Ocean migration of pop-up satellite archival tagged Atlantic salmon from the Miramichi River in Canada

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Keywords: Acoustic telemetry, Atlantic salmon, diving behaviour, Hidden Markov Model (HMM), marine migration, pop-up satellite archival tags (PSATs).

Abstract

The ocean migration of 16 post-spawned adult Atlantic salmon (*Salmo salar* L.) from the Miramichi River, Canada, tagged concurrently with pop-up satellite archival tags and acoustic transmitters was reconstructed using a Hidden Markov Model. Individuals exclusively utilized areas within the Gulf of St. Lawrence and the Labrador Sea, and showed little overlap with known distributions of European stocks. During the migration, individuals were generally associated with surface waters and spent more than 67% of the time in the upper 10 m of the water column. The Atlantic salmon occupied greater depths and showed more diving activity during the day than during the night, with a few exceptions. While residing in the Gulf of St. Lawrence, individuals used different geographical areas and displayed frequent dives to shallow depths (10-30 m). All fish that entered the Labrador Sea (n = 8) migrated through the Strait of Belle Isle (767 km from the river mouth), after spending 41-60 days in the Gulf of St. Lawrence. After exiting the Gulf of St. Lawrence, individuals utilized different areas in the Labrador Sea, and overlaps in spatial distributions among the individuals were largely limited to the Labrador Coast. This variation in area use was accompanied by individual differences in diving behaviour, with maximum depths recorded for individuals ranging from 32 to 909 m. Dives to depths exceeding 150 m were only performed by four individuals and mainly restricted to the central Labrador Sea (areas with water depths > 1000 m). Vertical movements were shallower and resembled those in the Gulf of St. Lawrence when fish migrated through shallower coastal areas along the Labrador Shelf. In conclusion, the large overall variation in migration routes suggests that post-spawners from the Miramichi River encounter different habitats during their ocean migration and that the growth and survival of

adults may depend on ecological conditions in multiple regions, both in the Gulf of St. Lawrence and in the Labrador Sea.

Introduction

Comprehensive descriptions of the movement and spatial distribution of individuals are essential in order to understand how animals interact with their environment (Hays *et al.* 2016). Studying large-scale marine migration and behaviour of fishes have become possible by the development of electronic tags that store information about the environment experienced by the fish (e.g. Howey-Jordan *et al.*, 2013; Guðjónsson *et al.*, 2015). For pelagic species that migrate over large spatial scales, the most common tag type used for describing migration is the pop-up satellite archival tag (PSAT, e.g. Block *et al.*, 2011). These tags are attached externally to the animals before they detach after a pre-programmed time period, surface, and transmit archived data and their current position to the Argos satellite system. The use of PSATs has facilitated great advances in examining the ocean distribution and migratory behaviour for pelagic fishes, providing indispensable information for management and conservation (e.g. Lacroix, 2013; Lea *et al.*, 2015)

For Atlantic salmon (*Salmo salar* L.), the number of large-scale studies of their ocean migration is increasing (Chittenden *et al.*, 2013; Lacroix, 2013; Guðjónsson *et al.*, 2015). Nonetheless, most knowledge regarding the marine distribution of Atlantic salmon still originates from conventional tagging studies based on reports of recaptures in fisheries (Dadswell *et al.* 2010, Jacobsen *et al.* 2012, Reddin *et al.* 2012). Studies based on reported recaptures provide invaluable information about the general distribution patterns of stock complexes, but fail to describe accurate space use and behaviour both on individual and population level, and are biased towards areas where fisheries have taken place. As a result, detailed knowledge of movement at sea is still required for many populations, particularly in light of the species' current conservation status (Hansen *et al.* 2012).

During the past decades, substantial declines in population sizes have been observed for numerous populations of Atlantic salmon, particularly in the southern part of the distribution range where many are currently on the brink of extinction (Chaput 2012, ICES 2015). On local and regional scales, the causal mechanisms behind the declines are diverse and include: parasite induced mortality from salmon lice infestation (e.g. Gargan *et al.*, 2012; Krkosek *et al.*, 2013), introduced parasites (e.g. Harris *et al.*, 2011), genetic introgression from farmed Atlantic salmon (e.g., Glover *et al.*, 2013), degeneration of freshwater habitats (Parrish *et al.*, 1998; Otero *et al.*, 2011), and overharvesting (e.g. Parrish *et al.*, 1998). On a broad scale, changes in marine ecosystems are considered prominent contributors to the recent declines, as decreasing return rates often correlate with increases in sea surface temperatures (Friedland *et al.*, 2009a; Otero *et al.*, 2011; Chaput, 2012). For European populations, it is perceived that these temperature induced population declines are associated with shifts in marine food web structure that reduce post-smolt growth during the first months at sea (McCarthy *et al.*, 2008; Friedland *et al.*, 2009a). This differs, at least in parts, compared to populations from the Northwest Atlantic where population declines can be linked to both temperature induced reduction on individual growth (Mills *et al.* 2013, Renkawitz *et al.* 2015), and/or changes in predator fields (Friedland *et al.* 2009b, 2012). Nevertheless, more information about the large-scale ocean distribution and migration routes of Atlantic salmon is needed.

To date, individual migration routes for North American Atlantic salmon have been addressed in only one published study, where the migratory behaviour of post-spawned adults, tagged with PSATs in the Bay of Fundy, varied among populations with the longest recorded migration terminating at the Labrador Coast (Lacroix 2013). Although studies on the migration of post-spawners do not address the most critical life stage (i.e. post-smolts), these studies are of great importance because post-smolts and previous-spawned Atlantic salmon show some overlap in marine distribution (Sheehan *et al.* 2012, Renkawitz *et al.* 2015), and repeat spawners play an important role in maintaining recruitment particularly in years with low post-smolt survival (Halttunen 2011). Consequently, novel information about the migration of post-spawned individuals is essential in developing a greater understanding of how Atlantic salmon interact with their environment – and of the ongoing process that has left a vast number of stocks at peril.

The Miramichi River, Canada, supports the largest Atlantic salmon population in North America. In recent decades the spawning stock in the river has collapsed despite monumental reduction in fishing pressure (Friedland *et al.*, 2009b; Chaput and Benoît, 2012). Here, we present a detailed analysis of the marine migration and behaviour of post-spawned Atlantic salmon from the Miramichi River, concurrently tagged with PSATs and acoustic transmitters. The combination of satellite and acoustic telemetry has previously been use for describing coastal movement in other salmonids (Teo *et al.* 2013), but the current study is the first to utilize both technologies in describing the large-scale oceanic migration of Atlantic salmon. Our primary aim was to reconstruct the movement of individual post-spawners using a Hidden Markov Model (HMM), which predicts the probability of individuals occupying different geographic positions on a daily basis and reconstructs movement tracks using data retrieved from individual tags (Thygesen *et al.*, 2009; Pedersen, 2010). We also investigated vertical profiles in relation to diel periods and spatial distribution in addition to temperature ranges experienced by the fish during the marine migration.

Material and Methods

Study area

The Miramichi River is located within the western Gulf of St. Lawrence (47.2°N, -65.0°W) and drains an area of approximately 12,000 km^2 (Figure 1). It is divided in two main branches, the Southwest Miramichi and the Northwest Miramichi, which join in the estuary before the river terminates in the Miramichi Bay. Over a four-year period, starting in 2012, post-spawned adult Atlantic salmon (kelts) were tagged with PSATs and acoustic transmitters. Kelts were caught in the Northwest Miramichi River by fly-fishing from 20 April to 16 May each year and brought to shore in live wells for tagging. All tagged kelts were at least 70 cm in length to accommodate the size of the tags. A total of 43 kelts were tagged (42 females, 1 male), with a mean total length of 78 cm (range 70-93 cm, SD ± 5 cm) and average mass of 3.5 kg (range 2.3-6.1 kg, SD ± 0.8 kg).

Tagging procedure

The fish were anaesthetized using clove oil (Hilltech Canada, Canada) at a concentration of 40 mg/l river water. During surgery, the fish were provided with a flow of fresh river water over their gills. Kelts were first fitted with an acoustic transmitters that was inserted into the body cavity through a 15 mm incision made slightly lateral to the mid-ventral line approximately 20 mm anterior to the pelvic fins. Two sutures (nylon, size 2-0, Ethicon Inc., Pennsylvania, USA) were used to close the incision.

