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Linkage Between Coastal Conditions, Detection Patterns, and Migratory Behavior of Atlantic Salmon Postsmolts across the Scotian Shelf

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Atlantic salmon *Salmo salar* migrate over long distances in the marine environment and are threatened by changes in oceans conditions linked to climate change. To better understand their migratory behavior and the linkages with local hydrographic and current conditions, we used acoustic telemetry in conjunction with concurrent oceanographic measurements collected from underwater gliders. We released acoustically tagged Atlantic salmon smolts in the Penobscot River (Maine, USA) from 2008 to 2014 (157 - 597 annually). A total of 339 of these fish were detected more than 500 km away, along an acoustic curtain of up to 256 hydrophones deployed over 180 km along the Halifax Line, across the Scotian Shelf. The arrival of postsmolts at the Halifax Line varied by more than two weeks depending on the year and was concurrent with the seasonal solar heating of the top 20 m of the water column. Detections were generally concentrated near-shore (within 40 km) but varied somewhat annually. Detections were negatively correlated to temperature and salinity, suggesting that Atlantic salmon postsmolts may be selecting colder and less saline water. The absence of a significant correlation with ocean currents indicated that local ocean circulation does not affect their spatial distribution. The migratory behavior of postsmolts was characterized by a localized detection pattern (75% of the fish were detected at two or less adjacent stations), and short residence time (75% of the postsmolts spending less than 25 min within the detectable range). The migratory heading was estimated between 50° and 120° North. These results provide the first empirical data on migratory routing of Atlantic salmon postsmolts during annual migration to ocean feeding grounds, and highlight important relationships with climate variables that are subject to change in the future.
Atlantic salmon *Salmo salar* in the Gulf of Maine (GoM) is listed as an endangered species, with stocks currently at record lows (Fay et al. 2006; ICES 2015). Atlantic Salmon spawn in coastal rivers and juveniles move seaward in the spring as smolts. Upon ocean entry, the fish, now termed postsmolts, migrate northward and spend the next year or more growing to adulthood at sea. Marine survival has been identified as a major factor in the population’s decline since 1990 (Chaput et al. 2005). Though investigating marine survival of GoM Atlantic salmon remains an important challenge, there is great difficulty in collecting data over a migration route that ranges from the GoM to the coast of Greenland (Chaput et al. 2005; Miller et al. 2012). As a result, the influence of environmental factors on spatial distribution and survival during ocean migration are poorly characterized.

While monitoring migration routes remains a challenge, the rapid development of fish tracking techniques using acoustic transmitters and fixed listening receivers deployed in arrays has improved opportunities to characterize Atlantic salmon behavior and survival. These advances have begun to shed light on the relationships between fish behavior and oceanographic variables in previously unattainable ways (Hussey et al. 2015). During the last decade, nearly 2,700 Atlantic salmon smolts have been released into the Penobscot River (Maine, USA) as part of ongoing acoustic telemetry studies (Holbrook et al. 2011; Stich et al. 2014, 2015). The exodus of these fish into the GoM has provided an opportunity to understand the early phase of the species' migration. The installation of an organized network of receivers on the Scotian Shelf has made tracking these fish at distant locations possible. As part of the Ocean Tracking Network (OTN), a series of acoustic receivers covering 180 km from shore seaward have been deployed across the Scotian Shelf, roughly along a traditional ocean monitoring transect called the Halifax Line (HL, Figure 1; Petrie 2004). These receivers have
detected, among other species, Atlantic salmon postsmolts from the Penobscot River (Cooke et al. 2011), providing spatial and temporal data for migrating postsmolts at sea. The OTN research program also includes an observational component that collected measurements of both the hydrography and circulation along the HL, providing a unique opportunity to characterize the local ocean conditions experienced by Atlantic salmon postsmolts.

Ocean climate variables, and particularly ocean temperature, are hypothesized to affect salmon postsmolts growth directly (Todd et al. 2008; Friedland et al. 2012) and indirectly, through a change in prey and predator distributions and interaction (Friedland et al. 2012; MacKenzie et al. 2012; Mills et al. 2013; Renkawitz et al. 2015). The GoM and the Scotian Shelf have rapidly warmed over the last decade (Hebert et al. 2013), putting local fish stocks at risk (Pershing et al. 2015; Hare et al. 2016). When postsmolts pass the HL in early spring, the hydrography is characterized by a coastally-trapped, wedge-shaped water mass composed of colder and less saline water exiting the Gulf of St. Lawrence and originating from the St. Lawrence River (Loder et al. 2003; Hebert et al. 2013; Dever et al. 2016). This water mass is separated by a sharp density front that results from warmer and more saline water covering most of the Scotian Shelf, and that is influenced by off-shelf water coming from the shelf break and the Gulf Stream (Dever et al. 2016). The location of the density front varies on the synoptic timescale, but generally outcrops about 45 km from shore, and intersects the bottom along the 100 m isobath, located roughly 30 km offshore (Loder et al. 2003; Dever et al. 2016).

This offshore density gradient leads to a strong southwestward buoyancy-driven alongshore current called the Nova Scotia Current (NSC; Drinkwater et al. 1979; Smith and Schwing 1991; Dever et al. 2016). The current speed is strongest near the surface, and can reach about 30 cm/s. It spreads between 30 and 60 km offshore on average, with the maximum
velocity located about 45 km from shore. The temperature and salinity in the top 20 m generally co-vary across the Scotian Shelf depending on the dominant water mass (colder and less saline vs. warmer and more saline; see Dever et al. 2016). In spring, the two variables decouple in the surface layer, due to the seasonal increase in surface heat fluxes that warm the upper layer and generate a sharper thermocline (Umoh and Thompson 1994; Loder et al. 2003; Dever et al. 2016).

