and escapement of silver-phase American eels in the St. Lawrence watershed. *In* Biology, Management, and Protection of Catadromous Eels. *Edited by* D.A. Dixon. American Fisheries Society Symposium, Bethesda, Md. pp. 235–242.

Caron, F., Dumont, P., Mailhot, Y., and Verreault, G. 2007. L'anguille au Québec une situation préoccupante. Nat. Can. **131**(1): 59–66.

Carr, J.W., and Whoriskey, F.G. 2008. Migration of silver American eels past a hydroelectric dam and through a coastal zone. Fish Manage. Ecol. **15**(5–6): 393–400. doi:10.1111/j.1365-2400.2008.00627.x.

Castonguay, M., Hodson, P.V., Couillard, C.M., Eckersley, M.J., Dutil, J.-D., and Verreault, G. 1994*a*. Why is recruitment of the American eel, *Anguilla rostrata*, declining in the St. Lawrence River and Gulf? Can. J. Fish. Aquat. Sci. **51**(2): 479–488. doi:10.1139/f94-050.

Castonguay, M., Hodson, P.V., Moriarty, C., Drinkwater, K.F., and Jessop, B.M. 1994*b*. Is there a role of ocean environment in American and European eel decline? Fish. Oceanogr. **3**(3): 197–203. doi:10.1111/j.1365-2419.1994.tb00097.x.

COSEWIC. 2012. COSEWIC assessment and status report on the American Eel *Anguilla rostrata* in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa. xii + 109 pp (www.registrelep-sararegistry.gc.ca/default_e.cfm).

Côté, C.L., Gagnaire, P.-A., Bourret, V., Verreault, G., Castonguay, M., and Bernatchez, L. 2013. Population genetics of the American eel (*Anguilla rostrata*): F_{ST} = 0 and North Atlantic Oscillation effects on demographic fluctuations of a panmictic species. Mol. Ecol. **22**(7): 1763–1776. doi:10.1111/mec.12142. PMID:23216918.

Couillard, C.M., Hodson, P.V., and Castonguay, M. 1997. Correlations between pathological changes and chemical contamination in American eels, *Anguilla rostrata*, from the St. Lawrence River. Can J. Fish. Aquat. Sci. **54**(8): 1916–1927. doi:10.1139/f97-097.

Daverat, F., Limburg, K.E., Thibault, I., Shiao, J.C., Dodson, J.D., Caron, F., Tzeng, W.-N., Iizuka, Y., and Wickström, H. 2006. Phenotypic plasticity of habitat use by three temperate eel species, *Anguilla anguilla*, *A. japonica* and *A. rostrata*. Mar. Ecol. Prog. Ser. **308**: 231–241. doi:10.3354/meps308231.

de Lafontaine, Y., Lagacé, M., Gingras, F., Labonté, D., Marchand, F., and Lacroix, E. 2009. The decline of the American eel in the St. Lawrence River: Effects of local hydroclimatic conditions on CPUE indices. *In* Eels at the edge. Science, status, and conservation concerns. *Edited by* J.M. Casselman and D. Cairns. American Fisheries Society, Bethesda, Md. pp. 207–229.

Dumont, P., LaHaye, M., Leclerc, J., and Fournier, N. 1997. Caractérisation des captures d'anguille d'Amérique dans des pêcheries commerciales de la rivière Richelieu et du lac Saint-François. *In* Compte Rendu du Deuxième Atelier sur les Pêches Commerciales. *Edited by* M. Bernard and C. Groleau. Ministère des Ressources Naturelles et Faune Québec, Québec City. pp. 25–34.

Forward, R.B., and Tankersley, R.A. 2001. Selective tidal-stream transport of marine animals. Oceanogr. Mar. Biol. Annu. Rev. **39**: 305–353.

Gibson, R.N. 2003. Go with the flow: tidal migration in marine animals. Hydrobiologia, **503**(1–3): 153–161. doi:10.1023/B:HYDR.0000008488.33614.62.