Next, a PSAT was attached using a similar method to that described in Courtney et al. 2016. First, the tags were attached to two 50 mm long cushioned rigid back plates using a nylon braid. The back plates were then wired through the dorsal musculature below the dorsal fin using two biocompatible plastic coated stainless steel wires. A part of the braid attaching the PSAT to the harness was encapsulated in plastic coating to lift the PSAT up from the back of the fish, reducing the chances of skin wounds from the tag scratching on the skin of the fish. This made the tag lie 1-2 cm above and behind the dorsal fin minimizing drag and buoyancy (Supplementary figure 1). A biocompatible silicon pad was glued on the inside of the plates to reduce abrasion on the skin and a small plastic tag (Floy Tag Inc., Washington, USA) was attached to one of the plastic plates with contact information for anglers in the event of recapture. The entire process to insert an acoustic transmitter and attach a PSAT lasted 4-5 minutes.

After tagging, fish were placed in holding boxes in the river and monitored for a minimum of one hour after tagging. Fish were upright between four and six minutes after PSAT attachment, and reacted to external stimuli shortly afterwards. No excessive bleeding was recorded. Once recovered, the fish were released into the river at the surgery site (n = 32) or, in 2014, placed in oxygenated tanks and trucked 2 km downstream to bypass large numbers of anglers in the tagging area (n = 11). The tagging was approved under licence by Department of Fisheries and Oceans Canada (license numbers SG-NBT-12-032A, SG-RHQ-13-036A, SG-RHQ-14-021, SG-RHQ-15-005).

Tag and tracking details

The PSATs used in this study were X-tags (12 × 3.2 cm, 40 g in air) manufactured by Microwave Telemetry, Colombia, Maryland. These tags record temperature, depth, and light intensity at two-minute intervals, and calculated a daily geolocation based on sunrise and sunset estimates for up to 16 months. The daily latitudes are calculated using the estimated day lengths, whereas longitudes are calculated by dusk-dawn symmetries. Similar to all other methods for geolocation based on light levels, this approach provides more accurate estimates of longitude than latitude, particularly in periods around the equinoxes (Hill and Braun 2001, Musyl *et al.* 2001).

Tags were programmed to release on 31 August, 30 September, and 31 October in the year of tagging, with deployment periods between 114 and 177 days. A failsafe release was also programmed to account for situations when pressure (depth) was constant (corresponding to a 2 m depth band) for more than 4-5 days, or if the fish dived to depths endangering the physical integrity of the tag (manufacturer specified at 1250 m). In addition, the tags were programmed to not detach during the first 22 to

25 days after tagging (22 days in 2012, 2013 and 25 days in 2014, 2015). This prevented detachment if the tagged fish remained at constant depths in the river. Temporal resolution of the data retrieved from X-tags depends on the deployment duration and whether or not the tags are physically retrieved. Tag recovery allows access to the full data set, whereas for non-recovered tags only a subset of the time series is accessible depending on the amount of data successfully transmitted to the satellites. A completely transmitted data set would include: daily geolocation estimates, daily sunrise and sunset estimates, daily summaries of temperature and depth, 15-min interval recordings of depth and temperature for the first 4 months of deployment, and 30-min interval recordings for the days after this threshold. Notably, for non-recovered X-tags, compression techniques implemented in the tags may cause reporting of delta-limited values (http://www.microwavetelemetry.com/fish/understanding_data_xtag.cfm). If present, these values represent distorted measurements of depth and temperature, and they occur when the changes exceeds a certain threshold. This causes underestimation of the true values during drastic increase in depth or temperature and overestimation of true values during drastic decrease in the same variables.

For the acoustic tracking, we used V9 transmitters (29 mm × 9 mm, VEMCO, Halifax, NS, Canada), which emit signals at 69 kHz and have a lifespan of 272 days. VEMCO VR2W and VR4 receivers were strategically deployed at positions covering the entry and exit points of the Gulf of St. Lawrence (Figure 1). This was done to increase the number of known position independent of the PSAT data, and decrease the uncertainty of the geolocation model. Acoustic receivers were deployed near the river mouth (n = 6), at the Miramichi Bay exit to the Gulf of St. Lawrence (n = 11) and at the two main exits from the Gulf of St. Lawrence, which were i) Strait of Belle Isle, between Newfoundland and Labrador (n = 23), and ii) the Cabot Strait, between Newfoundland and Cape Breton Island (n = 162) (Figure 1). Receivers at the Cabot Strait constitute the Cabot Strait Line, operated by the Ocean Tracking Network, Dalhousie University, Halifax, NS, Canada (Castonguay *et al.* 2009). In 2015, a second Strait of Belle Isle transect of receivers (n = 28) was deployed approximately 3.5 km northeast of the first gate to increase the likelihood of detecting tagged fish. All receivers were seasonal (deployed in spring and removed by fall), with the exception of the Cabot Strait line, which operates year round. The spacing distance between receivers in transects (Miramichi Bay, Strait of Belle Isle and Cabot Strait) was maximum 800 m, which is considered to provide complete detection coverage for V9 tags under ideal conditions.

Migration model

We modelled the movement of tagged Atlantic salmon using a discrete-time Hidden Markov Model (HMM), developed for geolocating fish (Thygesen *et al*., 2009; Pedersen, 2010). HMMs are state-space models in which location distributions are non-parametric and enable reconstruction of movement in non-linear environments, while accounting for the uncertainty of the data (Pedersen 2010). The non-parametric nature of the location distributions differ compared to Kalman filter techniques (e.g. Sibert *et al*., 2003; Nielsen *et al*., 2006), which despite being highly efficient in describing migration over open waters, often assign non-zero probabilities to positions on land in non-linear environment (Pedersen 2010). We chose the HMM framework because the tagged fish encountered areas with complex boundaries between land and ocean during large parts of their marine migration. Furthermore, since the quality of input data from the PSATs were occasionally compromised by the mode of transmission, we wanted to use a model that explicitly accounted for this uncertainty. In the following section, we describe our specific model, which could be replicated and improved in further studies. For the mathematical theory and assumptions behind geolocation using HMMs, we refer to Pedersen (2010). All model implementations were conducted in the R environment (R Core Team 2015).

In HMMs, the posterior distribution at each discrete time step is estimated by a two-step forward running Bayesian filter, followed by a backward smoothing step refining marginal distributions conditional on all data (Pedersen 2010). In the forward filter, non-parametric posterior distributions are calculated by coupling of two stochastic models: the process model (i.e. time update), which represents the movement scheme and predicts the underlying evolution of probability densities; and the observational model (i.e. data update) that refines these probability densities depending on the data (Thygesen *et al*., 2009; Pedersen, 2010).

HMMs rely on discretization of time and space, allowing posterior distributions to be estimated by a numerical solution of the underlying movement process. We used time-step length of one day, meaning that positional probabilities were estimated on a daily basis. For the process model we assumed fish to move according to a diffusion process, given by the diffusion equation (Codling *et al.* 2008).

$$\partial\phi(\mathbf{x},t)/\partial \mathrm{t} = \mathrm{D}\nabla^2\phi(\mathbf{x},t) \qquad (1)$$

where $\phi(\mathbf{x},t)$ is the probability that a fish is present at location $\mathbf{x}$ at time t, ∇ is the spatial gradient operator, and D represents the diffusivity parameter. Here, movement probabilities between days were constructed by solving equation (1) using the finite difference method (see Thygesen *et al.*, 2009 for solution) on the discretized grid multiple times for each time step. This was done in order to implement more realistic movement between days, allowing individuals to perform multiple short movements in a single day (Supplementary figure 2). For our final solution, we used an equidistant grid of 10 km in each direction at ten recursive solutions allowing individuals to move a maximum daily distance of 100 km. Movement onto land was prevented by setting transition probabilities onshore to zero. In order to avoid loss of probability mass the remaining transition probabilities were then normalized.