Because these environmental characteristics vary both spatially and temporally through the region, understanding where migrating fish are observed can help to characterize the conditions these fish may select or avoid. In this study, we sought to combine acoustic detections of Atlantic salmon postsmolts with oceanographic conditions to characterize the seascape through which these fish migrated. Our objectives were (1) to describe the spatial and temporal detection patterns of the Atlantic salmon postsmolts at the HL, (2) to investigate cross-shelf movements during the migration and (3) to relate migratory behavior to physical conditions in the ocean, including estimating the migration heading.

Methods

Tagging and release of smolts

From 2008 to 2014, Atlantic salmon smolts (n= 2,671) were surgically tagged with Vemco V9 transmitters (as described in Kocik et al. 2009 and Holbrook et al. 2011) and released in the Penobscot River (Figure 1). Tagging occurred from April to May, and included both female and male smolts (undetermined), as well as both wild and hatchery fish. The primary study objectives for these releases were to assess in-river management questions such
as dam impacts (Holbrook et al. 2011; Stich et al. 2014) and estuary survival, path choice, and
behavior (Stich et al. 2015). Therefore, smolts were released at various points in the river, with
some passing as many as eight dams, while others had no dams obstructing their seaward
migration. Transmitters were programmed to transmit at random intervals between 20 and 40 s
for the first 35 days and between 60 and 80 s afterwards to preserve battery life and increase the
probability of detecting the transmitter over longer times. Transmitter battery life was estimated
to be about 70 days, which exceeds the time required by the Atlantic salmon smolts to migrate
from the Penobscot River to the Halifax Line.

**Receiver Network**

The array of receivers transecting the Scotian Shelf included up to 256 acoustic
receivers, deployed about 800 m apart over the period 2008-2014 (Table 1; Figure 1). Each
receiving unit was equipped with a bottom-mounted Vemco VR3 or VR4 acoustic receiver
depending on the station. The first 73 stations from shore were deployed along the HL. To
minimize interactions with local commercial fisheries, the array changed direction at stations
HFX073 and HFX164, and can be separated into three sections:

1. **Inner Section** runs from HFX001 (63.533°W; 44.478°N) 60 km SE (141°) to HFX073
   
   (63.074°W; 44.066°N) with depths ranging from 45 to 200 m.

2. **Middle Section** runs from HFX074 (63.079°W; 44.060°N) 72 km SSW (208°) to HFX164
   
   (63.500°W; 43.500°N) with depths ranging from 95 to 210 m.

3. **Outer Section** runs from HFX165 (63.500°W; 43.493°N) 73 km S (180°) to HFX256
   
   (63.500°W; 42.837°N) with depths ranging from 140 to 190 m.
The receiver array was installed incrementally over several years (Table 1). From 2008 to 2010, the shoreward half of the Inner Section (up to HFX028) was deployed. In 2011, the remainder of the Inner Section was deployed (up to HFX073) and the line was completed in May 2012 (up to HFX256). Detection data were acoustically downloaded from the receivers. If a receiver was unresponsive, the acoustic release was triggered, the receiver was recovered and replaced. In those cases, data were downloaded directly from the receiver. Receivers were conservatively assumed to have failed immediately after the last logged detection. Less than 4% of the stations had failed at any given time and no adjacent stations failed simultaneously. Station failures, therefore, were assumed to have negligible effects on observed detection patterns.

Transmitter Detections

Of the 2,671 smolts released for the Penobscot River studies, the 339 postsmolts detected as postsmolts at the Scotian Shelf receiver array comprise our study. For V9 transmitters, the detection range is reported to be about 900 m in calm conditions but is affected by variables that increase the level of ambient noise (Kessel et al. 2014 and references therein), such as environmental factors (e.g., rain, wind, wave action, currents, hydrography); anthropogenic factors (e.g., boats and sonars); and biological factors (e.g., biofouling). However, under optimal conditions a single tag could theoretically be detected at two receivers simultaneously, although this was never observed in the dataset.

For this reason, we pooled individual detections into “sequences”, to characterize distinct encounters as opposed to treating each detection independently (Furey et al. 2015). Detection sequences were defined as a set of detections of a unique transmitter where
consecutive detections were not separated in time by more than one hour or in space by more than two receivers along the array.

**Oceanographic Variables**

Temperature, salinity, current strength, and current direction were measured from a variety of instruments along the HL over the period 2008-2014. We combined these data to better characterize the seascape during the ocean migration phase of Atlantic salmon postsmolts. The following sections describe the different data sources and the processing steps that we applied to the measurements.

*Current Profilers.* – Velocity measurements were made using bottom-mounted, upward-looking Acoustic Doppler Current Profilers (ADCPs) at three locations over the Inner Section of the HL (Figure 1). Currents were measured continuously from April 2008 to October 2014 at stations T1, T2 and T3, with infrequent data gaps representing between 10 and 15% of the time series due to either instrument failures or deployment delays (Dever et al. 2016). Currents were sampled every 30 min with a vertical bin size of 4 m, from 10 m off the bottom to 10 m from the surface. The horizontal components of the observed currents were rotated by an angle of 58° from North to obtain the alongshore and cross-shore directions from the Nova Scotia coastline (Dever et al. 2016). The stations T1, T2 and T3 are located around the onshore boundary, the current maximum and the offshore boundary of the NSC, respectively, and correspond to the stations HFX028, HFX048, and HFX069.

