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Spatial ecology of translocated American Eel (*Anguilla rostrata*) in a large freshwater lake

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Abstract
American Eel (*Anguilla rostrata*) undertake extensive migrations from their rearing grounds to spawn in the Sargasso Sea, and historically the upper St. Lawrence River and Lake Ontario provided an important source for large, fecund female eel. Following declines in the Lake Ontario population, glass eel were translocated from eastern Canada from 2006 to 2010. From 2016 to 2018, large, presumably translocated yellow eel ($N=230$) with the potential to begin maturing and out-migrating within their year of capture were collected in spring and fall and tagged with acoustic transmitters. Eel were released into eastern Lake Ontario and tracked to better understand their movement patterns prior to and during migration, and the timing of migration. Most eels successfully migrated out of Lake Ontario (64%). Timing of migration was consistent regardless of year or tagging season and primarily occurred in late summer or fall, with cooling water temperatures and decreasing sky illumination associated with initiation for fall tagged eel. Eels were mostly detected in eastern Lake Ontario and those in western Lake Ontario were mostly detected in shallow waters (< 20 m) close to shore. Eels were detected on fewer receivers in the winter, suggesting reduced movements during this season. Finally, larger individuals spent less time in the system, particularly when tagged in the fall. These findings confirm that translocated eels can migrate out of Lake Ontario; however, the weeks when migration occurred were more aligned with timing in their natal range (i.e., eastern Canada) than with naturally recruited eels from Lake Ontario. This temporal mismatch requires further consideration, since it may influence arrival times of translocated eel to the spawning grounds and their recruitment potential. These results can be used to inform future assessments of eel translocation efficacy and can also aid in the design of future tracking studies to more completely explore the downstream migration success of eel translocated into the highly productive waters of Lake Ontario.

Keywords Acoustic telemetry, Migration cues, Lake Ontario, Movement

Background

Effective management and conservation of fish populations requires an understanding of where and when a species lives and moves [13, 17, 59] and fundamental to this is describing the characteristics of a species' movement [1]. These characteristics include the shape or size of home ranges, the timing or distance of movements, or commonly used movement and migration pathways [1]. This information can then be used by fisheries managers to define the boundaries of protected areas or management zones [8, 26, 28], protect movement corridors or important habitat [53], evaluate migration success [56],

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and identify movement behaviours and patterns for more effective resource management [21, 72]. Further, a species' spatial ecology can be useful when assessing the efficacy of stocking or translocations since the movement of individuals in a novel environment may be distinct from their natal range or misaligned with remnant populations of the same species [9, 10, 36]. Despite the noted benefits of incorporating movement ecology into conservation and management decisions, this type of information remains underutilized [13, 17, 43].

American Eel (*Anguilla rostrata*) are an ecologically, culturally, and economically important species that has seen a marked population decline and is now listed as Threatened on the International Union for Conservation of Nature (IUCN) red list and assessed as Threatened by the Committee on the Status of Endangered Wildlife in Canada [14, 30]. They are a catadromous, semelparous, panmictic species that are thought to be comprised of a single population that make long migrations (> 5000 km) from their rearing habitats to reproduce in the Sargasso Sea and then die [15, 58]. As young (glass-stage, elvers, or early yellow-stage) eels they migrate to freshwater rivers or lakes, brackish estuaries, or nearshore coastal parts of the Atlantic Ocean [2, 55]. In their rearing habitats, yellow-stage American Eel are primarily benthic and found in nearshore lotic and lentic waters to depths of 10 m over a range of substrate types [55, 58]. They are thought to either overwinter in burrows or aggregate in bays/estuaries on mud substrates [60]; however, like many fishes, their winter ecology is poorly understood [41]. Once mature, silver-stage American Eel migrate back to the Sargasso Sea during the late summer or fall in northern latitudes and later for more southern latitudes [14, 23, 32], which is thought to ensure arrival times align among sub-populations. For American Eel and other congenerics (e.g., European Eel, *Anguilla anguilla*), environmental factors such as light, tidal directions, discharge, and lunar phase have been found to influence migration and movements [4, 61, 67]; however, there is considerable variation in the start and duration of migration among American Eel from different regions [14, 23]. Given the migration distances and life cycle complexity of the American Eel, understanding their movement ecology can assist in their conservation and management.

In the Lake Ontario—St. Lawrence River region, the American Eel sub-population has experienced a decline in recruitment by more than 99% since the early 1980s [11, 40]. Historically, this region only contained females and consequently was an important source of larger and more fecund female spawners that were believed to contribute significantly to the overall spawning biomass [11, 12]. As such, population impairments in this region are of concern for the conservation of the species as a whole. The decline in American Eel has been linked to a wide variety of factors including barriers to fish upstream migration (e.g., dams), commercial and recreational harvest, changing ocean conditions, as well as mortality at hydroelectric facilities during their downstream migration [19, 24, 40, 52, 65]. After long term declines in the Lake Ontario—St. Lawrence River region, a moratorium was placed on harvesting eel for Lake Ontario fisheries and the American Eel was listed as Endangered in Ontario's Endangered Species Act in 2007 [14].

In order to increase population abundance in Lake Ontario, 4.1 million glass eel from Nova Scotia and New Brunswick were successfully translocated between 2006 and 2010 [48], and the majority of the American Eel currently in Lake Ontario are a result of these efforts (T. Pratt, Fisheries and Oceans Canada, unpublished data). Little is known about successful migration of translocated eels back to the Sargasso Sea to spawn, and studies with European Eel have shown mixed support for successful [70] and unsuccessful [49, 71] migration. Across the range of American Eel, growth rates and length at maturity vary by both latitude and distance to spawning grounds with smaller adult females in areas like Nova Scotia (47–65 cm on average) compared to those historically in Lake Ontario and the upper St. Lawrence River (> 90 cm,[31]). Given this size discrepancy, Verreault et al. [66] questioned whether stocked American Eel that mature at a smaller size than naturally recruited eel would be able to travel the entire distance to the Sargasso Sea. Regardless of size, migration of translocated eel through the St. Lawrence River has been documented with initial evidence for synchrony in timing of migration with naturally recruited American Eel [7, 66], but information is limited on short-term movement ecology and migration timing for American Eel translocated further upstream in Lake Ontario. Thus, understanding the movement and timing of migration will inform management on the extent that these translocated American Eel migrate and what may influence said migration.

Since 2015, a small subset of American Eel incidentally caught by commercial fishers in eastern Lake Ontario and the upper St. Lawrence River were tagged with acoustic transmitters and re-released into Lake Ontario to explore the timing and success of their out-migration, primarily to support the downstream passage goals of the Eel Passage Research Center [47]. With the expansion of acoustic telemetry receivers throughout Lake Ontario in 2016, there was an opportunity to track these tagged American Eel to determine when they left the system and where else they may have traveled within the lake. The objective of this study was to explore the movements of American Eel following their capture, tagging, and release into Lake Ontario. Specifically, we document:

(1) the timing of the start of their migration from Lake Ontario into the St. Lawrence River, (2) the timing and extent of movements within Lake Ontario in the summer and winter, (3) whether environmental cues predict the start of migration, and (4) if smaller individuals were more likely to overwinter before migrating to the St. Lawrence River. Collectively, assessing these objectives will provide insight into the movement characteristics of American Eel translocated into a novel large lotic system, which can help managers assess the efficacy of these translocations as potential future recovery actions.