Daily likelihoods of each position in the grid were constructed using filtered daily geolocation estimates (i.e. latitude and longitude), daily mean temperature of PSAT recordings at the surface (>5m), and daily maximum depth. The raw geolocation estimates reported by the tags were filtered as follows: first, a subjective removal was conducted omitting days when time of sunrise and/or sunset were measured at depths exceeding 10 m. This threshold depth was chosen, as this was the only depth bin running from the surface with 10 m increments where less than 5 % of light values were influenced by vertical movements for all recovered tags with available light data. Second, an objective removal was implemented. Here, a generalized additive model (GAM) with day length as the dependent variable and Julian days as a smoother was fitted, rejecting days with residuals exceeding a set threshold (2 × residual standard deviation). Smoothing parameters of regression curves were selected using generalized cross validation. Latitude estimates 14 days prior and after the autumn equinox were omitted, as this period produces unreliable latitude estimates as day lengths are approximately equal across all latitudes (Hill and Braun 2001, Musyl *et al.* 2001). In estimating longitude, the equinox problem is negligible as they rely on the dusk and dawn symmetry, and measurement error is constant throughout the year (Hill and Braun 2001). Likelihood fields for the filtered raw geolocations were calculated assuming independent Gaussian distributions for latitude and longitude, using the filtered estimates as means. Standard deviation in longitudes was fixed to 0.5°, whereas for latitude the standard deviation was set to 1.5° for days with appropriate distance from the autumn equinox. These parameters were selected based on the expected uncertainties given by Microwave Telemetry for the X-tag used at latitudes between 65°S and 65°N, and the general variability of geolocation estimates by PSATs (Musyl *et al.* 2001).

Daily temperature observations at each position were modelled as Gaussian random variables, with daily observed values and measurement errors derived from the Operational Sea Surface Temperature and Sea Ice Analysis (OSTIA) database at that respective positions as the means and standard deviations (http://ghrsst-pp.metoffice.com/pages/latest_analysis/ostia.html). For the depth filter, a rejection algorithm was implemented, setting data likelihoods to zero if maximum depth recorded by the tag exceeded the bathymetry at that position, and to one otherwise (http://www.gebco.net/data_and_products/gridded_bathymetry_data/). The posterior distributions of the time and data update, $\phi(\mathbf{x},t)$, were then calculated:

$$\phi(\mathbf{x},t) = \frac{\phi(\mathbf{x},t\text{-}1) * \mathrm{TP} * \mathrm{L}(\mathbf{x},t)}{\lambda(\mathrm{t})} \qquad (2)$$

where $\lambda(t)$ denotes the normalization constant, $\phi(\mathbf{x},t\text{-}1)$ is the posterior distribution the previous day, TP is the convolution scheme (Supplementary figure 2) and $\mathrm{L}(\mathbf{x},t)$ is the product of the different likelihood fields.

The diffusivity parameter, D, was fixed to the highest possible value that prevented numerical oscillations and ensured that all probabilities were positive (i.e. stability criterion of the finite difference method). In order to filter the posterior distributions conditional on all data in the time series, the backward smoothing described in previous geolocation papers using HMM was applied (e.g. Thygesen *et al.* 2009, Pedersen 2010). Individuals' most likely movement paths were estimated using the Viterbi algorithm (Viterbi 2006) and overall space use was quantified by the overall residency distribution (Pedersen *et al.* 2011). The overall residency distribution, RD, is a cumulative distribution representing the expected amount of time an individual uses at all positions in the spatial domain, thus accounting for the spatial uncertainty in the estimates (Pedersen *et al.* 2011).

Vertical movement

For individual fish, diel differences in depth distributions and vertical displacements were investigated independently during occupancy of different oceanographic regions using one-way permutation tests (i.e. randomisation tests). The defined regions were the Gulf of St. Lawrence, and coastal and non-coastal waters in other areas. The division of the time series was based on the most likely movement path of individual fish. Segregation of waters outside the Gulf of St. Lawrence depended on whether the fish migrated over coastal shelves or non-coastal waters, categorized by a depth threshold of 1000 m, for consecutive days. This was implemented to prevent excessive partitioning of periods when fish migrated close to coastal shelves. Diel periods were determined by civil sunrise and sunset, which correspond to 30 min before sunrise and 30 min after sunset. For days with unreliable estimates, sunrise and sunset data were generated by linear interpolation.

Results

Fate of tagged fish and data recovery

Data from the marine migration were retrieved from 24 PSATs, whereas 4 tags were expelled prior to ocean entry and 15 PSATs did not transmit data for unknown reasons. The tags with successful data retrieval were i) successful detachments at programmed pop-up date (n = 6), ii) premature pop-ups after ocean entry (n = 16: 7 reporting for unknown reasons and 9 with temperature and depth profiles associated with ingestion by marine predator), or iii) retrieved from fish returning to the river as consecutive spawners in the same year as they were tagged (n = 2).

Of the 24 fish tagged with reporting PSATs, 22 were detected by the acoustic receivers when leaving the river, 3 fish were recorded by acoustic receivers when passing the Strait of Belle Isle and none were recorded leaving the Gulf of St. Lawrence via the Cabot Strait. For the fish tagged with non-reporting PSATs, 13 of

15 individuals were detected leaving the river and 6 were detected passing the Strait of Belle Isle. Hereafter, only data from fish tagged with reporting PSATs are described. The median time spent in the river after tagging was 14 days (range = 6-42 d, SD ± 10 d), with individuals entering the sea between 2 May and 7 June. For the three fish that were detected by acoustic receivers when passing the Strait of Belle Isle, residency times in the Gulf of St. Lawrence were 41, 45, and 51 days. The two consecutive spawners spent 70 and 38 days reconditioning in the Gulf of St. Lawrence before returning to the river.

Quantity of transmitted data varied between tags, largely dependent on the fate of the fish and pre-programmed pop-up date, with the total number of logged days ranging from 7 to 141. Only fish that spent more than 30 days at sea had their migration reconstructed (n = 16: 6 reaching the due date, 7 with temperature and depth profiles associated with predation, 1 surfacing prematurely after a period on the ocean floor, and 2 fish returning to the river in the same year as tagging). For these fish, 4 tags were physically retrieved, whereas data from 12 tags were recovered from satellites (range = 43 – 100 %).

The start points of the HMM were set as individuals' last acoustic fix in the estuary or bay, or by investigating the tags temperature profile if fish were not acoustically detected entering the Gulf of St. Lawrence. For the tags reporting as scheduled and for the tag dwelling on the ocean floor, end points were set as the first reported Argos position and treated as certain in the HMM. This was a reasonable assumption for the sinking tag, as depth recordings prior to surfacing were constant and corresponded with the bathymetry at the surfacing position. For tags with temperature and depth profiles corresponding with ingestion by a predator, end points were not fixed and candidate positions were represented by their probability at the day of predation along a time series including the post-predation period. For individuals recorded passing the acoustic gates at the Strait of Belle Isle, acoustic fixes were treated as certain.

Horizontal movement

For the tracked individuals, end points of migrations were in the Labrador Sea for eight fish, whereas the remaining tracks ended in the Gulf of St Lawrence (Figure 2 and 3). For all tracked individuals, the overall and daily residency distributions were densely centred, with most of the probability mass occupying a small spatial region throughout the migrations (Supplementary figure 3; Supplementary video 1 and 2). For the three fish that were detected by acoustic receivers when passing the Strait of Belle Isle (straight line distance of 767 km from river mouth) the estimated timing of passage, calculated by running the HMM ignoring the acoustic detection, were identical to the actual passage times (41, 45, and 51 days after leaving the river). This confirms the reliability of the HMM.

The most likely tracks for the geolocated fish that entered the Labrador Sea without being detected by acoustic receivers (n = 5) indicated that these fish also passed through the Strait of Belle Isle, after an estimated median residency time in the Gulf of St. Lawrence of 44 days (range = 42-60 d, SD ±7 d). For all fish that migrated through the Strait of Belle Isle, passage dates were between 27 June and 12 July (n = 8).

During the residency in the Gulf of St. Lawrence, individuals utilized different areas shortly after ocean entry. The most likely tracks and daily residency distributions indicated overall utilization of areas spanning from waters adjacent to Prince Edward Island towards waters north of Anticosti Island (Figure 2 and 3; Supplementary figure 3). For fish entering the Labrador Sea, average migration speeds from the river mouth to the Strait of Belle Isle ranged from 19.4 – 26.1 km/d (n = 8, median = 23.9 km/d, SD = ± 2.3 km/d), based on the most likely movement paths.