*Glider Measurements.* – From June 2011 to September 2014, 59 transects were completed along the HL using Teledyne Webb Research Slocum electric gliders. Gliders
sample the water column to depths of 200 m in a triangle wave sampling pattern. The horizontal and vertical resolution of the glider datasets were not uniform and depended on the angle of attack of the glider (about 22 to 26° from the horizontal), average relative and ground speeds (~0.3 m/s), and depth of the water column. The resulting average vertical resolution was about 0.3 m, while the finest horizontal resolution was 850 m. It took from 3 to 11 days for the glider to complete a survey of the HL, depending on spatial coverage, and it recorded pressure, temperature, and conductivity during each mission.

Both salinity and potential density were computed using the Gibbs Seawater toolbox in MATLAB (McDougall and Barker 2011). Observations made by the glider along each transect were gridded on a 0.5 m × 1 km grid in the vertical and horizontal directions, respectively. Because the glider sampled at 0.5 Hz (i.e., each transect included between 150,000 and 450,000 data points), no interpolation was necessary to bin the glider data onto the spatial grid, and a simple two-dimensional averaging block was used while still preserving the main hydrographic features.

Two estimates of currents were retrieved from Slocum gliders: The first estimate was depth-averaged and solely based on the flight characteristics of the glider. The other was based on in situ temperature and conductivity measurements collected by the glider, and estimated geostrophic currents across the glider’s path (Dever et al. 2016). It is worth noting that individual glider transects are not to be considered as instantaneous snapshots of the cross-shelf conditions, because of the time required to complete a transect (Dever et al. 2016).

To directly compare hydrographic data collected at the HL (Figure 1) to acoustic detections as a function of distance from shore, the HL was projected onto the receiver array
formed by the acoustic receivers. The projection follows the alongshore direction defined in previous work by a heading of 58° (Dever et al. 2016; see Figure 1). This projection was selected among several other projections techniques by maximizing the correlation coefficient in the hydrographic fields of two glider transects completed consecutively along both the receiver array and the HL in the spring of 2014. Because of this projection, and for readability reasons, the acronym HL is used interchangeably to denote both the oceanographic transect and the receiver array. The distance from shore is calculated for both datasets based on a reference point located on Sambro Head (63.534°W, 44.482°N).

*Satellite-derived Sea Surface Temperature (SST).* – For each individual year over the period 2011-2014, the daily averaged SST along the HL was extracted from observations collected by the MODIS\(^1\) satellite. At the time of crossing of the Atlantic salmon postsmolts, the thermocline depth is located between 20 and 30 m, with a relatively homogeneous mixed-layer (see supplementary materials). Because postsmolts are thought to spend most of their time in the upper 20 m of the water column, SST is therefore assumed to be more representative of the temperature experienced by the postsmolts. Satellite-based SST is used to complement glider-based measurements by providing a higher temporal resolution.

**Analysis of arrival timing at the HL**

An objective was to characterize the variability in arrival timing of Atlantic salmon postsmolts at the HL at inter-annual timescales. For each individual year, the timestamp

\(^1\) Data available at https://oceancolor.gsfc.nasa.gov/
corresponding to the first detection of a transmitter was extracted to record the arrival of an individual postsmolt at the HL. Detections were then grouped into 1-day bins, and normalized by the total number of transmitters detected that year to obtain a daily “detection percentage” denoted as $D$. A 5-day moving average was used to suppress the daily variability in the temporal distribution for two reasons: (1) the timescales of interest are on the order of inter-annual, and (2) it is difficult to associate daily variability in detections with migratory behaviors, as detection efficiency can also vary on daily timescales due to a change in environmental conditions (Kessel et al. 2014 and references therein). Finally, a Gaussian model was fitted to the smoothed yearly temporal distribution of the detection percentage to extract the yearly mean and standard deviation of the arrival timing at the HL, using the following equation:

$$D(t) = a \times e^{\left(-\frac{(t-\mu)^2}{2\sigma^2}\right)}$$  \hspace{1cm} (1)

where $D(t)$ is the temporal distribution of the detection percentage, $t$ is the day of year and $a$, $\mu$, and $\sigma$ are the regression coefficients and represent the amplitude, mean, and standard deviation of the Gaussian distribution, respectively. The same analysis was conducted for the period 2008-2014 to characterize the statistics of Atlantic salmon postsmolts arrival timing at the HL in any given year.

**Analysis of spatial patterns of detection and environmental factors**

Because the complete HL was not in place until the 2012 Atlantic salmon migration
period, only 2012 to 2014 data were used to analyze the spatial variability of the detections. The average distribution of detection sequences along the HL was calculated based on 309 detection sequences logged over the period 2012-2014.

To better quantify the relationship between the spatial detection patterns and oceanographic variables, a multiple regression analysis was applied to the detection count. For each variable, the top 20 m of the water column was averaged to obtain the temperature, salinity, and alongshore currents. The variables were then standardized by subtracting the average for all years and scaling by the standard deviation. The linear model can be written as:

$$D(x) = \beta_1 \overline{T}(x) + \beta_2 \overline{S}(x) + \beta_3 \overline{V}(x)$$

where $D(x)$ is the detection percentage at a location $x$, and $\overline{T}$, $\overline{S}$, and $\overline{V}$ are the averaged temperature, salinity and alongshore flow anomalies over the top 20 m for each observed detection sequence.

This multiple regression analysis has strengths and limitations; firstly, it is worth noting that oceanographic variables alone cannot be expected to explain all the spatial variability in the acoustic detections. Other parameters such as fish size (Handeland et al. 2008), the chemical signal of water masses (Døving and Stabell 2003), and navigation and orientation (Burke and Byron 2014; Byron et al. 2014) are also likely to influence migratory behavior of fish.