Methods

Study site

Lake Ontario, one of the five Laurentian Great Lakes, drains directly into the St. Lawrence River. It has an average depth of 86 m, maximum depth of 245 m, and a surface area of ~ 19,000 km^2. The eastern region is considerably deeper than the western region (Fig. 1), but the shorelines in the eastern region are also more complex with numerous islands and bays. In contrast, shorelines at the western region of the lake are less complex and have greater anthropogenic disturbance and shoreline alteration. Although the lake is generally cool and deep, sheltered areas such as Hamilton Harbour and Toronto Harbour in the western region, and the Bay of Quinte in the eastern region, historically supported productive fisheries for a variety of species.

To better understand lake dynamics and potential impacts on American Eel (herein "eel") behaviour, we defined seasonality of the lake using thermocline delineation and temperature changes based on the seasons

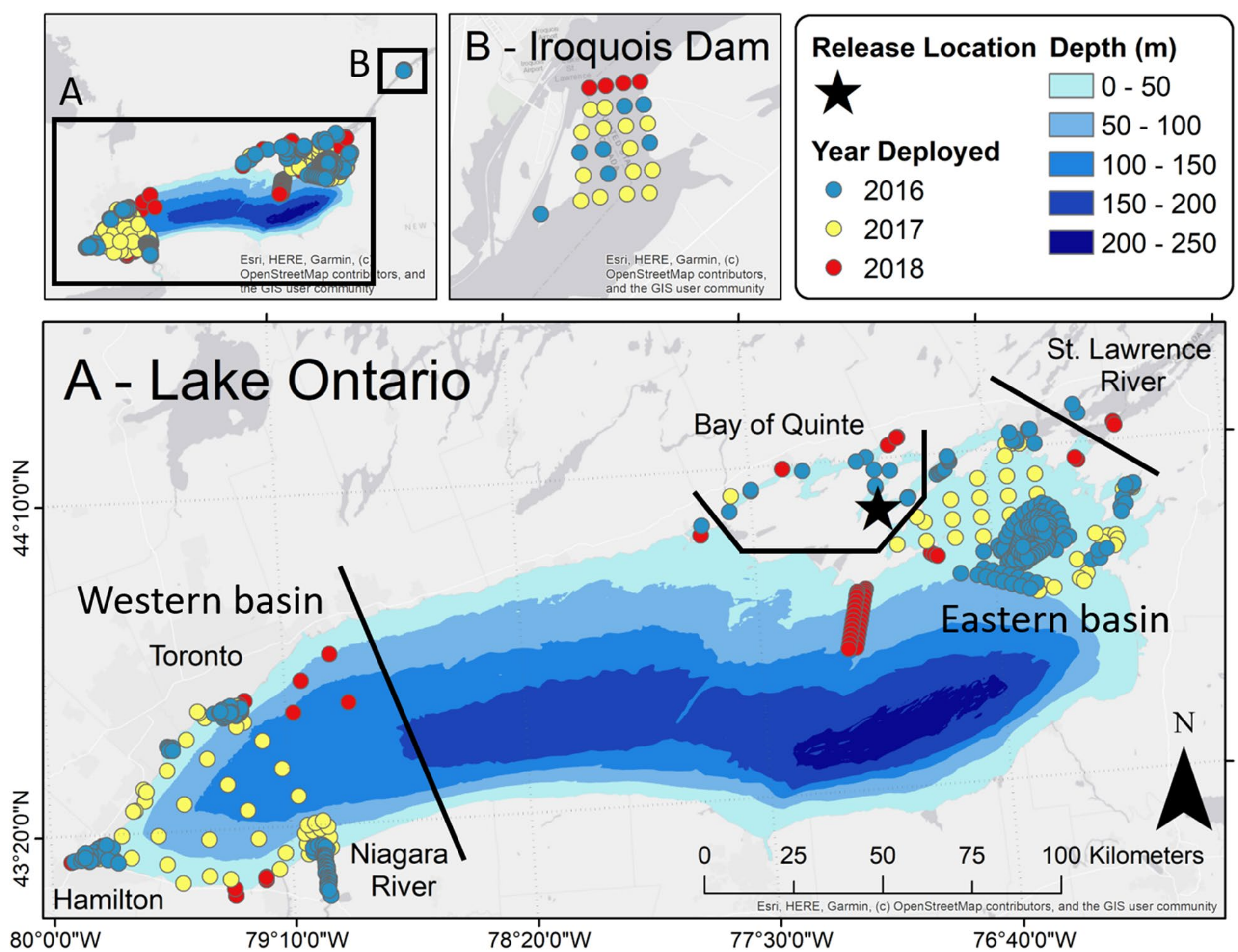

Fig. 1 Map of the acoustic receiver array in Lake Ontario and the St. Lawrence River. The array is represented for the duration of the study (2016–2018), the year initially deployed indicates when the receiver was originally deployed, but all were held in the same position until the end of the study. Receiver groupings are split into eastern and western regions, Bay of Quinte, and the St. Lawrence River (also includes receivers at the Iroquois Dam (inset B))

defined in Larocque et al. [37]. Briefly, data were compiled from temperature chains deployed in Toronto Harbour (43.637, − 79.392) and in the open lake near Ajax, ON (43.767, − 79.984). From these data, the start and end dates for seasons in each year were defined as follows: winter—water temperatures are consistently less than 5 °C, spring—temperatures are increasing (> 5 °C) until they surpassed 15 °C, summer—temperatures were consistently above 15 °C, and fall—temperatures decreasing (< 15 °C) until they stabilized at 5 °C [37].

Eel capture and tagging program

Eels were captured in the Bay of Quinte, eastern Lake Ontario, and the upper St. Lawrence River by local commercial fishers as part of an adult eel trap and transport program that has been underway since 2008 [45]. A subset of the eel were acoustically tagged and released in Lake Ontario in the spring and fall of 2016 and 2017, and spring of 2018. Previous studies on eels in the Bay of Quinte included an examination of otolith bones for the oxytetracycline 'stocking mark'; 94.8% of eels examined between 2015 and 2020 had this mark ($N = 451$, total length = 0.85 ± 0.07 m, range: 0.57–1.12 m), indicating that the vast majority of eels were translocated glass eels that originated in Nova Scotia and New Brunswick (T. Pratt, Fisheries and Oceans Canada, unpublished data). Since examining the otoliths for an oxytetracycline mark is lethal, the status of eels as stocked or native could not be explicitly assessed during acoustic tagging. Captured eels were measured for total length (m) and subsequently tagged. A V13 69-kHz acoustic transmitter (Innovasea, Bedford, NS; hereafter called tag; tag specifications varied among batches (see Additional file 1: Table S1), but were all high-power output, length 36 mm x diameter 13 mm, and 6.3 g mass in water; nominal delay was typically 60 s [range 40–120] and an estimated battery life of 331 days [range 256–653]) was surgically implanted in each eel following methods outlined by Béguer-Pon et al. [7]. Briefly, captured eels were anesthetized using clove oil (60 ppm) and then further immobilized with electrofishing gloves (Smith-Root, Vancouver, WA) before being placed ventral side up in a trough. A 2–3 cm incision was made mid-ventral anterior to the anal fin, the transmitter was inserted, and the incision was closed using one or two simple interrupted sutures. Following recovery (typically 2–4 h in an aerated recovery tank), eels were released at the OMNRF Glenora Fisheries Station in the Bay of Quinte (44.0416, − 77.0579; Fig. 1). Since eels were tagged over multiple years and seasons, from here on a 'tagging session' refers to a season and year where eels were tagged and released into the lake (e.g., Spring 2017) while a 'tagging season' refers to multiple tagging sessions that happened during the same season (e.g., the spring tagging season includes the tagging sessions Spring 2016, Spring 2017, and Spring 2018).