For individuals passing the Strait of Belle Isle (n = 8), tags logged for 18-94 days after entering the Labrador Sea, with most likely movement paths and residency distributions of individuals spanning from coastal waters of Newfoundland, towards Baffin Bay and the west coast of Greenland (Figure 2; Supplementary figure 3). Despite large variation in individual movement paths after exiting the Gulf of St. Lawrence five individuals displayed similar migratory trajectories during initial residency in the Labrador Sea, with persistent migration northwards along the Labrador Coast. For the remaining fish (n = 3), two individuals migrated towards deeper waters in the central Labrador Sea shortly after strait passage, whereas one fish resided in areas of the coast of Newfoundland for an extended period before migrating to the central Labrador Sea (Figure 2). Notably, neither of the similarities in migratory behaviours remained consistent throughout the occupancy of the Labrador Sea, with further diversification during the periods leading up to tag detachments (Figure 2). The most distant location from the Strait of Belle Isle for these individuals was median 1070 km (n = 8, range = 404 – 1590 km, SD ± 416 km), and average individual migration speeds after passing the strait ranged from 17 – 35.8 km/d (median = 28.3 km/d, SD ± 5.2 km/d), based on the most likely migration routes.

Vertical movement and temperature range

Individuals were generally associated with surface waters during their marine migration, with all fish spending more than 67% of the time in the upper 10 m of the water column (Figure 4). Maximum depths recorded by the 16 tags ranged from 38-909 m (median = 97 m, SD ± 331 m). Only four fish performed deep dives exceeding 150 m. The overall temperature experienced by the fish ranged from -1.3°C to 17.9°C, with all recordings below 0°C occurring during vertical movements in stratified waters.

Within the Gulf of St. Lawrence, all fish exhibited frequent vertical movements to various depths in the upper 50 m of the water column (Figure 2 and 3). Dives exceeding 30 m were rare, and maximum depths within the Gulf of St. Lawrence were between 38-163 m (median = 83 m, SD ± 39 m). All fish occupied greater depths and exhibited greater vertical movements during the day than during the night when residing within the Gulf of St. Lawrence (permutation-tests; p-values < 0.025, median depths day = 0.7-7.4 m, median depths night = 0-2.7 m). Water temperatures experienced by the fish during these periods ranged from 0°C to 17.9°C, with individual mean temperature ranging from 6.3°C to 11.1°C.

After entering the Labrador Sea, maximum depths ranged from 32-909 m (median = 362 m, SD ± 410 m). Here, temperatures experienced by the fish ranged from -1.3°C to 14.9°C, and individual mean temperatures ranged from 4.2°C to 8.5°C. For fish entering the Labrador Sea, mean temperatures were significantly lower than those experienced in the Gulf of St. Lawrence (Wilcoxon signed-rank test; p-value < 0.025).

For the five fish that migrated northwards along the Labrador Coast after entering the Labrador Sea, all individuals displayed frequent shallow dives, occupied greater depths, and displayed greater vertical movements during the day than night (permutation-test; p-values < 0.025, median depths day 1.3-2 m, median depths night 0-1 m). In contrast, for the remaining fish ($n = 3$), no general trend in diurnal behaviour was present during the initial residency over the coastal shelf of Newfoundland and Labrador (permutation-tests).

When distributed over waters with depths greater than 1000 m, all fish performed occasional deep dives exceeding 150 m ($n = 4$, Figure 2). During these periods, only the fish that migrated across the Labrador Sea towards the west coast of Greenland displayed both deeper depth distribution and greater vertical movement during the day (permutation-tests) (Figure 2).

For the three fish that re-entered coastal waters, residency periods over non-shelf areas lasted for 26, 27, and 31 days. After re-entering shelf waters, all fish ($n = 3$) performed frequent shallow dives (Figure 2), with one individual utilizing significantly greater depths during the day, and two fish displaying significantly greater vertical displacement in periods of daylight (permutation-tests). The longest residency time over non-shelf waters was 55 days for the fish that remained over deep water until tag detachment.

Discussion

Horizontal movement

This is the first study to provide detailed descriptions of movement of multiple Atlantic salmon in the Gulf of St. Lawrence and Labrador Sea. Here, we show that individual migration routes diversify immediately after leaving the river, with an escalating degree of spatial diversification for the tagged fish that entered the Labrador Sea through the Strait of Belle Isle. Migrations to the Labrador Sea using the Strait of Belle Isle were expected, as Atlantic salmon from the Miramichi population are known to enter the Labrador Sea via this passage (Ritter 1989). Furthermore, the estimated timing of Gulf of St. Lawrence exit observed in the present study corresponded well with data from conventional tagging studies on previous spawners from the Miramichi River, where most fish were recaptured in proximity to the strait in July (Ritter 1989).

For Atlantic salmon that migrated to the Labrador Sea, the reconstructed tracks and residency times in the Gulf of. St. Lawrence indicate that they were foraging in these areas because both the most likely movement paths and residency distributions show non-directional movements at slow rates. Since the 1990s, the biomass of small fish suitable as Atlantic salmon prey has increased in southern parts of the Gulf of St. Lawrence (Benoît and Swain 2008). This increase in food availability has had a positive effect on consecutive spawners by increasing the proportion of individuals returning to the river after only one summer at sea (Chaput and Jones, 2006; Chaput and Benoît, 2012). In comparison, alternate spawners are seemingly unaffected, indicating a lower overall reliance on the Gulf of St. Lawrence food web for adult Atlantic salmon spending one winter at sea before returning (Chaput and Benoît 2012). In context of the present study, it is therefore likely that the growth of alternate spawners is predominately determined by ecological conditions in the Labrador Sea, and it is possible that the positive effects from increased prey abundance in the Gulf of St. Lawrence are masked by the reduced food availability in these areas (Mills *et al*. 2013, Renkawitz *et al*. 2015).

The Labrador Sea is considered the primary overwintering area for North-American Atlantic salmon populations, and utilization of this region has been documented in both conventional tagging studies (Ritter, 1989; Miller *et al.*, 2012) and pelagic surveys that have targeted Atlantic salmon (Reddin and Short 1991, Sheehan *et al.* 2012). Despite this, no detailed information exits on how migratory trajectories vary among individuals when distributed in these areas. We show that individuals differentiate in their area use in the Labrador Sea during summer and autumn, and that their total distribution area covers regions known to be utilized by Atlantic salmon (Miller *et al.* 2012, Sheehan *et al.* 2012). This suggests that the growth and survival of adult Atlantic salmon from the Miramichi River likely depends on foraging conditions in multiple regions of the Labrador Sea, during at least parts of their residency in these waters.

To what extent the observed distribution patterns are maintained in the winter remains unknown because all fish that entered the Labrador Sea experienced tag detachments before 4 October. It is possible that adult Atlantic salmon show more similarities in their spatial distributions later on in their migration, particularly in areas at the west coast of Greenland, which are known as important areas for both maiden and previous spawned individuals (Renkawitz *et al*. 2015). In our study, only one fish entered these waters, after crossing the Labrador Sea in September, and it is possible that a higher proportion of the surviving fish eventually migrated to these areas.

For Atlantic salmon in general, it has been suggested that the migration may follow the North-Atlantic Sub-polar gyre (Dadswell *et al*. 2010). This hypothesis is largely based on conventional tagging studies on smolts, and suggests that North-American Atlantic salmon that enter the Labrador Sea eventually join the south-flowing Labrador Current (Dadswell *et al*. 2010). In our study, the reconstructed tracks provided no evidence to suggest that migrations follow oceanic currents. Instead, tagged fish that entered the Labrador Sea either displayed migrations against the south-flowing Labrador Current or northwards migrations in the central Labrador Sea. The migratory behaviour displayed by the fish arriving at the west coast of Greenland particularly questions the generality of this hypothesis, as this individual performed counter current migration throughout most parts of its time at liberty. A similar result suggesting that migration of post-spawners is independent of oceanic gyres has previously been recorded for PSAT tagged fish from the Bay of Fundy (Lacroix 2013), indicating that horizontal movement of adult Atlantic salmon may be more directly linked to environmental cues governing foraging.

The overall migration pattern displayed by the post-spawners from the Miramichi strengthens the evidence that Atlantic salmon from North America generally utilize areas farther west in the Atlantic Ocean (Ritter, 1989; Miller *et al*., 2012) than European populations (Jacobsen *et al*. 2012, Jensen *et al*. 2014). Some European

Atlantic salmon are known to migrate to areas along the west coast of Greenland (Hansen and Quinn 1998, Reddin *et al.* 2012, Renkawitz *et al.* 2015), but the Northeast Atlantic Ocean is regarded as their primary destination – with individuals utilizing areas from the Barents Sea to the east coast of Greenland, partially depending on their river of origin (Jacobsen *et al.*, 2012; Jensen *et al.*, 2014). For Atlantic salmon from the Miramichi River, migrations to areas at the Faroe Island have been recorded, indicating that parts of the population utilize areas outside the Labrador Sea (Hansen and Jacobsen 2003). However, in the present study, there was no evidence of trans-Atlantic migrations. This suggests that the spatial overlap between post-spawners from the Miramichi River and individuals from European stocks is limited to areas along the west coast of Greenland. However due to the low sample size and limited duration of the time series, we cannot exclude that some post-spawned individuals migrate to the Northeast Atlantic.