Secondly, glider-based measurements are a function of distance and time and are therefore not necessarily concurrent to the detection data. This model therefore approximates that the temporal variability of the regressed variables in the top 20 m over the duration of a
transect is smaller than their spatial variability across the shelf, compensating for the time
difference between glider and detection observations.

Finally, the model assumes that the regressed variables are independent. This
assumption is only valid from June to September, where the correlation between temperature
and salinity in the top 20 m is below 0.6 ($p \ll 0.01$). However, this assumption is not valid over
the rest of the year because temperature and salinity are strongly coupled across the Scotian
Shelf from the colder and less saline watermass coming for the Gulf of St. Lawrence to the
warmer and more saline watermass coming from the shelf break ($r > 0.8$, $p \ll 0.01$; Loder et al.
1997; Dever et al. 2016). The weaker correlation between temperature and salinity in the upper
water column during spring and summer can be explained by the influence of surface heat
fluxes, that primarily drive the temperature field (Umoh and Thompson 1994). Atlantic salmon
postsmolts were detected during late spring and early summer, therefore temperature and
salinity were considered as two independent variables.

While the model is therefore not fitted for predictive purposes, useful information can
still be deduced from the regression’s coefficients. The sign and relative amplitude of $\beta_i$ as well
as the error associated with the coefficients provide insights into the environmental preferences
of Atlantic salmon postsmolts.

**Migratory behavior and cross-shelf movements**

We analyzed detection sequences of Atlantic salmon postsmolts individually to
investigate their migratory behavior when detected at the HL. We calculated estimates of the
time spent, the ground covered, and the net cross-shelf movements of the animals along the HL,
by using first and last detections of each detection sequence to represent arrival and departure
of individual fish. Magnitude of the distance covered is only an estimation based on our
assumption that the fish location was identical to the station’s coordinates where the transmitter
was detected. However, the fish could be located within a receiver’s detection radius
(approximately 450 m) but varies in time and space (Kessel et al. 2014).

A Sinuosity Index (SI) was also developed to provide more information on the behavior of the
fish while migrating. SI was used to evaluate whether fish tended to swim back-and-forth
between two receivers, or demonstrated a more substantive cross-line movement. In this study,
the SI was defined as the net difference in the station number between the first and last
detections (i.e., “net station change”) divided by the total number of station changes:

\[
SI = \frac{\text{net station change}}{\text{total number of station changes}}
\]  

SI was therefore only defined for detection events covering more than a single station, and can
be interpreted as follows:

(1) SI = 0; the fish left the HL in the same location it was first detected, therefore exhibiting
no net cross-line movement

(2) SI < 1; the fish principally zigzagged, with some small cross-shelf movement

(3) SI = 1; the fish completed a cross-shelf movement along the HL and has been detected
consecutively at each station along the way

(4) SI > 1; the fish completed a significant cross-shelf movement away from the HL, and has
therefore not been consecutively detected along the array
The hypothesis that observed cross-shelf movements are driven by local currents was tested over the Inner Section, where current measurements were available, and most detections of postsmolts were recorded. The direction of cross-shelf currents measured in the top 20 m of the water column at the three T-stations was thus compared to the observed cross-shelf movements of the fish to assess a possible correlation. The comparison was completed over different speed ranges, to ensure that the relationship between cross-shelf fish movements and current directions did not change depending on the current speed.

**Results**

**Oceanographic Variables**

Temperature and salinity distributions in the upper 50 m collected along the HL before, during, and after the detection period of Atlantic salmon postsmolts were analyzed to identify changes in the seascape that could be related to the arrival of the Atlantic salmon postsmolts (Figures S1, S2, and S3). Across all years, a substantial temperature difference was noticed between transects collected before and during the detection period (Figure S1). Water temperature in the first 20 m of the water column (i.e., where postsmolts spend most of their time; Renkawitz et al 2012) averaged about 7°C before postsmolt arrival and 10°C during the detection period. No relevant changes occurred in the salinity field in the periods before, during, and after the detection periods (Figure S2).

No low-frequency differences in current strength or position that would explain the timing of crossing of the HL by the postsmolts were noticed (Figure S3). Daily detections
logged over the Inner Section of the HL were also compared to the alongshore transport associated with the NSC and computed from the three ADCP stations (not shown). The results confirmed that the strength of the NSC can significantly vary on different timescales (daily to inter-annually) and that the variability in the NSC was not correlated to the timing of arrival of the postsmolts.

When comparing the hydrography along the HL during the detection period, we see that the distribution of low-salinity water across the HL varied between years in the study (Figure 2). Low-salinity water at the surface was more widely distributed in 2013, than in 2012 or 2014 when the low-salinity water was more confined to the Inner Section.

The magnitude, standard error, t-test, and p-value for each coefficient in Equation 2 are reported in Table 2. The coefficients $\beta_1$ and $\beta_2$ are significant, indicating that the percentage of postsmolts detections on the HL was related to temperature and salinity. The value of $\beta_3$ has the same order of magnitude as the standard error, meaning that the regression failed to detect a correlation between percentage of detections and alongshore flow. Overall, these relationships explained about 35% of the variation in the distribution of postsmolt detections ($R^2 = 0.35$, $df = 435$, $p \ll 0.01$).