Acoustic receiver array

During the study period (April 2016 to April 2019), a total of 283 (2016), 359 (2017), and 379 (2018) acoustic telemetry receivers (69-kHz VR2W and VR2AR, Innovasea, Bedford, NS, Canada) were deployed throughout Lake Ontario and the St. Lawrence River as part of ongoing acoustic telemetry projects coordinated through the Great Lakes Acoustic Telemetry Observation System (GLATOS) network (Fig. 1; [35]). Since GLATOS is a collaborative network, the number of receivers and array coverage in certain regions changed annually. Receiver groupings covering the open waters of Lake Ontario were located in the western (12 in 2016; 48 in 2017; 51 in 2018) and eastern regions ($n = 147$ in 2016; 182 in 2017; 206 in 2018), with additional receivers in the Bay of Quinte, Toronto Harbour, Hamilton Harbour, and the Niagara River. Receivers were also placed at the entrance to the St. Lawrence River and further downstream at the Iroquois Dam to monitor downstream migration of eels (Fig. 1). In Lake Ontario, receiver spacing varied from 1 to 15 km apart, with grid patterns used in the western and eastern regions, and a bathymetry driven design around the St. Lawrence Channel in the eastern region. Bathymetric depth of receivers deployed in Lake Ontario ranged from 4 to 120 m during the time of the study (Fig. 1). Due to logistical challenges, there was a lack of receiver coverage in the central region of Lake Ontario. For more details on the receiver moorings see Klinard et al. [33] and Ivanova et al. [29].

Detection data during the study period were filtered for false detections, which removes any detections of an individual tag that is detected on a single receiver and separated by more than 30 times the nominal delay of the tag [46]. Any detections that happened outside of our study zone (i.e., Lake Ontario and the upper St. Lawrence River to the Iroquois Dam; Fig. 1) were also removed. Detection data were further filtered to check for mortality or expelled tags, and those individuals were subsequently removed from analyses [34]. Fish were inferred to be dead if they stayed within the same area of the array and/or moved less than 1.5 km for an extended period of time without a change in this detection pattern by the end of their tag life. This distance was selected to represent separation among receivers that is likely beyond typical detection ranges for receivers in Lake Ontario [33, 69]. All data preparation was conducted with the assistance from the R package "glatos" [27].

Analyses

General movement patterns

All analyses were completed in R version 4.0.2 [51]. Eel detection data were visualized to explore patterns in their spatial ecology on the Lake Ontario telemetry array. We plotted the detection patterns for each individual eel through time and noted when they moved among four general areas: Bay of Quinte, eastern Lake Ontario, western Lake Ontario, and the St. Lawrence River (Fig. 1; Additional file 1: Fig. S1). We summarized the total number of eels from each tagging session that were detected in each part of the lake and determined the day of last detection in the lake. As eels left the Bay of Quinte, we investigated migration movements and their timing into the St. Lawrence River as well as movements in Lake Ontario. In order to reach the St. Lawrence River, eels needed to move through eastern Lake Ontario and would be captured on the receivers located in that part of the lake. We quantified the number of eels that moved into the St. Lawrence River to migrate shortly after tagging; overwintered in Lake Ontario and then moved to the St. Lawrence River; and those that stayed in Lake Ontario and did not migrate by the time the battery life ended. To explore movement patterns in the eastern part of Lake Ontario prior to migration, we plotted detection patterns for eels tagged in spring 2017 and 2018; these two tagging sessions were selected because array coverage in the east was more spatially comprehensive than in 2016.

For each tagging session, we assigned seaward migration status for each individual (e.g., out-migration, no migration) based on whether eels were or were not detected on the St. Lawrence River receivers. This provided a general indication of the minimum number of eels that were confirmed to migrate during the period when their tags were active; for those assigned to the no migration group, they might have made a seaward migration after their tag stopped working or moved undetected past the river-based receivers, but these alternatives cannot be confirmed.

Based on the observed movements of eels to the western region of Lake Ontario, we compared whether eels that went into the St. Lawrence River (i.e., out-migrants) and those that went to the west end (i.e., west migrants) started their migration and were subsequently migrating at similar times. Timing of the start of migration would ideally have been assessed based on detections at the start of the St. Lawrence River; however, this was not always possible as there was not complete receiver coverage in this area and a majority of out-migrating eels were not detected until further downstream. Similarly, no receivers were deployed in central Lake Ontario and westward moving eels were not detected until in the western region. Instead, we used departure from the Bay of Quinte as a proxy for migration initiation with fall and spring tagged eel analyzed separately based on the more sporadic nature of spring-tagged eel movements (see Additional file 1: Figs. S1 and S2). To determine if peak migration initiation was synchronous for out-migrant and west migrant eels, we calculated the cross correlation (covariance) of the weekly number of eel in each group last detected in the Bay of Quinte with the function "ccf" from the R package "tseries" [62]. To determine if peaks in movement through the St. Lawrence River or in the western region of Lake Ontario were synchronized, we calculated the cross correlation (covariance) of the weekly number of eels based on the first day of detection on the Iroquois Dam (Fig. 1) or at any west end receivers, respectively. Finally, we determined the cross correlation (covariance) of the weekly number of eels leaving the Bay of Quinte and entering the St. Lawrence River (albeit with highly reduced sample sizes) for both fall and spring release seasons to verify that eels leaving the Bay of Quinte, during the fall in particular, is synchronous to entering the St. Lawrence River and migration initiation.

We used the number of receivers an eel was detected on as a proxy to determine the activity levels of eels and how that varied over time. When eels were detected anywhere in Lake Ontario (i.e., all receivers except St. Lawrence River receivers), we calculated the number of receivers an eel was detected on each Julian day and then measured a rolling average over 7 days to remove unwanted noise. We then plotted the mean number of receivers eels were detected at per Julian week, grouped by season to study trends in the activity of the eels. Periods of increased activity were then visually compared with documented migration windows of June to October (approximately weeks 23 to 43) for eels in Lake Ontario [14] and August to November (approximately weeks 31 to 48) for eels in Nova Scotia or New Brunswick [14].

For eels that overwintered in Lake Ontario and specifically for the eels that went to the west end of the lake, we determined if they were detected more frequently closer to shore than offshore in order to better understand their movement corridors. To do this we calculated the number of individual eels detected by each receiver per season. Since our focus was primarily on movements within Lake Ontario, we combined all receivers deployed in Hamilton Harbour, Toronto Harbour, and the Niagara River arrays into distinct single points, and assigned these points the maximum number of individual eels detected on each array during each season. We used a generalized linear model (GLM) using a Poisson distribution to relate the number of eels detected by each receiver to the square root of the distance to shore. Distance to shore was measured in ArcPro using the near tool (v2.4.2, ESRI, Redlands, CA). We also collected bathymetric depth data for each receiver from the National Oceanic and Atmospheric Administration (NOAA) digital elevation model [42]; however, distance to shore and bathymetric depth were highly correlated (0.91) and thus only distance to shore was used in the final model. Assumptions of normality and heteroscedasticity of the model were verified and a bubble plot of the residuals was used to verify that no spatial autocorrelation remained in the residuals of the model.