Vertical movement

Diving behaviour in Atlantic salmon is generally not well understood, and no study has explicitly addressed the underlying mechanisms of vertical movement. It is likely that diving is driven by foraging, predator avoidance, temperature regulation, and orientation, and that the frequency of dives depends on the stage of migration and the environment that individuals occupy (Reddin *et al.* 2004, 2011, Godfrey *et al.* 2015). Despite this uncertainty, the general consensus regarding continual diving behaviour to shallow depths, typically during the hours of daylight, is that this specific behaviour is associated with foraging in the epipelagic zone (Reddin *et al.*, 2011; Lacroix, 2013). In the present study, this type of behaviour was evident for both consecutive and alternate spawners in the Gulf of St. Lawrence and for alternate spawners when distributed over continental shelves in the Labrador Sea. Given that frequent dives to shallow depth during the day is an appropriate proxy of foraging, the behaviour displayed by the tagged fish is likely to reflect foraging over large geographical areas.

In the current study, shallow dives and diel effects on vertical movements were mostly absent during periods of deep diving behaviour, and consequently an alternative behavioural mode during these periods can be assumed. The function of deep diving behaviour in Atlantic salmon remains largely speculative, but overall it is likely that they have multiple functions, including foraging, predator avoidance, and searching behaviour. Overall the proportion of fish performing deep dives was low with only 4 of 16 fish analysed showing depth recordings deeper than 150 m. Drag and/or lift caused by the tag may have affected the diving behaviour. In a recent study on Atlantic salmon kelts, Hedger *et al.* (in press) concluded that PSAT tagged fish from European rivers dived less frequently and to shallower depths than individuals tagged internally with small archival tags. Hence, the vertical movements observed here are likely to some extent altered by tagging, but we argue that the observed proportion of fish performing deep dives is likely unaffected, because utilization of depths greater than 150 m was mostly limited to periods of occupancy of waters exceeding 1000 m in depth. This conclusion, supported by the lack of occupancy of depths greater than 50 in a previous tagging experiment on adult North-American using small archival tags (Reddin *et al.* 2011), indicates that deep dives are not performed by all adult Atlantic salmon.

Geolocation method

Despite the increasing availability of Hidden Markov models (HMM) to researchers, only one published study has applied this framework for studying the marine migration of Atlantic salmon tagged with archival tags (Guðjónsson *et al.* 2015). For studies aiming to geolocate Atlantic salmon, HMMs could be considered a favourable framework because it can, in addition to estimate migration in coastal areas, also be applied in scenarios without or with poor light-based geolocation estimates (Pedersen *et al.*, 2008; Thygesen *et al.*, 2009; Neilson *et al.*, 2014). Many Atlantic salmon populations migrate to polar areas (Jensen *et al.* 2014), where geolocation from light level algorithms is impossible for large parts of the year, making HMMs applicable throughout the species' distribution range.

For the daily posterior distributions, the overall uncertainties estimated from our model covered large spatial areas (Supplementary video 1). This was expected, as our model treats uncertainties in a pure sense, creating daily likelihood fields depending on Gaussian random variables without a preset cut-off point. However, it is more important that the centres of the daily probability distributions were dense, indicating high certainty. This is evident by the reduced spatial dispersion of the 95% confidence limits of the daily probabilities (Supplementary video 2), which suggests that the current framework is highly suitable for geolocating Atlantic salmon at these latitudes. This suitability was highlighted by the identical residency times in the Gulf of St. Lawrence when running the model with and without the acoustic detections at the Strait of Belle Isle line for the three fish detected by acoustic receivers when entering the Labrador Sea.

In comparable studies using HMMs, a directional element in movement is occasionally included by modelling movement as an advection-diffusion process (Pedersen *et al*., 2011; Neilson *et al*., 2014). We did not include a directional element in the model, because the persistence of a biased random walk is unlikely in the complex geography that our fish migrated. However, in areas that allow a persistent bias, and where assuming a constant directional preference is reasonable, the fit of both movement schemes should be investigated, because this would potentially decrease the uncertainty of the posterior distributions and reconstructed tracks (Pedersen *et al*. 2011).

Conclusion

The present study demonstrates the value of performing long distance tracking studies on pelagic fish using PSATs, as the results show several novel aspects of the marine migration of adult Atlantic salmon. The individual variation displayed throughout the tracking periods suggests that reconditioning success of individual fish likely depends on local ecological conditions, while large spatial areas are important for the population as a whole. This in combination with the spatial differentiation between the North American and European stock complex, add to the consensus that partially different mechanisms are causing the ecosystem driven population declines in the different regions (Friedland *et al*. 2009a, 2009b). Furthermore, we show evidence of consistent diving behaviour during occupancy of different environments, with frequent shallow diving behaviour present along the continental shelf and execution of deeper dives when residing in deeper waters of the Labrador Shelf. This suggests that post-spawned Atlantic salmon display general behavioural modes in different oceanographic environments.

Supplementary materials

The following supplementary material is available at ICESJMS online: I) Supplementary figure 1 illustrates the release of an Atlantic salmon tagged with a pop-up satellite archival tag; II) Supplementary figure 2 depicts the convolution scheme of the applied Hidden Markov model, which represents the underlying transition probabilities of the individual movement process from time i to time $i+1$; III) Supplementary figure 3 illustrates the overall residency distributions of the tagged fish that successfully entered the Labrador sea; IV) Supplementary video 1 visualizes the evolution of the daily residency distributions for one Atlantic salmon including the full probability spectra; and V) Supplementary video 2 visualizes the evolution of the daily residency distributions for the same individual with 95 % confidence limit on the daily probabilities (i.e. 95 % of the daily probability mass).

Acknowledgments

The authors would like to thank the Miramichi Salmon Association, Mark Hambrook, Holly Labadie, the Atlantic salmon Conservation Foundation, and especially the volunteer anglers and tag sponsors without whom the fieldwork could not have been undertaken. We also thank Serena Wright and Martin W. Pedersen for helpful correspondences regarding the model development, Richard Hedger for generating

the spatial grid, and two anonymous reviewers for constructive comments on an earlier draft of the manuscript.