**Analysis of arrival timing at the HL**

Based on years where the HL was complete (2012-2014), no clear spatio-temporal relationship could be established in postsmolt arrival at the HL. As a result, the entire time series (2008-2011) was considered to study the timing of Atlantic salmon postsmolts arrival at the HL, despite a partially-deployed HL (see Table 1).
The overall mean date of detection ($\mu$) among all years, as estimated by the Gaussian model ($R^2 > 0.96$), was June 5 (week 23, SD = 9.6 days), and ranged from May 15 (week 20) to July 1 (week 26) during the years studied (Figure 3). Annual analyses indicated a high degree of inter-annual variability in mean date of arrival at the HL. Variability observed on daily timescales might not be representative of real migratory behavior, but rather associated with poor detection efficiency variability due to environmental conditions. For example, the bimodal distribution observed in 2011 and 2013 was possibly due to a short period of high winds (> 10 m/s), therefore affecting the detection efficiency.

Annual timing of Atlantic salmon postsmolt detection at the HL revealed two different modes (Figure 3): early arrivals in 2010, 2012 and 2013 and later arrivals in 2008, 2009, 2011 and 2014. Again, the Gaussian model performed well for describing annual distributions of postsmolts arrival ($R^2$ between 0.88 and 0.99). Early arrivals were usually centered on the last few days of May, while late arrivals corresponded to a detection peak about 2 weeks later, between June 12-17, depending on the year. Annual SD for detections estimated by the Gaussian models ranged from 3 to 6.8 days, but was not correlated with the timing of arrival. Although the detection peak was earlier in 2014 (June 9), it was considered as a “late year” as there were no detections recorded before June 1, similarly to other “late years”. Detection efficiency (and thus numbers of detections recorded) after June 15, 2014 may have been artificially lowered due to strong winds recorded at a nearby weather station from June 15-21. A similar event was observed around June 15, 2011, where detections decreased likely due to strong winds (>10 m/s) at that time. The yearly standard deviations of the Gaussian model provide information on how long the Atlantic salmon postsmolts populations took to cross the HL during their northeastern migration for a particular year. The standard deviation of the
average distribution, however, includes additional information on the inter-annual variability in the mean arrival timing. Satellite-based SST at time of Atlantic salmon arrival were recorded for each year over the period 2008-2014. SST ranged between 6.5 and 10.8 °C (mean = 8.5 °C, SD = 1.2 °C) and was relatively consistent across late and early years.

Analysis of spatial patterns of detection and environmental factors

Our analysis revealed that 53% (163/309) of the detection sequences were located over the Inner Section of the line with 25% (76/309) inshore of station T1 (station 28, < 26 km from shore). About 38% (118/309) of the detections were logged over the Middle Section, and only 9% (28/309) over the Outer, even though the Outer Section covered more distance than the other sections (Figure 4). The average distribution also exhibited a local minimum in the detection percentage around station T2 (station HFX050; 45 km offshore) for all years.

All three years show a significantly different spatial distribution (Figure 4). While distributions of detections were similar across the HL in 2012 and 2014 (56-62% over the Inner Section, 33-39% over the Middle Section, and 5-6% over the Outer Section); they differed within the Inner Section. In 2012, most of the detections were located onshore of station T1, shoreward of the average onshore boundary of the NSC. In 2014, detections were more evenly spread throughout the Inner Section, as indicated by a median distance of 47 km in 2014 vs. 29 km in 2012 (p < 0.01). This increase in detection percentage within the NSC (i.e. between stations T1 and T3) is intriguing, given that the NSC transport averaged over the detection period was -0.30 Sv in 2014 compared to -0.21 Sv in 2012, (p << 0.01). Fewer detections were
logged over the Inner Section during 2013 (41%; 46/113); Middle Section detections accounted for 43% (49/113) of the detections and the Outer Section 16% (18/113) during 2013. A local minimum was also observed between the stations T1 and T2, even though the transport associated with the NSC was weaker in 2013 (-0.17 Sv) than in 2012 (-0.21 Sv; p ≪ 0.01).

**Migratory Behavior and Cross-Shelf Movements**

The majority of postsmolts (92%) were detected more than once, with an average of 18 detections per detection sequence. This was an encouraging sign that the detection efficiency of the acoustic curtain at the HL was somewhat reliable. While 60% (281/472) of the detection sequences were logged over a single station, 28% (134/472) were detected over two adjacent receivers and 12% (57/472) were recorded at more than 2 adjacent stations.

The average time spent along the HL was relatively short (21 min), but varied from 32 s to 4.3 h (Figure 5). Almost 75% of the animals spent less than 25 min at the HL, and half of the multi-detected postsmolts passed the HL within 12 min of their initial detections. As expected, sequences detected over several receivers (i.e., multi-station sequences (MSS), representing 40% of the population) corresponded to longer residence times at the HL. With an average time of 37 min, 75% of the MMS fish spent less than 36 min at the HL and 50% left within 24 min of their initial detection.

For all 472 detection sequences of postsmolts, the average distance traveled along the HL was about 500 m, ranging from 0 m (i.e., fish detected at a single station) to 5.6 km (~ 7 stations). The median value was logically 0 km, as more than half the detection sequences were logged over a single station (60%). This skews the probability distribution towards lower
values. As such, we also calculated descriptive statistics for MMS fish only (N=191, Figure 5).

The average distance covered increased to 1.2 km in this group, with half of the individuals covering no more than 850 m. This indicates that most of the observed cross-shelf movements occurred over two to three adjacent stations.

When estimated for all 472 detection sequences, the SI varied from 0 to 1, with an average of 0.6 (25th percentile = 0.20, median = 0.5, 75th percentile = 1.00). According to Equation (3), SI is only defined for detection events covering more than a single station (N=191). The SI for detection sequences inherently cannot be greater than 1, due to the condition that a fish detected more than 2 stations away from the previous detection constitutes a new detection sequence. For this reason, it is also important to calculate the SI on an individual basis, as opposed to detection sequences, because it characterizes the migratory behavior of the fish as an animal. It therefore allows the SI to be greater than 1. When estimated for all 339 fish detected along the HL, the SI varied from 0 to 111, averaging 3.8 (25th percentile = 0.27, median = 1.00, 75th percentile = 1.10).