Hain, J.H.W. 1975. The behaviour of migratory eels, *Anguilla rostrata*, in response to current, salinity and lunar period. Helgoländer Wissen. Meeresun. **27**: 211–233. doi:10.1007/BF01611808.

Han, G., Loder, J.W., and Smith, P.C. 1999. Seasonal-mean hydrography and circulation in the Gulf of St. Lawrence and on the eastern Scotian and southern Newfoundland shelves. J. Phys. Oceanogr. **29**(6): 1279–1301. doi:10.1175/1520-0485(1999)029<1279:SMHACI>2.0.CO;2.

Haro, A., Richkus, W., Whalen, K., Hoar, A., Busch, W.D., Lary, S., Brush, T., and Dixon, D. 2000. Population decline of the American eel: implications for research and management. Fisheries, **25**(9): 7–16. doi:10.1577/1548-8446(2000)025%3C0007:PDOTAE%3E2.0.CO;2.

Helfman, G.S., Stoneburner, D.L., Bozeman, E.L., Christian, P.A., and Whalen, R. 1983. Ultrasonic telemetry of American eel movements in a tidal creek. Trans. Am. Fish. Soc. **112**: 105–110. doi:10.1577/1548-8659(1983)112<105:UTOAEM>2.0.CO;2.

Heupel, M.R., Semmens, J.M., and Hobday, A.J. 2006. Automated acoustic tracking of aquatic animals: scales, design and deployment of listening station arrays. Mar. Freshw. Res. **57**(1): 1–13. doi:10.1071/MF05091.

Hintze, J.L., and Nelson, R.D. 1998. Violin plots: a box plot-density trace synergism. Am. Stat. **52**(2): 181–184. doi:10.1080/00031305.1998.10480559.

Hollander, M., and Wolfe, D.A. 1973. Nonparametric statistical methods. John Wiley & Sons, New York.

Jellyman, D., and Tsukamoto, K. 2002. First use of archival transmitters to track migrating freshwater eels *Anguilla dieffenbachii* at sea. Mar. Ecol. Prog. Ser. **233**: 207–215. doi:10.3354/meps233207.

Joyce, W.N., Campana, S.E., Natanson, L.J., Kohler, N.E., Pratt, H.L.J., and Jensen, C.F. 2002. Analysis of stomach contents of the porbeagle shark (*Lamna nasus* Bonnaterre) in the northwest Atlantic. ICES J. Mar. Sci. **59**(6): 1263–1269. doi:10.1006/jmsc.2002.1286.

Knights, B. 2003. A review of the possible impacts of long-term oceanic and climate changes and fishing mortality on recruitment of anguillid eels of the Northern Hemisphere. Sci. Total Environ. **310**: 237–244. doi:10.1016/S0048-9697(02)00644-7. PMID:12812748.

Lucas, M.C., and Baras, E. 2000. Methods for studying spatial behaviour of freshwater fishes in the natural environment. Fish Fish. **1**(4): 283–316. doi:10.1046/j.1467-2979.2000.00028.x.

McCleave, J.D., and Arnold, G.P. 1999. Movements of yellow- and silver-phase European eels (*Anguilla anguilla* L.) tracked in the western North Sea. ICES J. Mar. Sci. **56**(4): 510–536. doi:10.1006/jmsc.1999.0478.

Okamura, A., Yamada, Y., Yokouchi, K., Horie, N., Mikawa, N., Utoh, T., Tanaka, S., and Tsukamoto, K. 2007. A silvering index for the Japanese eel *Anguilla japonica*. Environ. Biol. Fishes, **80**(1): 77–89. doi:10.1007/s10641-006-9121-5.

Pankhurst, N.W. 1982. Relation of visual changes to the onset of sexual maturation in the European eel *Anguilla anguilla* (L.). J. Fish Biol. **21**(2): 127–140. doi:10.1111/j.1095-8649.1982.tb03994.x.