Figures

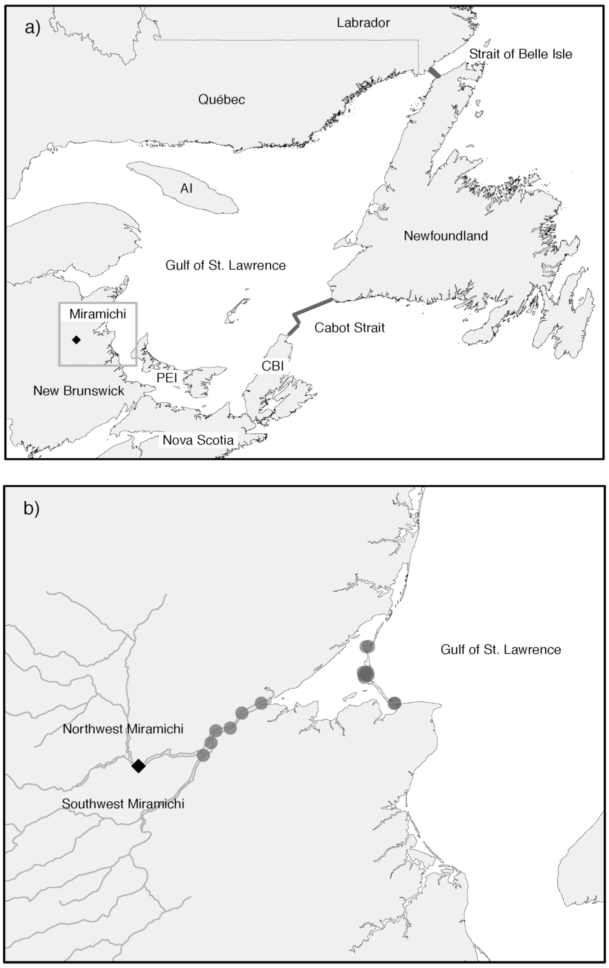
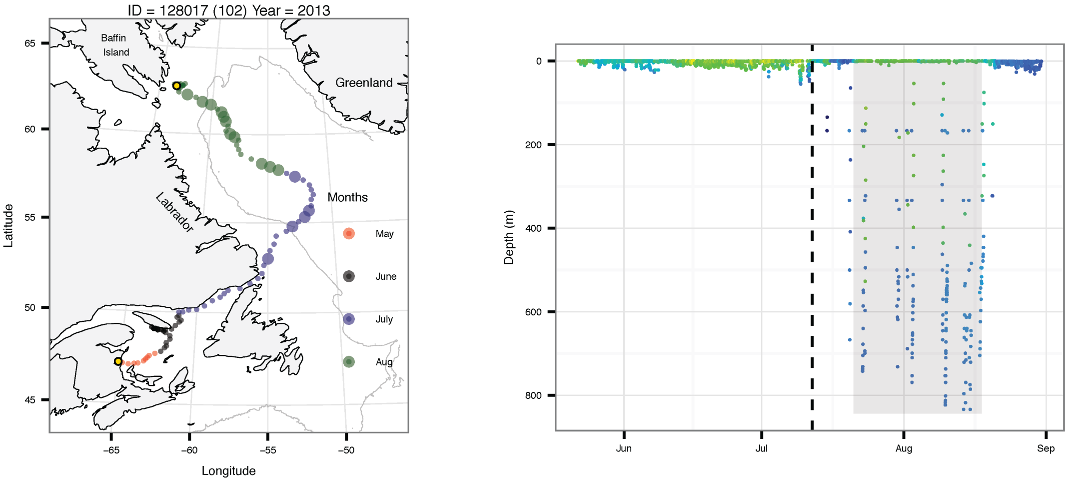