We analyzed cross-shelf movements of Atlantic salmon postsmolts to detect any significant patterns that would provide more information on the postsmolts’ migratory behavior. These data include 34, 29, and 4 fish detected over the Inner, Middle, and Outer Sections of the HL. We found a clear pattern in cross-shelf movement patterns of postsmolts that migrated through different sections of the HL (Figure 6). About 76% (26/34) of the fish detected over the Inner Section of the OTN line moved in an offshore direction (i.e., increasing station number), while 80% (23/29) of the postsmolts detected over the Middle Section moved onshore (i.e., decreasing station number). Too few fish (N=4) were detected over the Outer
Section of the HL to allow a reliable interpretation.

Since postsmolts typically spent less than 1 hour around the HL (Figure 5), the next logical step was to test the hypothesis that these cross-shelf movements were driven by local currents experienced by the fish at the time of crossing. We failed to detect statistical correlations between cross-shelf movements and current direction. Atlantic salmon are strong swimmers and while weaker currents might not dictate the swimming direction of the fish, periods where the currents were stronger might have influenced the along-array movements of the detected fish. The same analysis was therefore applied to fish experiencing stronger currents only. The result persisted: along-array movements were not correlated to the flow direction, and occurred independently of the current speed.

Discussion

Temporal variability of detections

The arrival of Atlantic salmon postsmolts at the HL appears to be under the control of seasonal warming and temperature conditions. Atlantic salmon postsmolts were only detected at the HL once the surface warming has started in spring (Figures 3 and S1). The satellite-based SST at the time of the first detection of postsmolts at the HL ranged between 6.5 and 10.8 °C (mean = 8.5 °C, SD = 1.2 °C). Glider-based temperatures in the top 20 m of the water column increased from an average temperature of about 7°C, with a weak thermocline before the detection period, to a temperature of about 10°C and a better-defined thermocline during the detection period. These results parallel extensive evidence in the freshwater migration literature
that Atlantic salmon smolts migration is modulated by the onset of a 10°C threshold temperature (Hayes and Kocik 2014; Zydlewski et al. 2005, and references therein). It also corresponds to the estimates of optimal temperature for postsmolts growth and food conversion efficiency (Handeland et al. 2008; Minke-Martin et al. 2015). More importantly, this temperature-dependence is consistent over the period 2011-2014, independently of whether the migration timing was classified as a late or an early year. This constitutes evidence that some of the inter-annual variability observed in the arrival of postsmolts at the HL is influenced by the temperature in the upper water column, where the fish are present.

We found no similar trends when comparing transects of salinity collected before, during, and after the detection period. The salinity variability at the HL in the regions Atlantic salmon postsmolts transit is relatively small compared to the range of salinities experienced by the salmon during the migration from a freshwater to a saltwater environment. This suggests that salinity is not an important variable when defining ocean habitat for Atlantic salmon, although it could have an impact on their swim speed (Byron and Burke 2014).

Previous research has demonstrated correlations between ocean currents and adult return rates of Atlantic salmon over inter-annual timescales (Thomson et al. 1992; Byron and Burke 2014). However, we observed no significant changes in the alongshore ocean currents along the HL that could explain the migration timing in postsmolts. The alongshore transport associated with the NSC is highly variable over timescales ranging from daily to inter-annually, but was always southwestward at the time of detection, suggesting that Atlantic salmon may use positive rheotaxis during migration, even in the marine environment, although the nature of the present study does not permit investigation of such causative mechanisms. Studies indicate
that salmon migration may (Booker et al. 2008; Mork et al. 2012) or may not (Burke et al. 2014; Byron et al. 2014) be affected by ocean currents, suggesting population-specific migratory behavior (Døving and Stabell 2003).

Our findings confirm the role of ocean temperature as one of the environmental cues influencing Atlantic salmon postsmolts during their oceanic migration (Friedland et al. 2000, 2005; Handeland et al. 2008; Minke-Martin et al. 2015). We suggest that Atlantic salmon postsmolts migrate northward once surface water has warmed in the spring, and may follow this heating as it propagates to higher latitudes. This hypothesis is supported by findings of Minke-Martin et al. (2015), who found that Atlantic salmon captured west of Greenland experienced a relatively constant temperature throughout their ocean migration.

**Spatial variability of detections**

Distribution of postsmolts along the HL showed significant inter-annual variability, but was consistently lower near the maximum of the NSC (Dever et al. 2016). The important role of oceanic fronts in shaping large ecosystems has been previously recognized by Le Fevre (1986) and Belkin et al. (2009). It has also been determined that biomass tends to accumulate along oceanic fronts due to converging flows (Houghton and Marra 1983; Franks 1992).

Conversely, studies focusing on Pacific salmon found that fish prefer specific thermal and halo-limits, and are not more abundant within a riverine plume front, despite the larger concentration of prey organisms (Robertis et al. 2005; Azumaya et al. 2007). Two possible mechanisms could explain the local minimum in transmitters detections: either postsmolts tend to avoid the NSC and the associated front located between stations T1 and T3, or they prefer the colder and less
saline inshore water associated with the outflow coming from the Gulf of St. Lawrence (Loder et al. 1997; Dever et al. 2016).