Parker, S.J., and McCleave, J.D. 1997. Selective tidal stream transport by American eels during homing movements and estuarine migration. J. Mar. Biol. Assoc. U.K. **77**(3): 871–889. doi:10.1017/S0025315400036237.

Petrie, B., Toulany, B., and Garrett, C. 1988. The transport of water, heat and salt through the strait of Belle Isle. Atmos.-Ocean, **26**(2): 234–251. doi:10.1080/07055900.1988.9649301.

R Core Team. 2013. R: A language and environment for statistical computing. Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org/.

Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. **191**: 1–382.

Svedäng, H., and Wickström, H. 1997. Low fat contents in female silver eels:

indications of insufficient energetic stores for migration and gonadal development. J. Fish Biol. **50**(3): 475–486. doi:10.1111/j.1095-8649.1997.tb01943.x.
Tesch, F.-W. 1978. Telemetric observations on the spawning migration of the eel (*Anguilla anguilla*) west of the European continental shelf. Environ. Biol. Fishes, **3**(2): 203–209. doi:10.1007/BF00691944.
Tesch, F.-W. 1989. Changes in swimming depth and direction of silver eels (*Anguilla anguilla* L.) from the continental shelf to the deep sea. Aquat. Living Resour. **2**: 9–20. doi:10.1051/alr:1989002.
Tesch, F.-W. 1992. Insignificance of tidal currents for silver eel migration as studied by eel trackings and current measurements. Ir. Fish. Invest. Ser. A, **36**: 105–109.
Tesch, F.W. 2003. The eel. 3rd ed. Blackwell Publishing.
Therriault, J.-C. 1991. The Gulf of St. Lawrence: small ocean or big estuary? Can. Spec. Publ. Fish. Aquat. Sci. **113**: 359.
Thorstad, E.B., Kerwath, S.E., Attwood, C.G., Økland, F., Wilke, C.G., Cowley, P.D., and Næsje, T.F. 2009. Long-term effects of two sizes of surgically implanted acoustic transmitters on a predatory marine fish (*Pomatomus saltatrix*). Mar. Freshw. Res. **60**: 183–186. doi:10.1071/MF08191.
Thorstad, E.B., Økland, F., Westerberg, H., Aarestrup, K., and Metcalfe, J.D. 2013. Evaluation of surgical implantation of electronic tags in European eel and effects of different suture materials. Mar. Freshw. Res. **64**(4): 324–331. doi:10.1071/MF12217.
Verreault, G., Pettigrew, P., Tardif, R., and Pouliot, G. 2003. The exploitation of the migrating silver American eel in the St. Lawrence River Estuary, Québec, Canada. *In* Biology, management, and protection of catadromous eels. *Edited by* D.A. Dixon. American Fisheries Society Symposium, Bethesda, Md. pp. 225–234.
Verreault, G., Mingelbier, M., and Dumont, P. 2012. Spawning migration of American eel *Anguilla rostrata* from pristine (1843–1872) to contemporary (1963–1990) periods in the St Lawrence Estuary, Canada. J. Fish. Biol. **81**(2): 387–407. doi:10.1111/j.1095-8649.2012.03366.x. PMID:22803716.
Vollestad, L.A., Jonsson, B., Hvidsten, N.-A., and Naesje, T.F. 1994. Experimental test of environmental factors influencing the seaward migration of European silver eels. J. Fish Biol. **45**(4): 641–651. doi:10.1111/j.1095-8649.1994.tb00930.x.
Weihs, D. 1978. Tidal stream transport as an efficient method for migration. J. Cons. Int. Explor. Mer, **38**: 92–99. doi:10.1093/icesjms/38.1.92.
Westerberg, H., and Sjöberg, N. 2011. Migration behaviour of stocked and naturally recruited eel. Working Paper ICES/EIFAC WGEEL 2011.
Westerberg, H., Lagenfelt, I., and Svedang, H. 2007. Silver eel migration behaviour in the Baltic. ICES J. Mar. Sci. **64**(7): 1457–1462. doi:10.1093/icesjms/fsm079.