Movement cues

We explored possible environmental cues for movement out of the Bay of Quinte for all eels tagged in the fall as well as whether the size of eels was related to the duration of time spent in Lake Ontario before outmigrating. Based on the movement synchronicity analysis described above, leaving the Bay of Quinte provided a relatively accurate time for moving towards and into the St. Lawrence River. However, for comparison, we also assessed environmental cues related to movements into the St. Lawrence River (at the start of the river only) with the smaller sample size of eels detected there. To assess movement out of the Bay of Quinte and into the St. Lawrence River, a daily presence (0) or absence (1) in the Bay (or start of the St. Lawrence River) was assigned to each eel, in which a 1 was given when the eel was last detected on Bay of Quinte receivers (some eels left and re-entered the bay) or first detected at the start of the St. Lawrence River. Data were trimmed to a limited period each year based on water temperature availability and to only cover before and during the migration period. Data for fall eels leaving the Bay of Quinte spanned from their date of release (range September 7–29) until December 1 and data for eels entering the St. Lawrence River spanned from July 1 to December 1 for 2016 and 2017, and from July 1 to November 18 for 2018. Environmental variables to predict when eels left the Bay of Quinte or entered the St. Lawrence River included: daily surface water temperature (°C) as measured by buoy #45012 located in eastern Lake Ontario (43.621 − 77.401); total sky illumination at these same coordinates (hours), calculated as the number of hours of daylight including both sunrise and sunset; and moon fullness as a continuous variable (ranging from 0 to 1, or new moon to full moon, respectively) based on the function "lunar.phase" of the R package "lunar" [38]. Pearson's correlations among the environmental variables indicated that water temperature and total sky illumination were highly correlated (0.97) and only water temperature and moon fullness were included in the models. Logistic regression analyses were performed for the fall tagging season using a generalized linear mixed model (GLMM) with a binomial distribution to assess if water temperature and moon fullness were related to the probability of eels leaving the Bay of Quinte, with tag ID as a random effect. A similar logistic regression was performed for eels entering the St. Lawrence River. Assumptions of normality and heteroscedasticity for the models were verified with the R package "DHARMa" [25]. Conditional R^2 of the models were calculated using the R package "MuMIn" [5].

We determined if there was a relationship between the length of eels at tagging and whether they migrated that fall or overwintered and then migrated (both considered a "migration") or stayed in Lake Ontario until the end of the tag's battery life (no migration). For each eel, we calculated the duration of their stay in the lake based on the number of days between their time of release and last detection on the Lake Ontario array. We tested the relationship between length of eels (at tagging) and the length of stay within the lake using an ANCOVA (analysis of covariance) on the square root of the duration of stay, with the length, tagging season, and whether or not they migrated to the St. Lawrence River as explanatory variables. An interaction between tagging season and migration status was included in the model since eels tagged in spring or fall may naturally spend different durations in the lake before migration. Normality and homoscedasticity were verified through visualization of the residuals.

Results

General movement patterns

A total of 230 eels were tagged from 2016 to 2018 (Table 1), with a mean (± standard deviation) total length of 0.91 ± 0.08 m (range: 0.74–1.03 m). Of the 230 tagged eels, 28 were presumed to be dead and of the 202 remaining eels, 130 (64%) left Lake Ontario (14 of which were not detected at the Iroquois Dam but were last detected leaving Lake Ontario and entering the St. Lawrence River). Seventy-two (36%) eels remained within the lake until their tag likely ran out of battery power. For each tagging session, at least one eel was detected in each location (Table 1). More eels were detected in the eastern region of the lake (towards the St. Lawrence River outflow) or in the Bay of Quinte (where they were released), while western Lake Ontario had the lowest number of individual eels detected. That said, of the 72 eels that remained in the lake, 55 of them went to western Lake Ontario at some point.

Several general movement patterns were evident and described as: (1) eels that migrated out of Lake Ontario in the late summer or fall; (2) eels that overwintered in Lake Ontario and then migrated the following year; (3) eels that remained in Lake Ontario until their transmitters stopped working; and (4) eels that were rarely detected (see Additional file 1: Figs. S1a–e). Although tagging sessions occurred in either the spring or fall, the majority of

Table 1 Summary of number of American Eel released in Glenora for each tagging session

Number of eels	Tagging session					
	Spring 2016	**Fall 2016**	**Spring 2017**	**Fall 2017**	**Spring 2018**	**Total**
Tagged	39	40	49	50	52	230
Detected	39	40	49	50	52	230
Dead	7	3	6	3	9	28
1st year migrants *(Migrated post release)*	13	19	26	32	26	116
2nd year migrants *(Overwintered and migrated)*	7	3	2	2	–	14
No evidence of migration	12	15	15	13	17	72
Number of Eels detected in						
Bay of Quinte	32	37	43	47	43	202
Eastern Lake Ontario	30	35	41	45	37	188
St. Lawrence River	19	20	22	34	25	120*
Western Lake Ontario	8	8	11	19	9	55

The number of individuals that were presumed to be dead as well as the number detected in different parts of Lake Ontario are shown; the division of Lake Ontario into the four areas can be found in Fig. 1. Here a "– " denotes when tag battery life was insufficient to fully capture a movement pattern

* Not all eel deemed to have migrated were detected in the St. Lawrence River at the Iroquois Dam

eels that migrated out of Lake Ontario did so in the late summer through to the early winter of the year they were tagged (89%; $n=116$), 7% ($n=9$) overwintered and then migrated in this same time period the following year, and 3% ($n=5$) overwintered and migrated during spring or early summer (Table 1). The eels that overwintered in the lake before migrating or had no record of out-migrating and stayed in Lake Ontario until their tag battery ran out, were primarily detected in the eastern region (Additional file 1: Figs. S1a–e).

Although successful downstream migration necessitates passage through eastern Lake Ontario, some eels left Bay of Quinte and were detected in the western region of the lake; however, their time of departure from Bay of Quinte appeared to match well with that of eels that went straight towards the St. Lawrence River (Fig. 2). The cross-correlation between departure dates for fall tagged eel from the Bay of Quinte showed significant synchronization at multiple lags, but the strongest correlation was 0 weeks (Additional file 1: Fig. S3); a similar pattern (strongest correlation at -1 week) was also evident between timing of arrival at the Iroquois Dam and Western Lake Ontario (Fig. 2). This indicates that departure and arrival times for out-migrating or westward migrating eels tended to co-occur at the same time of year (i.e., largely within one week but with some variability). Spring released eels did not have the same synchronization when leaving the Bay of Quinte (Additional file 1: Fig. S3). Similarly, the cross-correlation of eels (tagged in either spring or fall) leaving the Bay of Quinte and arriving at the start of the St. Lawrence River had significant synchronization with the strongest correlation at -1 week lag for both the fall and spring release groups; however, spring was more sporadic and not as tightly synchronized as fall, indicating that timing of departure from the Bay of Quinte for fall released eels is consistent with initiation of migration (Additional file 1: Fig. S3c and d).

Seasonally, eels were detected on the most receivers during the fall (weeks 43 to 47; Fig. 3), suggesting greater activity during a narrow temporal window. Eels were detected on the fewest receivers in the winter, suggesting a decrease in activity or reduced long-range movements during this season, with increasing activity in the spring, starting around week 16 (Fig. 3). When plotted spatially, spring tagged eels moved from the Bay of Quinte into eastern Lake Ontario in May and June, but were still primarily focused near the eastern shore of the Bay of Quinte and the north shore of the eastern region for much of the summer (Fig. 4; Additional file 1: Fig. S4). More eels were located at the entrance of the St. Lawrence River from September and October as they started migrating, and fewer eels were detected in November and December as most had either left the system and those that remained had reduced movements/activity (Fig. 4; Additional file 1: Fig. S4). Eels that remained in the lake for an extended period of time and went to western Lake Ontario were primarily detected at receivers closer to shore (Additional file 1: Fig. S5). This result was corroborated by the GLM, where more eels were detected at near-shore receivers than receivers further offshore ($p<0.001$; Table 2).