Atlantic salmon postsmolts seemed to prefer colder and less saline water during this phase of their migration. However, these results must be interpreted with caution, as colder and less saline water corresponds to the previously described inshore water mass emanating from the Gulf of St. Lawrence (Loder et al. 2003; Dever et al. 2016). While the preference of the postsmolts for this water mass can be observed in the temperature and salinity fields, postsmolts might also be responding to other characteristics associated with this water mass such as the presence of prey organisms or a more suitable chemical signature (Le Fevre 1986; Døving and Stabell 2003; Robertis et al. 2005). Unfortunately, no concurrent observations of food availability are available along the HL to investigate this further.

We failed to document a relationship between postsmolt detection and alongshore currents. This supports the hypothesis that the migratory behavior of Atlantic salmon postsmolts is not hindered by ocean currents, and that the decrease in detections between stations T1 and T3 is linked to changes in water properties, with the water getting warmer and more saline, rather than related to the presence of the NSC. A similar observation was made by Robertis et al. (2005), where more fish were localized in the Columbia River plume region than in the more marine shelf waters.

Migratory behavior and cross-shelf movements

The time spent and the area covered during each detection sequence reveal that the migratory behavior of Atlantic salmon postsmolts is characterized by a rapid migration, as
opposed to a lingering foraging behavior that would be indicated by longer residency times. This conclusion is further supported by the Sinuosity Index that demonstrates that a large majority of the fish crossed the HL over a relatively small area and that the habitat covered by the fish can be explained by a generalized back-and-forth movement over a limited number of receivers.

Too few detections are available over the Outer Section of the line to reduce the heading range any further. However closer to shore, we found a significant number of fish exhibit significant cross-shelf movements as characterized by SI>1. When the direction of the cross-shelf movement was compared to the station where the fish was first detected, we found postsmolts moved offshore within the Inner Section and onshore within the Middle Section. This convergence towards the edge of the NSC suggests that Atlantic salmon postsmolts may use positive rheotaxis and the NSC to both orient and navigate. Because these cross-shelf movements were not correlated with ocean currents, the different orientation of the two sections of the line can be used to define a general heading of the migration. Using the orientation of the Inner Section (141°) and the Middle Section (208°), and assuming that postsmolts were headed northeast, the migration heading ranged between 51° and 118° from True North. These relationships of postsmolt movements to the NSC may also provide insights into the next steps of migration for post smolts to more common nursery areas off the Newfoundland and Labrador coast (Reddin and Shearer 1987) or occasional entry into the Gulf of St. Lawrence (Friedland et al. 1999).

Conclusions
The current study provides evidence on the conditions experienced by Atlantic salmon postsmolts from the Gulf of Maine during their ocean migration. We learned that the postsmolts arrival at the HL significantly varies from year-to-year, and that some of the variability is modulated by the warm-up of the surface layer through solar heating in spring. The ocean temperatures observed along the HL at the time of crossing (8.5 ± 1.2°C) tend to be warmer than previously reported Atlantic salmon habitat use (4 – 8°C, Reddin and Shearer 1987; 3.9 – 9.7°C, Minke-Martin et al. 2015). The study also demonstrates a postsmolts preference for colder and less saline water, while avoiding the frontal region; despite evidence that high concentrations of prey organisms are usually present along ocean fronts (Le Fevre 1986; Franks 1992; Robertis et al. 2005). The observed cross-shelf movements of the fish do not present any correlation with local ocean currents and can therefore be attributed to a migratory behavior. These findings led to the hypotheses that (1) inter-annual variability in postsmolts migration timing is driven by the increase of surface heat fluxes associated with spring; (2) postsmolts favor colder and less saline river plume water; and (3) local oceanic currents have minimal impact on the migratory behavior of the postsmolts. These could be tested with more refined arrays deployed in key regions such as Browns Bank, where the southern Atlantic salmon postsmolts are expected to change their migratory heading from eastward to northeasterward as they migrate around the southern tip of Nova Scotia. The acoustic array could be deployed during the migration period of the postsmolts only (April to July), established from the results of this study. Greater numbers of tracked fish as well as the use of depth tags that would provide more information on the vertical movements would also be beneficial. Finally, a more extensive study of the variability in detection efficiency using sentinel tags would provide more confidence in the representativeness of observed fish.
Our study highlights the potential of combining animal tracking and oceanography to better understand the factors driving postsmolts ocean migration and affecting their marine survival. Networks like these would not only benefit salmon, but any other highly migratory species. They also provide valuable observations to further inform models that use temperatures and ocean currents to simulate migratory behaviors.

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References

Azumaya, T., T. Nagasawa, O. S. Temnykh, and G. V. Khen. 2007. Regional and seasonal
differences in temperature and salinity limitations of Pacific salmon (Oncorhynchus spp.).


Atlantic salmon (Salmo salar). Canadian Journal of Fisheries and Aquatic Sciences 65:352–
361.


Byron, C. J. and B. J. Burke. 2014. Salmon ocean migration models suggest a variety of

Byron, C. J., A. J. Pershing, J. D. Stockwell, H. Xue, and J. Kocik. 2014. Migration model of
post-smolt Atlantic salmon (Salmo salar) in the Gulf of Maine. Fisheries Oceanography

taking account of non-stationarity in productivity of Atlantic salmon (Salmo salar L.) in the

Whoriskey. 2011. Ocean Tracking Network Canada: A Network Approach to Addressing
Critical Issues in Fisheries and Resource Management with Implications for Ocean

coastal circulation along the Halifax Line and the connections with the Gulf of St. Lawrence.