Figure 1: Map of study area, including tagging site (black diamond) and acoustic receivers (grey points). Abbreviations listed are: AI = Anticosti Island, CBI = Cape Breton Island, PEI = Prince Edward Island. a) Gulf of St. Lawrence, with acoustic receiver arrays at the Cabot Strait and Strait of Belle Isle (grey box indicates the Miramichi area). b) Miramichi area, including the Miramichi River (grey lines) and acoustic receivers in the river and bay.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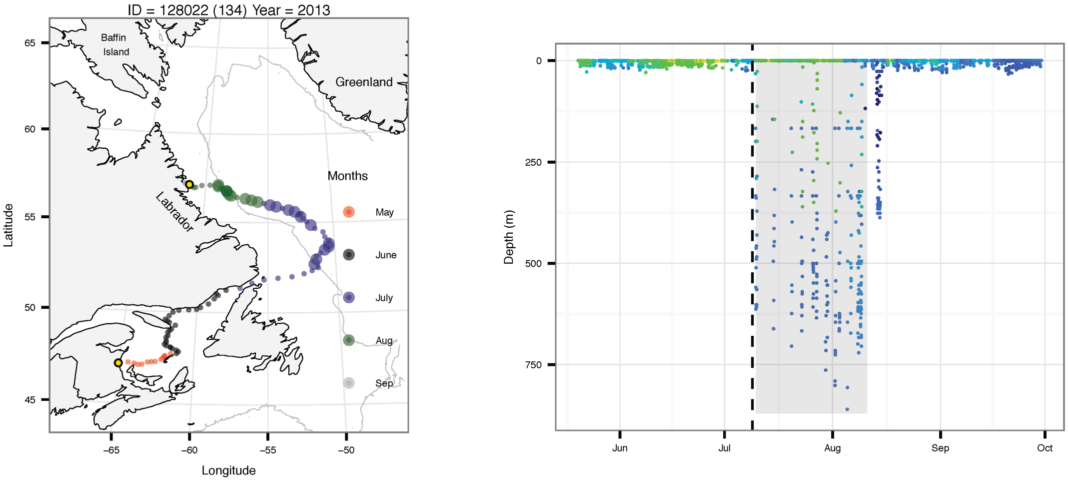
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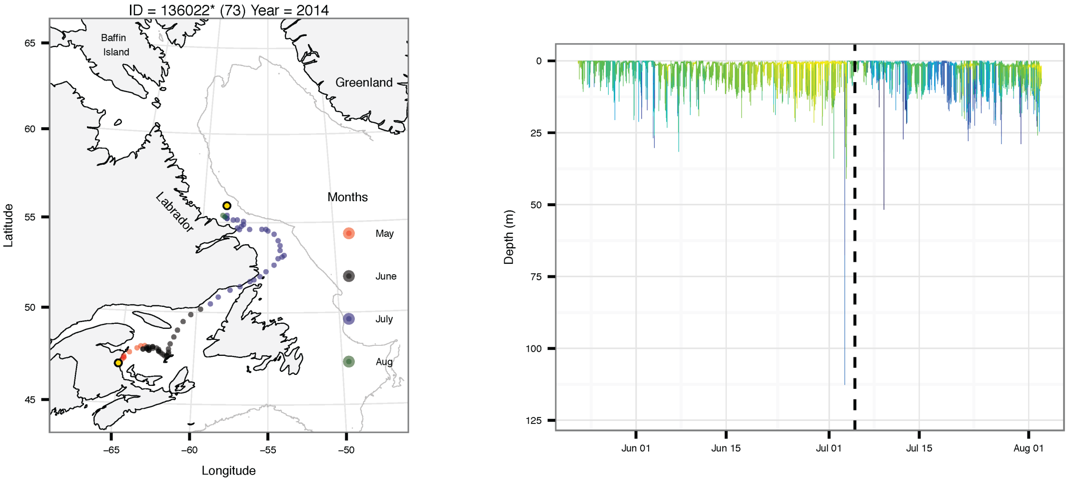
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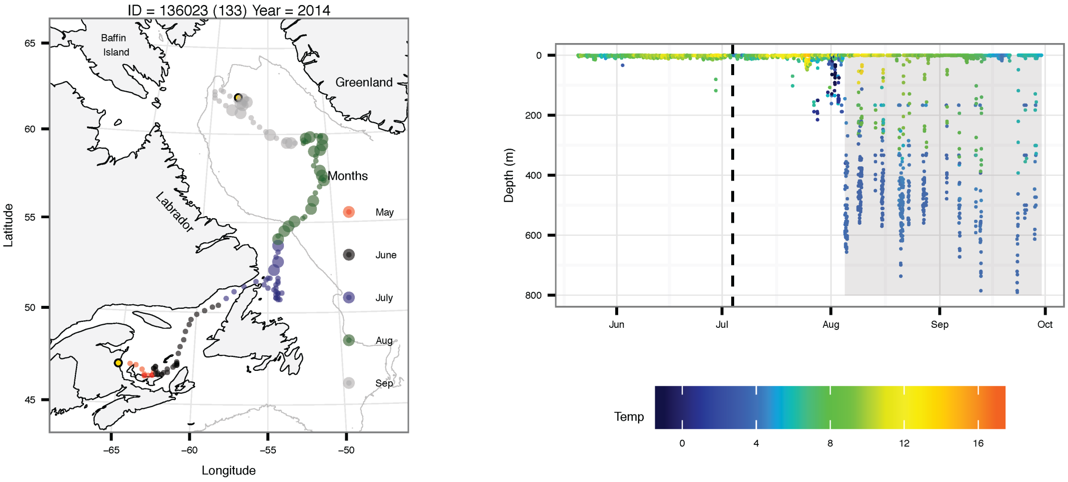
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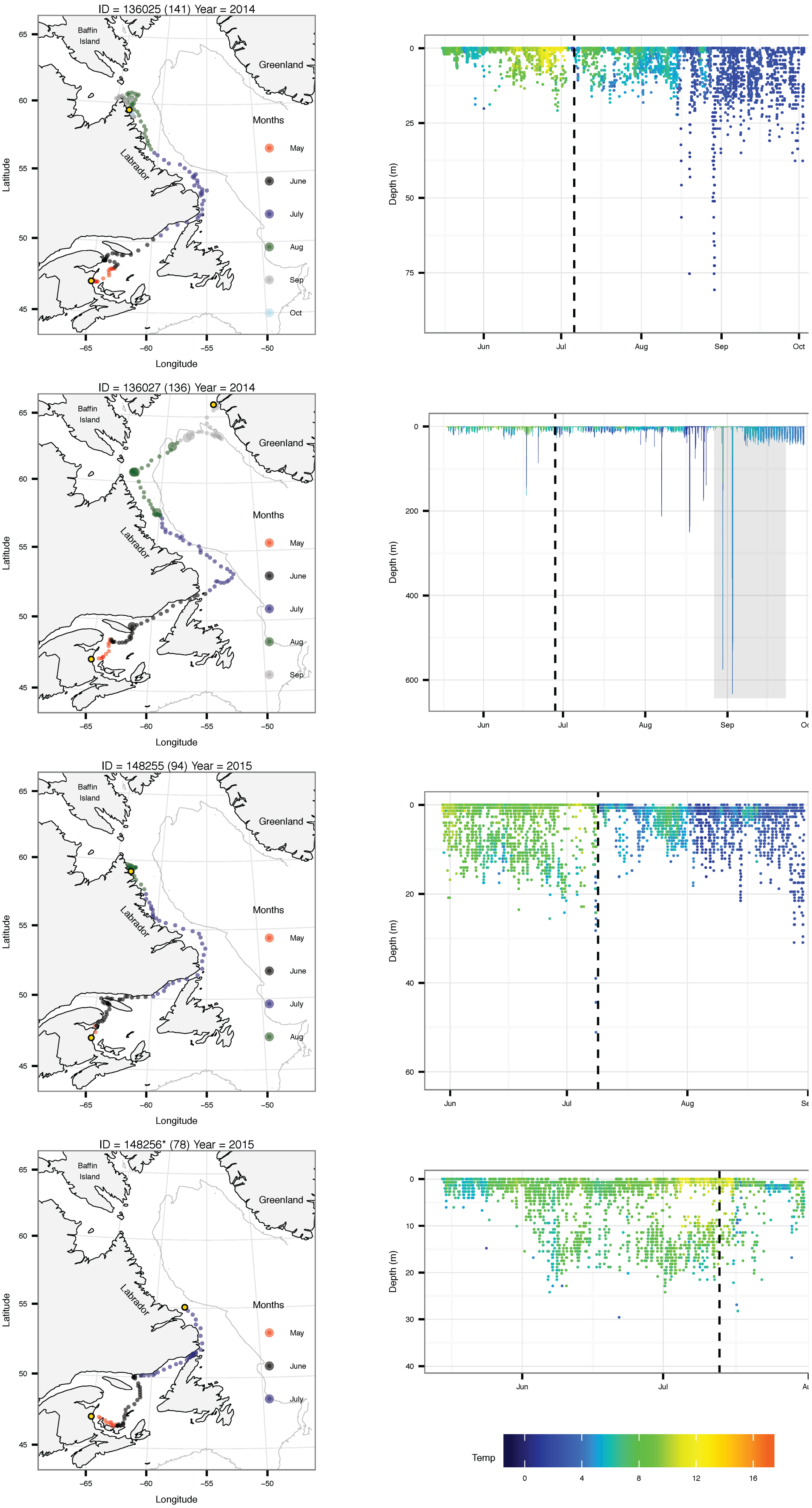
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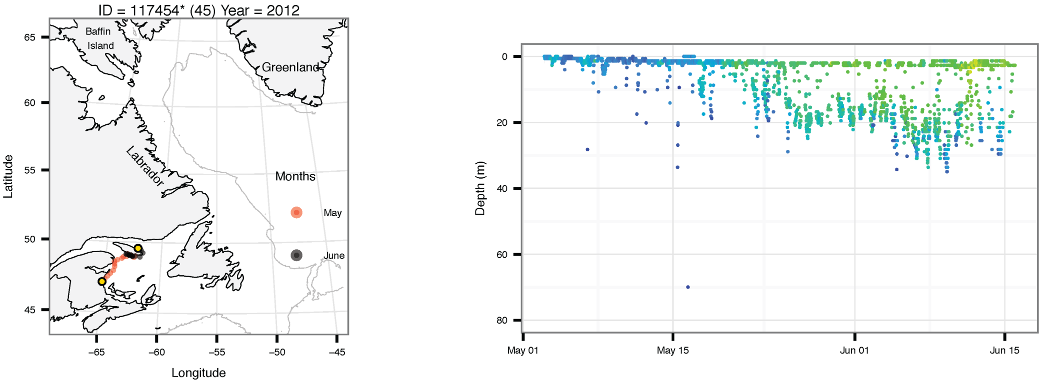
Figure 2: Detailed behaviour for the 8 tagged Atlantic salmon that entered the Labrador Sea. Fish experiencing premature tag detachment are noted by *. Left panels: Most likely movement path of individual fish (colour coded by month, yellow circles indicate start and end point of migration, number in parenthesis indicates duration of the marine migration). Large points illustrate days with maximum depths exceeding 150 m, whereas small points indicate days with maximum depths of less than 150 m. Grey line represents the 1000 m bathymetry contour. Right panels: Vertical profiles with corresponding temperatures for the marine migration (illustrated as lines for recovered tags and points for tags that were not retrieved). Colour keys indicate temperatures. Hatched vertical lines demonstrate time of exit from the Gulf of St. Lawrence and shaded areas indicate periods of residency over waters with depth > 1000 m.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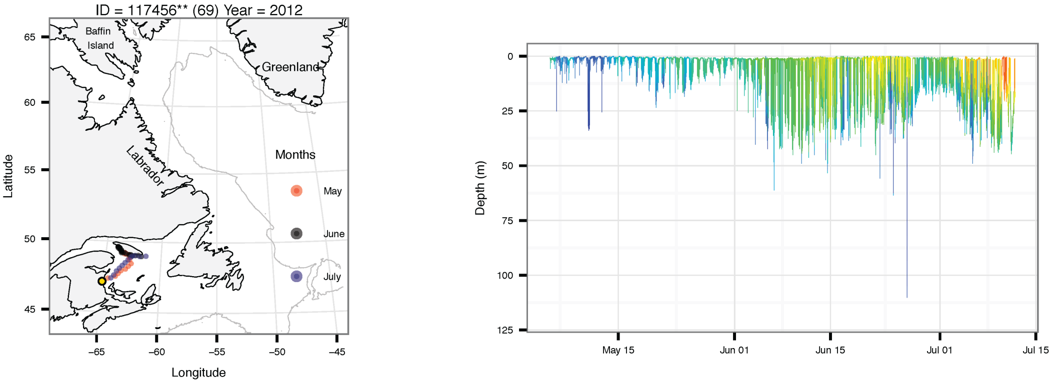
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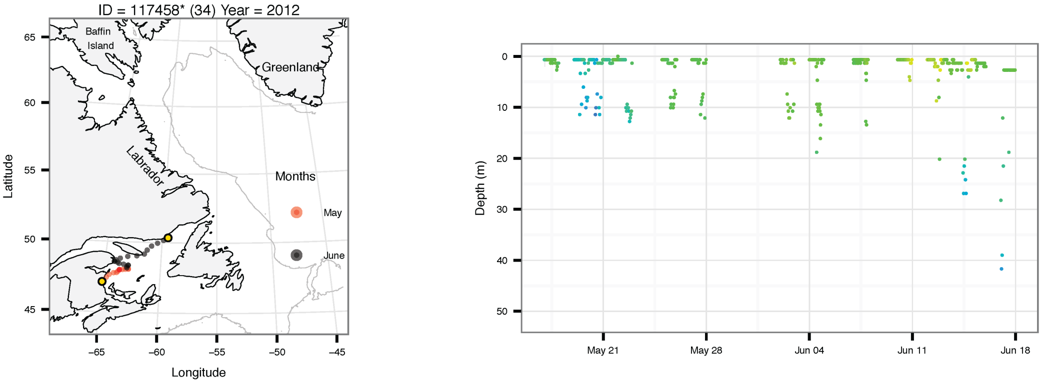
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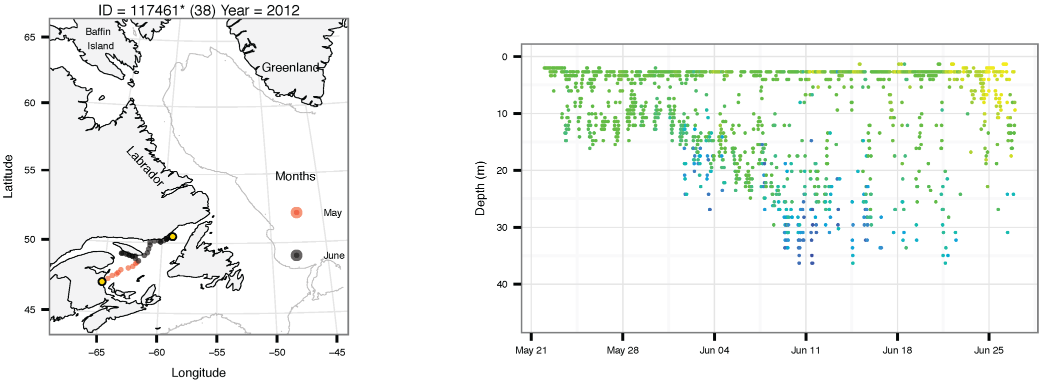
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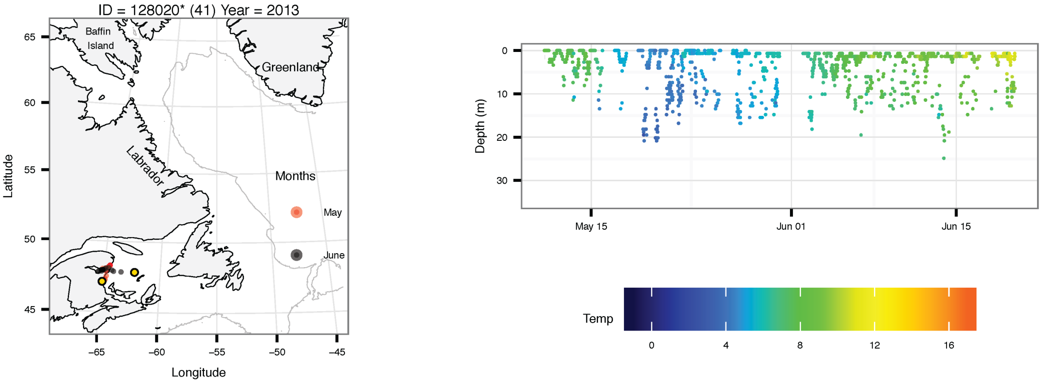
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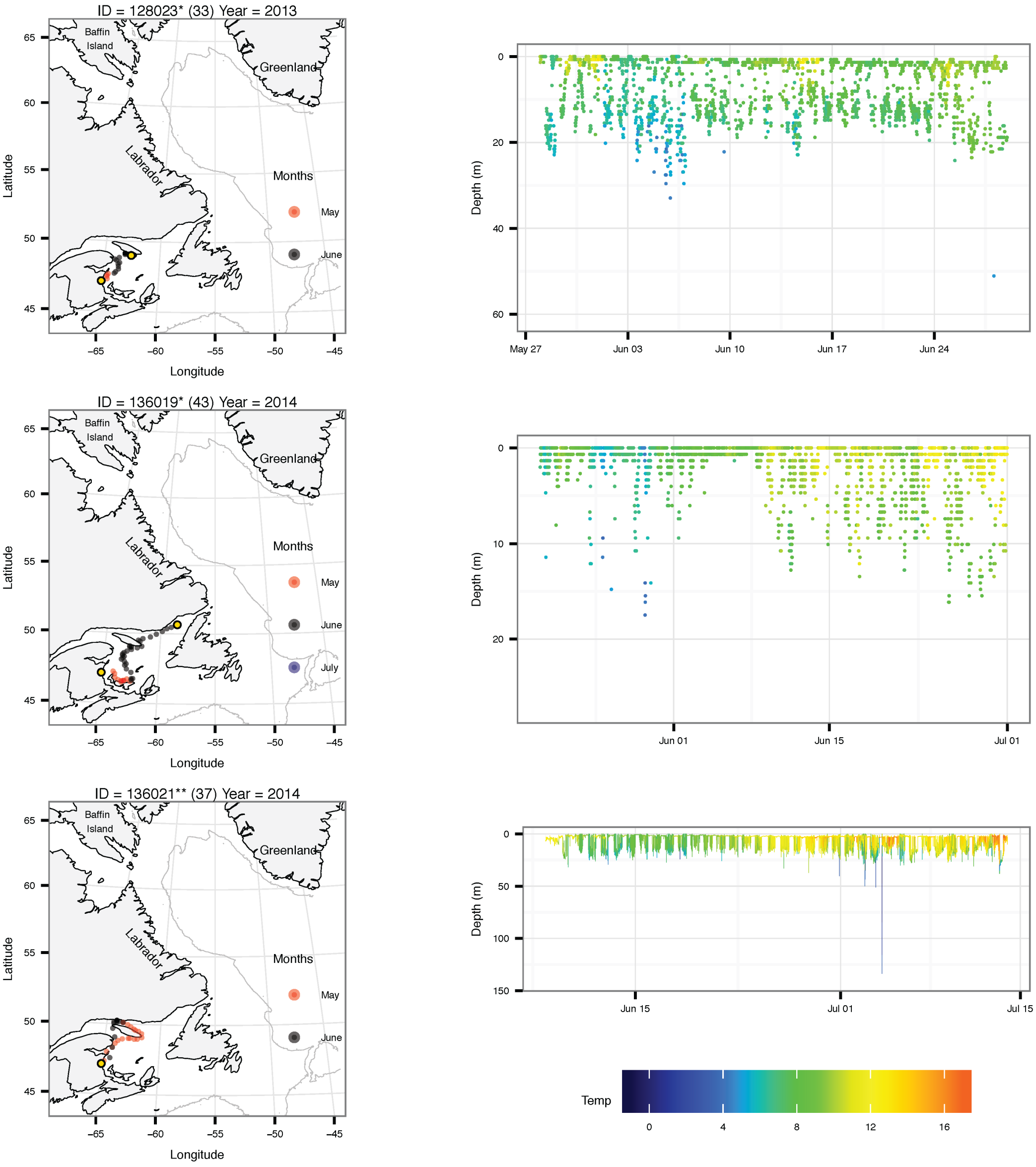