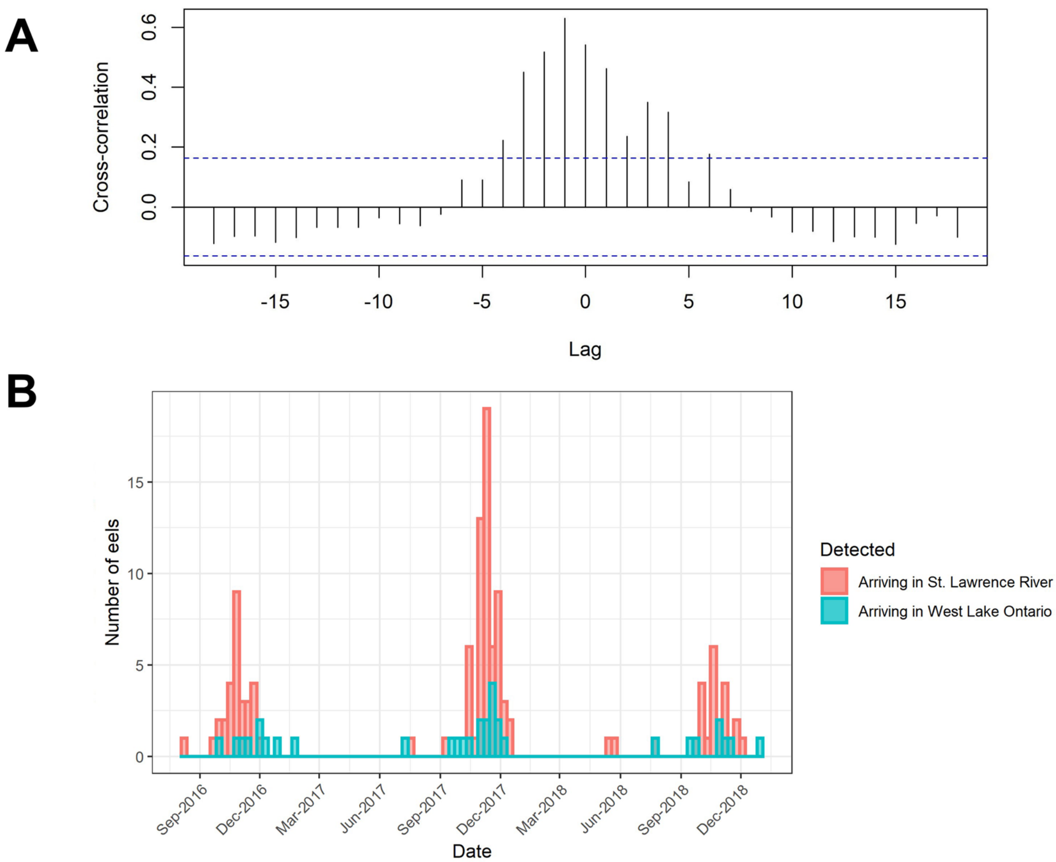

Fig. 2 Graphs related to the synchronization of the migration. **A** Cross-correlation plot showing the synchronization of the migration of weekly arrival times to the St Lawrence River and to the western region of Lake Ontario. There is a significant correlation if the bars go beyond the dotted blue lines; the largest correlation is -1 week between arriving at the Iroquois Dam in the St. Lawrence River and in western Lake Ontario. **B** Number of American Eel detected arriving at the Iroquois Dam in the St Lawrence River and to the western region of Lake Ontario over the study duration. N.B. The majority of receivers in western Lake Ontario were not deployed until spring/summer 2017

Movement cues

We explored environmental factors predicting the timing of eel movements out of the Bay of Quinte (fall released eel only) and into the St. Lawrence River (both spring and fall released eel). Fixed variables in the models explained 34 and 38% of the overall variance in the Bay of Quinte and St. Lawrence River models, respectively. Water temperature decreased with increasing probability of eels migrating out of the Bay of Quinte ($p < 0.001$) and entering the start of the St. Lawrence River ($p < 0.001$; Table 2; Additional file 1: Fig. S6). Moon fullness was also significant but with a very weak trend that varied between the two models (Additional file 1: Fig. S6). As moon fullness decreased, there was an increasing probability of eels migrating out of the Bay of Quinte ($p = 0.001$), but the opposite trend occurred for eels migrating into the start of the St. Lawrence River ($p < 0.001$; Table 2; Additional file 1: Fig. S6). There was a significant, negative correlation between length of the eels and duration of stay in Lake Ontario ($p < 0.05$; Table 2), and an interaction between tagging season and migration status ($p < 0.001$; Fig. 5). Shorter eels were more likely to spend a longer period of time in the lake. For eels tagged in spring, their migration status did not have a significant impact on the duration of their stay ($p = 0.27$; Table 2); however, for eels tagged in fall, non-migrating eels stayed for a longer duration ($p < 0.001$; Table 2). Although eels that migrated shortly following their release into the lake and those that overwintered had similar mean lengths (0.88 ± 0.06 m and 0.86 ± 0.05 m, respectively), there was considerably more spread in the range of lengths for eel that migrated earlier (Fig. 5).

Discussion

As the Lake Ontario—St. Lawrence River region was historically a critical rearing ground for the American Eel population as a whole [12], recovery of this

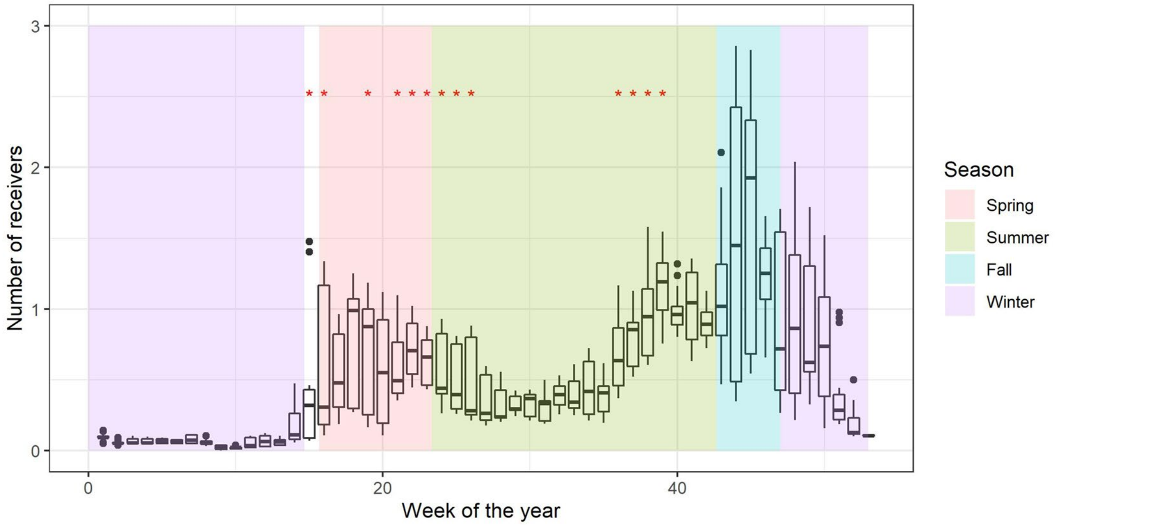

Fig. 3 Average eel activity throughout the year. Rolling daily average of the number of receivers an American Eel was detected at plotted depending on the week of the year. Release dates of the American Eels are indicated with a red '*'. Background colors indicate the average seasonal dates between 2016 and 2018