Mills, K. E., A. Pershing, T. F. Sheehan, and D. Mountain. 2013. Climate and ecosystem
linkages explain widespread declines in North American Atlantic salmon populations. Global

estimates of marine temperature use by West Greenland Atlantic salmon (Salmo salar). ICES

2012. Modelling the migration of post-smolt Atlantic salmon (Salmo salar) in the Northeast


Pershing, A. J., M. A. Alexander, C. M. Hernandez, L. A. Kerr, A. Le Bris, K. E. Mills, J. A.
Nye, N. R. Record, H. A. Scannell, and J. D. Scott. 2015. Slow adaptation in the face of rapid


Renkawitz, M. D., T. F. Sheehan, and G. S. Goulette. 2012. Swimming Depth, Behavior, and
Survival of Atlantic Salmon Postsmolts in Penobscot Bay, Maine, Transactions of the
American Fisheries Society 141:1219-1229.

structure and energy dynamics in the Northwest Atlantic: implications for Atlantic salmon
feeding at West Greenland. Marine Ecology Progress Series 538:197–211.

Robertis, A. D., C. A. Morgan, R. A. Schabetsberger, R. W. Zabel, R. D. Brodeur, R. L.
Emmett, C. M. Knight, G. K. Krutzikowsky, and E. Casillas. 2005. Columbia River plume
fronts. II. Distribution, abundance, and feeding ecology of juvenile salmon. Marine Ecology
Progress Series 299:33–44.


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TABLE 2: Coefficients of the multiple regression analysis linking the detection percentage of Atlantic salmon postsmolts to the temperature, salinity, and current speed (Equation 2).

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<th>Standard error</th>
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Figure captions

Figure 1. Map of the region connecting the Penobscot River System to the Halifax Line on the Scotian Shelf. Inset shows the Halifax Line, which corresponds to the average glider track, the receiver array composed of 256 receivers (black dots) with the station numbers where the array changes direction (black squares), as well as the projection used for the spatial analysis (see Section 2). The locations of the three ADCP stations (T1, T2 and T3) are marked by black triangles, and the red circle represents the location of the reference point on Sambro Head (see Section 2). Bathymetric contours are shown for the 100, 500, 750, and 1000 m isobaths (for inset - the 100, 200, 500, 750, and 1000 m).

Figure 2. Glider-based transects of temperature (top row, in °C), salinity (middle row) and alongshore velocity (bottom row, in m/s, negative means southwestward) collected during the detection period in 2012 (left panels), 2013 (middle panels) and 2014 (right panels). Stations T1, T2 and T3 are indicated in each transect by dotted lines, while the dashed lines mark the separation between the different sections of the Halifax Line.

Figure 3. Smoothed first detections percentage of Atlantic salmon postsmolts along the HL for individual years, as well as averaged over the period 2008-2014. In each panel, the Gaussian model fitted to the smoothed temporal distribution using equation 1 is represented (thick black line) and the model’s average (μ) and standard deviation (σ) are indicated. The sample size (N) and the coefficient of determination (R²) of the model are also shown in each panel. Note the change in scale in the last panel. The Sea Surface Temperature (in °C) from MODIS is super-imposed (dashed line).

Figure 4. Average spatial distribution of Atlantic salmon postsmolts detection sequences along the Halifax Line over the period 2012-2014, as well as for each individual year. On each panel, the 10-km moving average (thick line) is super-imposed, and the median distance from shore is indicated.

Figure 5. Bi-dimensional boxplots showing the distributions of the time spent (in h) on the horizontal axis and the total distance covered (in km) along the Halifax Line on the
vertical axis for (a) all the detection sequences and (b) the detection sequences that spread over at least two stations (i.e., multi-station sequences). The horizontal axis shows the 25th (left-most thick black line), 50th (green line), and 75th (right-most thick black line) percentile of the distribution of time spent at the HL (grey dots). The vertical axis shows the 25th (lower-most thick black line), 50th (red line), and 75th (upper-most thick black line) percentile of the distribution of distance covered at the HL (grey dots). Maximum time spent and total distance covered are also indicated.

Figure 6. Difference in the station number between the first and last detection recorded for animals logged over at least three adjacent or two non-adjacent receivers over the period 2008-2014 (N = 67). A negative station change indicates an onshore movement while a positive change illustrates an offshore movement. Horizontal dashed lines indicate where the HL changes direction and delineates the three sections. The right-hand-side panel shows a zoom-in of the distribution over the first 10 stations.

Figure S1. Glider transects of temperature (in °C) collected along the Halifax Line before (left panels), during (middle panels) and after (right panels) the Atlantic salmon postsmolts detection period in 2011 (1st row), 2012 (2nd row), 2013 (3rd row) and 2014 (4th row). The positions of the ADCP stations are indicated by vertical dashed lines.

Figure S2. Glider transects of salinity collected along the Halifax Line before (left panels), during (middle panels) and after (right panels) the Atlantic salmon postsmolts detection period in 2011 (1st row), 2012 (2nd row), 2013 (3rd row) and 2014 (4th row). The positions of the ADCP stations are indicated by vertical dashed lines.

Figure S3. Glider transects of alongshore current velocity (in m/s) collected along the Halifax Line before (left panels), during (middle panels) and after (right panels) the Atlantic salmon postsmolts detection period in 2011 (1st row), 2012 (2nd row), 2013 (3rd row) and 2014 (4th row). The positions of the ADCP stations are indicated by vertical dashed lines.
Figure 1.
Figure 2.
Figure 3.
Figure 4.
Figure 5.
Figure 6.
Supplementary Material

This supplementary material includes figures showing the temperature, salinity and alongshore currents as measured by underwater gliders for the period immediately before, during and immediately after the detection period of Atlantic salmon postsmolts along the Halifax Line. These figures are included to visualize the change, or lack of, in oceanographic variables that is coincident with the arrival of Atlantic salmon postsmolts at the Halifax Line.
**Figure S1.**
Figure S2.
Figure S3.