Figure 3: Detailed behaviour for the tagged Atlantic salmon that experienced premature tag detachment in the Gulf of St. Lawrence (n = 6, noted by *) or returned to the river the same year as tagging (n = 2, noted by **). Left panels: Most likely movement path of individual fish (colour coded by month, yellow circles indicate start and end point of migration, number in parenthesis indicates duration of the marine migration). Grey line represents the 1000 m bathymetry contour. Right panels: Vertical profiles with corresponding temperatures for the marine migration (illustrated as lines for recovered tags and points for tags that were not retrieved). Colour keys indicate temperatures.

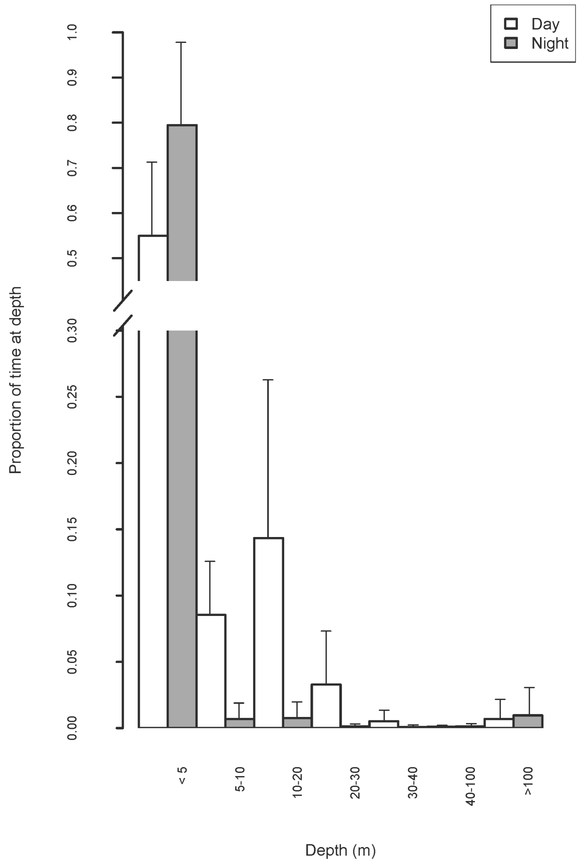

Figure 4: Mean of individuals' mean time spent at different depths during day and night for the entire marine migration (n = 16). Whiskers indicate standard deviation of individual means.

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