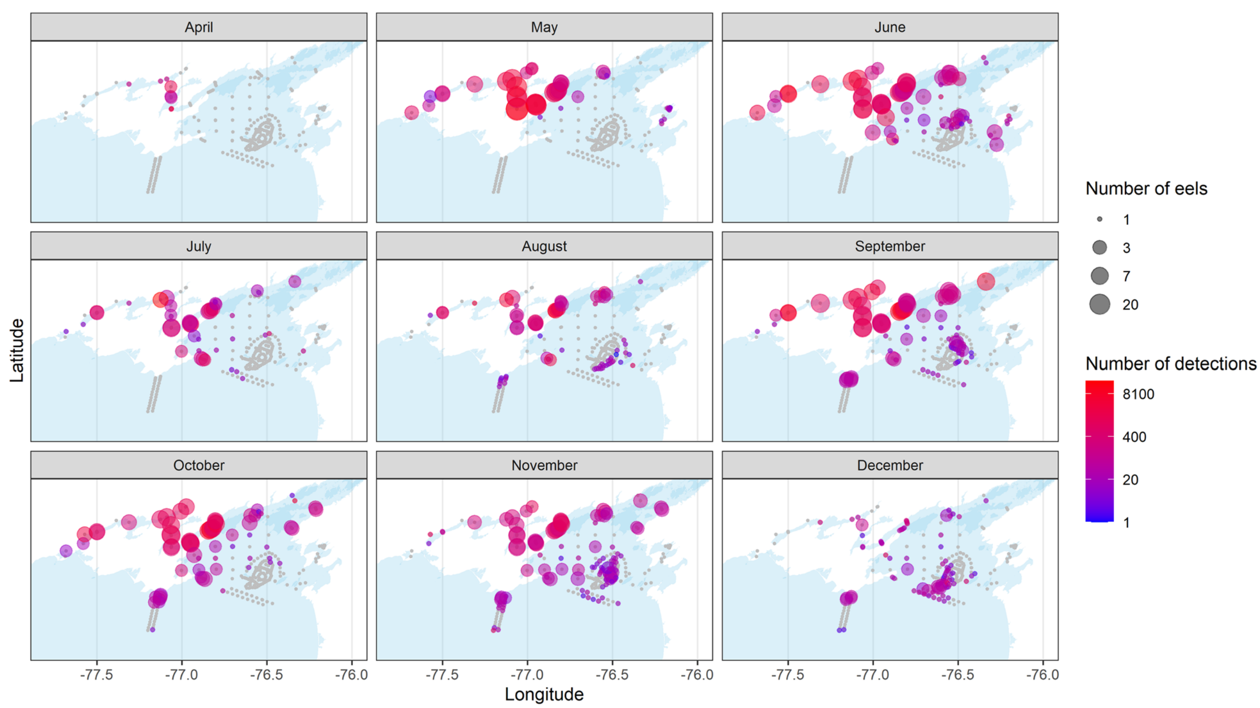

Fig. 4 Monthly map of total detections and number of eels detected in 2018. Maps of the east end of Lake Ontario with a point for each receiver deployed in 2018, for each month between April and December 2018. The size of the point depends on the number of American Eels detected by the receiver and the color of the point depends on the number of detections at the receiver. Both the color and size scales are logarithmic. Grey points indicate a receiver that did not detect any eel

sub-population is essential for meeting population-level recovery objectives. The present study explored the movement ecology and timing of movements of presumably translocated American Eel. Development of a non-lethal technique to determine the origin of the tagged eels, such as examining fin rays for the stocking

Table 2 Estimated regression parameters, standard error, *F*-values or *Z*-values, and *P*-values for the models presented

Location of detection (western Lake Ontario)	**Estimate**	**Std.error**	***Z*-value**	***p*-value**
Intercept	2.45	0.06	39.6	< 0.0001
Distance	− 5.64E^{-5}	1.09E^{-5}	− 5.2	< 0.0001
Migration cues (fall Bay of quinte model)	**Estimate**	**Std.error**	***F*-value**	***p*-value**
Intercept	34.33	2.35		< 0.001
Water temperature	− 2.11	0.11	452.06	< 0.001
Moon fullness	− 0.99	0.32	9.63	0.002
Marginal R^2	0.34			
Migration cues (St. Lawrence River model)	**Estimate**	**Std.error**	***F*-value**	***p*-value**
Intercept	16.25	1.08		< 0.001
Water temperature	− 0.94	0.03	869.08	< 0.001
Moon phase	0.51	0.16	10.37	0.001
Marginal R^2	0.39			
Duration of stay by body length	**Estimate**		***F*-Value**	***p*-value**
Intercept	17.77		18.6	< 0.0001
Length	− 10.68		5.3	0.022
Release season	4.88		49.8	< 0.0001
Migration status	5.64		38.0	< 0.0001
Release season: migration status	− 4.82		16.8	< 0.0001

Location of detection model was fit using a generalized linear model with a Poisson distribution, migration cue models used a generalized linear mixed model with a binomial distribution, and the duration of stay by body length model was fit using an analysis of covariance

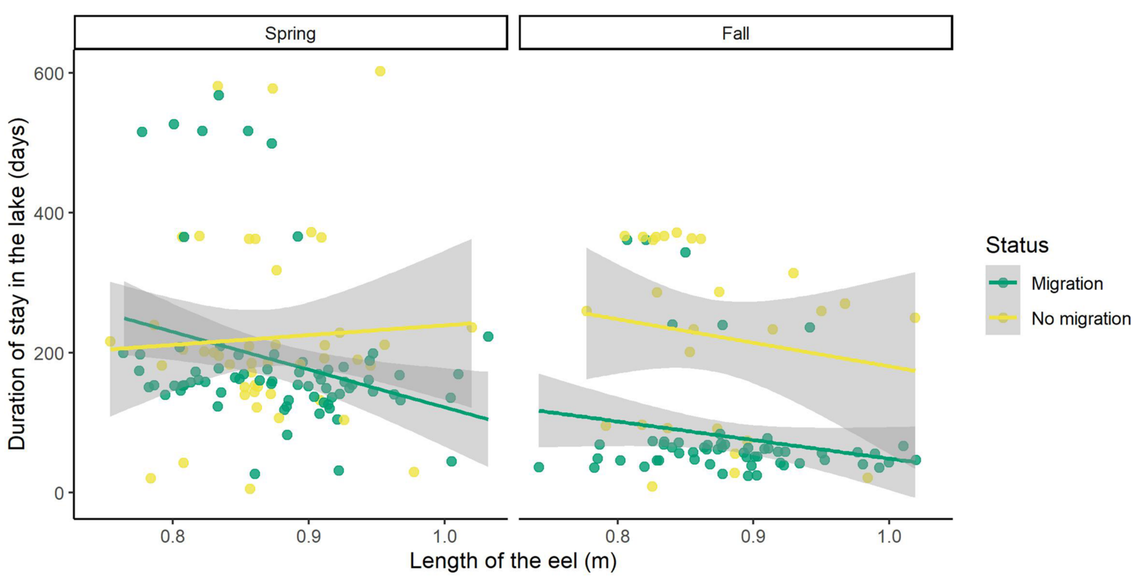

Fig. 5 Relationship between length of the eel and the duration of its stay in Lake Ontario. Length of the American Eel is measured in meters. The duration of its stay in Lake Ontario is calculated as the time in days between time of release and last detection. The eels were grouped depending on the tagging season. Colours represent the migration status of the eels; green for migration, yellow for no migration. Linear trends for each group were also plotted

mark, would reduce this uncertainty. However, there were 10 × more eels translocated into Lake Ontario than have naturally migrated since 2006, therefore it is likely the majority of our tagged eel were translocated. Most acoustically tagged American Eel in Lake Ontario migrated to the St. Lawrence River in the late-summer or fall of the year they were tagged. Most movements were within eastern Lake Ontario and the Bay of Quinte; however, longer distance movements occurred to western Lake Ontario, particularly for eels that overwintered in the lake. During these western movements, eels generally stayed close to shore. Environmental variables influenced eel movements in the fall both as they exited the Bay of Quinte and entered the St. Lawrence River. There was also an indication that eels that were smaller at the time of tagging were more likely to spend a longer period of time in the lake and potentially delay migration, as predicted. Understanding the initiation of migration and the number of eels that undergo migration after translocation is informative for management by helping to assess whether translocating wild caught glass eels from areas of higher abundance to areas of low abundance is a useful management option; estimate migration success of these translocated individuals; and ultimately determine their potential contribution to the spawning stock.

Our results confirm the findings of past works that American Eel translocated into Lake Ontario can migrate out of the Lake into the St. Lawrence River [7]. The successful migration of tagged eels (64%) into the St. Lawrence River indicates that despite being translocated and not completing a normal upstream migration into the lake, most eels are capable of initiating downstream migrations to complete their life cycle. Although 36% of the eels could not be confirmed to have migrated within the battery life of their acoustic tags, they could have eventually migrated after their tag battery ran out or moved into the St. Lawrence River undetected. As a result, successful migration rates out of Lake Ontario are likely higher than reported here and our values should be interpreted as conservative estimates of the proportion successfully migrating. As the timing of both the peak number of eels departing from the Bay of Quinte and subsequent detections at either the St. Lawrence River or western Lake Ontario were coincident, one possible explanation is that a portion of the eels may be disoriented and searching for a downstream exit in the wrong direction. However, we cannot discount other explanations since we do not know for certain when translocated yellow-stage eel will silver and begin their migration. Therefore, an equally plausible explanation is that individuals that moved to the western region did so in search of overwintering habitat. Regardless of the reason for westerly movements, management can potentially improve the efficacy of eel translocations by accounting for this inherent lack of migration success when establishing how many glass eels to move if future translocations are considered.

The broad geographic distribution of American Eel means that, like other temperate eels, there is a wide range in the onset of spawning migration depending on distance to the spawning ground [58]. Given that Lake Ontario is over 5000 km from the Sargasso Sea, naturally recruited eels are observed initiating spawning migrations as early as June, with the majority out-migrating in August and September [6, 14]. These eels synchronize their arrival in the St. Lawrence River estuary in late-October [66]. In contrast, eel that rear in closer proximity to the Sargasso Sea tend to have narrower migration windows that begin in late summer or early fall,this includes eel from the donor rivers in the Maritimes [14].

In the present study, tagged eels were detected on the most receivers, suggesting greater activity, during the fall (weeks 43 to 47; Fig. 3), which coincides with the end of the typical migration period for eels naturally recruited in Lake Ontario (approximately weeks 23 to 43; [14]), but overlaps with the later and shorter migration period of eels from their stocking origin of Nova Scotia and New Brunswick (approximately weeks 31 to 48,[14]). While the reason for this apparent delay is challenging to determine, it may be related to their stocking origin, their individual physiology or metabolism (i.e., growth rates—discussed below), magnetic imprinting [20], or the underlying method used to determine migration timing (i.e., commercial fishing capture timing vs acoustic telemetry). Confirming the driver of this apparent discrepancy is critical, however, since such a delay in the start of migration for translocated American Eel may have unknown consequences for migration survival and arrival on their Sargasso Sea spawning grounds. This is an area of future work that will be essential to understand if future translocations are to be considered.

Results from tracking studies further downstream in the St. Lawrence River have noted synchronous migration for translocated eel [7, 66], albeit at smaller than expected body sizes [66]. The pattern of downstream migration (i.e., continuous or discontinuous) and its duration are variable among individuals [6], so it may be possible that translocated eels can move more quickly downstream to ensure their arrival at the spawning grounds coincides with the larger population. Indeed, Béguer-Pon et al. [7] did not find any difference between wild or translocated eel in terms of migration speed through the Gulf of St. Lawrence or where they crossed at the Cabot Strait into the Atlantic Ocean. While this suggests that translocation did not impair their seaward migration, the timing of passage was not explicitly assessed. Therefore, further downstream tracking of eels all the way to their spawning grounds will help determine if translocated eels' arrival times are synchronous with naturally reared individuals. From a movement ecology perspective, this will be a critical determinant of whether moving eels into Lake Ontario to replace lost recruitment is an effective management approach for population recovery.

Eels were most active during the fall, which coincides with their spawning migration. However, translocated eel behaviour can also be informed by their seasonal habitat use and activity in Lake Ontario. Following the spring tagged eels through time identified increased activity in the spring and early summer as well as expanded spatial use of the Bay of Quinte and coastal waters of Lake Ontario prior to migrating into the St. Lawrence River. Yellow-stage European Eel can swim at speeds of ~ 1.5 km/hr [50], which, if similar for American Eel, means it would have taken less than two days to migrate to the St. Lawrence River from their release location. This suggests eels remained in shallow areas near their release site until it was time to migrate and that their activity was not restricted by any limitations related to their ability to move or speed of movement.

A proportion of eels did stray to western Lake Ontario, showing longer distance movements, and this was generally coincident with the migration period of those that went to the St. Lawrence River. Individuals that moved into western Lake Ontario were primarily detected at receivers deployed in shallow waters (< 20 m) in close proximity to shore, which is consistent with their documented preference for shallow waters (< 10–15 m; [14]). The ecology of American Eel during the winter season is not well known and we found limited activity/detections during this season. This is consistent with the assessment of reduced motility or quiescence during the winter [68], but does not clarify the types of habitat used during this season nor does it provide information on their small-scale behaviour (i.e., using burrows, or mud flats, being dormant or active in a very confined area [60]. Telemetry does hold promise as a means for assessing these types of behaviours during the winter through the use of fine-scale positioning arrays or other methods [41], as opposed to the large-scale movement patterns determined in our study for Lake Ontario.

The cues that influenced the initiation of fall movements out of the Bay of Quinte or into the St. Lawrence River, and length of eels vs duration of stay in Lake Ontario, indicate both an innate ability to know when to migrate and the size of eels to focus on for migratory studies. Generally, we found that eels initiated movements out of Bay of Quinte and into the St. Lawrence River during periods of decreasing water temperatures in the late summer or fall. Being highly correlated (0.97) with water temperature, total illumination was also an important driver with movements coinciding with fall declines in light conditions (reduced daylight hours). Moon fullness, although a significant model variable, did not have a strong trend. This may, in part, be related to the method of analyses and few years of data and warrants further study since it could still be a significant factor in the timing of movement as has been shown for European Eel [4]. Overall, the variance explained in the models was moderate ($R^2 = 34–38\%$), and results matched well with what is known for European Eel, particularly movements during lower temperatures [4, 22, 39]. If available, other factors such as water levels and water flow, which has been shown to also influence European Eel migration [4, 54, 63, 64], could improve our models and estimates of when eels begin to migrate. However, there is an indication that environmental cues drive the initiation of migration for eels in Lake Ontario. If these cues differ from historic Lake Ontario eels and if this disparity results in an unsuccessful migration, then stocks from locations that migrate at similar times as historic populations may need to be considered.

As anticipated, smaller eels remained in the lake longer. Larger eels were preferentially selected for tagging as they were anticipated to be more likely to out-migrate during the battery life of their tag. Eels may need to reach a sufficient size prior to migrating, and earlier assessments of these translocated eels showed unusually small silver-stage eels resulting from the translocation in comparison to historic, naturally recruiting eels [57, 66]. However, the size of eels in the present study were similar to naturally recruiting eels, and larger than migrating eels from the donor rivers in Nova Scotia/New Brunswick [14, 31]. Female eels may adjust their size requirements for migration based on habitat conditions since they must balance the potential for increased growth and ultimately higher fecundity with the potential for pre-spawning mortality, which increases the longer they delay migration [60]. Smaller eels in the present study may therefore be extending their duration in historically favourable Lake Ontario conditions since it allows them to grow larger to meet the energetic requirements of the > 5000 km migration [16], and consequently be more fecund [3]. Similarities in the timing of movements from the donor rivers suggest that while the environmental factors dictating when to start their migration are retained, size at migration or even gender from their stocking origin is not always. This more adaptive life history for translocated eels is promising since it suggests that some individuals from other systems may benefit from increased growth potential in Lake Ontario and, if they can reach the spawning grounds, will be larger and more fecund individuals than if left to rear in the source rivers.

A challenge with the present study, however, is that tagging efforts were focused on larger eels that were thought to be more likely to migrate, which likely reduced our regression slopes. Tagging smaller individuals may have strengthened the statistical relationship, but similar to Oliveria [44] we observed considerable variation in lengths within migrants and non-migrants, so a fixed value for migration likely does not exist; rather, a more general pattern for increased probability of migration with increasing lengths is evident. Length was not predictive of migration status for spring-tagged eels, and this may suggest that individuals have grown at different rates within Lake Ontario such that their initial length was no longer representative of their size during the migration period. Based on these factors, future studies of migration success for stocked eels from Lake Ontario should focus tagging efforts in the fall for the largest individuals possible, as this will increase the likelihood of capturing near-term migration and providing greater tracking potential during their movements through the St. Lawrence River.

The American Eel population is declining in the Lake Ontario—St. Lawrence River region; however, understanding the movement ecology of translocated eels can assist in management strategies to improve survival to reproductive success in the Sargasso Sea. Based on the relative timing of migration to the St. Lawrence River, the majority of translocated eels maintain the migratory timing of their rivers of origin, which could have repercussions towards a successful migration. However, the eels are generally larger, which may counterbalance this potential limitation by having more energy for a longer migration and ultimately greater fecundity upon arrival to the spawning grounds. The potential for translocated eels to have disparate migration timing as the natural population is an important consideration for management and, as noted, requires further study of the duration of their downstream migrations to determine whether they can make up for this delayed start and still reach the spawning grounds in time to contribute.

The small proportion of individuals that did not migrate or strayed by going to western Lake Ontario is noteworthy since it suggests that some base level of delay or failed migration is to be expected for translocated individuals. Using transmitters with longer battery life would help provide a final assessment of spawning migration success since an eel that migrates out of the lake might not make it to the sea. There are two large hydroelectric generating stations that cumulatively cause 40% mortality on out-migrating eels, a commercial silver-eel fishery in Québec that induces 10% fishing mortality, as well as natural mortality that all act to reduce the number of eels arriving on the spawning grounds [18]. Thus, in the short-term, ensuring survival past dams is the most critical factor limiting translocated American Eel in Lake Ontario from contributing to the spawning stock, and considerable work is underway to develop mitigation measures to reduce mortality at hydroelectric facilities [47]. Studies towards improving dam passage as well as our study on understanding movements of translocated eels will provide important information on large-scale movements of American Eel, which will be able to inform management decisions towards the recovery of this species.

Conclusions

Prior to migration, eels moved throughout Lake Ontario with most detections in the eastern portion of the lake. Eels that moved to the western end of Lake Ontario were primarily detected on receivers in shallower waters (<20 m) close to shore. Eels were detected on fewer receivers in the winter, suggesting reduced movements during this season. A majority of the tagged eels ($N=116$) migrated in their release year and a smaller subset ($N=14$) overwintered and migrated the following year; however, for the remainder ($N=72$) there was no direct evidence of migration. While limited battery lifespans likely contributed, some base level of failed migration may be expected for translocated individuals. For those that did migrate, larger individuals spent less time in the system, particularly when tagged in the fall. Timing of migration was consistent regardless of year or tagging season and primarily occurred in late summer or fall, with factors such as cooling water temperatures and decreasing sky illumination associated with initiation. The weeks when migration occurred, however, were more aligned with timing in their natal range (i.e., eastern Canada) than with naturally recruited eels from Lake Ontario. This temporal mismatch requires further consideration, since it may influence arrival times of translocated eel to the spawning grounds and ultimately their recruitment potential. Collectively, these results can be used to inform future assessments of eel translocation efficacy and can also aid in the design of future tracking studies to more completely explore the downstream migration success of eel translocated into the highly productive waters of Lake Ontario.

Abbreviations

ANCOVA	Analysis of covariance
CA	Canada
COSEWIC	Committee on the Status of Endangered Wildlife In Canada
GLM	Generalized linear model
GLMM	Generalized linear mixed model
IUCN	International Union for Conservation of Nature
NOAA	National Oceanic and Atmospheric Administration
NS	Nova Scotia

OMNRF	Ontario Ministry of Natural Resources and Forestry
WA	Washington (state)

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s40317-022-00308-9.

Additional file 1: Table S1. Transmitter specifications. **Figure S1.** Individual American Eel detection history for each tagging session. **Figure S2.** Number of eels when first detected by julian date in different areas of Lake Ontario or in the St. Lawrence River based on different migration groups and release groups. All eels released in fall (fall 2016; fall 2017 columns) leave the Bay of Quinte at roughly the same time as the beginning of migration whereas spring released eels enter eastern Lake Ontario prior to fall migration. Bars are stacked. Outmigrants = detected in the St. Lawrence River; West migrant = if it did not out migrate and was detected in western Lake Ontario; Nonmigrant = was never detected in the St. Lawrence River or western Lake Ontario. **Figure S3.** Cross-correlation plot showing the synchronization of the eel migration based on weekly departure times from the Bay of Quinte if migrating to the St. Lawrence River or western region of Lake Ontario when released in the fall (A) or spring (B), and weekly departure times of eels leaving the Bay of Quinte and arriving at the mouth of the St. Lawrence River for all fall (C) or spring (D) released eels. There is a significant correlation if the bars go beyond the dotted blue lines; For fall released eels (A), the largest correlation is 0 weeks between the two groups of eels leaving the Bay of Quinte indicating the majority of eels are leaving at the same time. For spring released eels (B), the largest correlation is -12 and -13 weeks and leaving the Bay of Quinte is not well synchronized. Fall and spring released eels leaving the Bay of Quinte have the largest correlation -1 week for reaching the mouth of the St. Lawrence River (C and D); however, timing was more sporadic for spring released eels (D). **Figure S4.** Monthly map of total detections and number of eels detected in 2017. **Figure S5.** Map of the number of eels and eel detections at receivers in the west end of Lake Ontario in 2017 and 2018. **Figure S6.** Graphs reflecting the predicted logistic regression relationship between environmental variables (surface water temperature - panels A and B; and moon fullness - panels C and D) and probability of American Eel leaving the Bay of Quinte in the fall (panels A and C) and entering the St. Lawrence River (SLR; panels B and D).

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Author contributions

Data curation: AS, AM, TCP, SS. Formal analysis: AS, SML. Funding acquisition: AM, TCP, SS. Methodology: AS, SML, JG-C, JDM, AM, TCP, SS. Project administration: AM, TCP, SS. Visualization: AS, SML. Writing—original draft: AS, SML, JG-C, JDM. Writing—review & editing: AS, SML, JG-C, AM, TCP, SS, JDM. All authors read and approved the final manuscript.

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Availability of data and materials

Datasets used and/or analyzed during the current study are available from the corresponding author upon reasonable request.

Declarations

Ethics approval and consent to participate

Our research adheres to the ASAB/ABS Guidelines for the Use of Animals in Research. Tagging of American Eel followed the procedure outlined in Béguer-Pon et al. [7] as well as standard operating procedures for the Great Lakes Laboratory for Fisheries and Aquatic Sciences-Water Science Technology Directorate (GLLFAS-WSTD) Animal Care Committee related to fish tagging (GWACC-130) and anesthesia (GWACC-105). At the start of the study the Ontario Ministry of Natural Resources and Forestry used standard animal care procedures through their monitoring programs and did not require internal Animal Care approvals; however, starting in 2018, tagging was completed under the GLLFAS-WSTD Animal Care Permit #1850.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no financial or non-financial competing interests.

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