Title: Atlantic salmon movement patterns and habitat use during colonization of novel habitat

Running head: Salmon movement during colonization

Author list:

Danielle M. Frechette*, Institut National de Recherche Scientifique, Centre Eau Terre Environnement, Québec, Québec, Canada, G1K 9A9, danielle.frechette@ete.inrs.ca

Mélanie Dionne, Ministère des Forêts, de la Faune et des Parcs, Direction de la faune aquatique, Québec, Québec, Canada, G1S 4X4, Melanie.Dionne@mffp.gouv.qc.ca

Julian J. Dodson, Université Laval, Québec, Québec, Canada, G1V 0A6, Julian.Dodson@bio.ulaval.ca

Normand E. Bergeron, Institut National de Recherche Scientifique, Centre Eau Terre Environnement, Québec, Québec, Canada, G1K 9A9, normand.bergeron@ete.inrs.ca

*Corresponding author; present address: Maine Department of Marine Resources, 650 State Street, Bangor ME, 04401

This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1002/TAFS.10284

DR. DANIELLE M. FRECHETTE (Orcid ID : 0000-0002-3344-6338)

Article type : Article

Abstract

Allowing reproductive individuals to colonize novel habitat or recolonize previously occupied habitat is increasingly being considered as a tool for recovery of depleted populations of anadromous salmon. Successful application of these techniques requires thorough understanding of how adults use the riverscape during colonization to ensure that programs achieve desired outcomes. We examined movements and habitat use of adult Atlantic Salmon *Salmo salar*, during colonization of novel habitat in an eastern Canadian river using a novel combination of acoustic telemetry, remote sensing, ground surveys, and continuous records of river temperature and discharge. Females moved less than males regardless of river temperature or discharge, whereas males engaged in more extensive movements except at elevated temperature and discharge. Probability of movement was lower during the summer, coincident with individuals holding in pools during high heat/low discharge events. River temperature, discharge, and day of year were influential in predicting whether salmon held in pools, and size was the most important physical characteristic identifying "suitable" holding pools. Observed movement patterns may reflect different evolutionary strategies employed by each sex to maximize reproductive fitness. Because spawning behavior is highly conserved within salmonids, these findings may 1) provide a generalized picture of how Atlantic Salmon use space during colonization of unoccupied habitat and 2) be used to optimize future reintroduction and assisted migration programs.

Introduction

Salmon populations have decreased dramatically throughout much of their North American and European ranges due to over-harvest, loss and degradation of freshwater habitat, construction of dams that block access to spawning and rearing habitat, and decreased survival in the ocean (National Resource Council 1996; Gustafson et al. 2007; Jonsson and Jonsson 2011; ICES 2018). Recovery programs for depleted salmon populations have predominantly relied on supplementation using hatchery-reared salmon (Kostow 2009; Fisch et al. 2015). Reintroduction and assisted migration are gaining popularity for salmon recovery because of genetic and ecological risks related to hatchery propagation (Kostow 2009; Anderson et al. 2014; Fisch et al. 2015).

Salmon reintroduction programs facilitate access to upstream spawning and rearing areas previously used by salmon that were made inaccessible by dams or other anthropogenic features (Anderson et al. 2014). In assisted migration, (hereafter, “colonization”), salmon are given access to river reaches that have appropriate spawning and rearing habitat but were historically inaccessible because of natural barriers to migration, (e.g., large waterfalls; Bryant et al. 1999). The primary methods used to accomplish reintroduction and colonization for salmon are volitional passage and translocation. Volitional passage is facilitated by removal or alteration of a migration barrier (e.g., through installation of a fish ladder or fish lift), which allows upstream migrating salmon to pass the obstruction and reach spawning habitat (Bryant et al. 1999; Pess et al. 2011; Pess et al. 2012; Izzo et al. 2016). Translocation (also referred to as “trap and haul”) entails capturing salmon and physically transporting them via truck or barge (Anderson et al. 2014).

Introducing adults to previously inaccessible habitat can enhance population productivity by allowing the breeding population to expand into unoccupied, high quality habitat, thereby reducing density-dependent effects on juvenile growth and survival (Pess et al. 2011; Anderson et al. 2014). Without a detailed understanding of how salmon exploit novel habitat during colonization, reintroduction and colonization programs may not achieve this desired outcome.

Migration and habitat use by adult salmon are influenced by a variety of intrinsic and extrinsic factors. Fish sex, size, proximity to the spawning season and river temperature all affect migration patterns (Baglinière et al. 1990; Baglinière et al. 1991; Dahl et al. 2004; Thorstad et el. 2008; Richard et al. 2014; Martin et al. 2015). River hydrology and geomorphology shape river habitat and influence spawning migrations by affecting the difficulty of upstream passage and the time and energy it takes to reach spawning grounds (Milner et al. 2012). Such features also may limit the availability of pools where salmon stop to rest and recover during upstream migration or between spawning attempts (Bardonnet and Bagliniere 2000; Milner et al. 2012).

Despite many studies of upstream migration of returning adult salmon, a general mechanism for predicting the migratory response of salmon to environmental conditions (e.g., river temperature and discharge) has not been developed (Thorstad et al. 2008; Bendall et al. 2012). Links between migration patterns and temperature or discharge are likely river- and context-specific, and relationships between these variables are complex and often correlated (Jonsson 1991, Bendall et al. 2012, Martin et al. 2015). Differences in methods (e.g., counts at fish ladders vs. telemetry) make comparison among studies difficult, and studies carried out in regulated rivers may not be representative of conditions experienced by salmon in free-flowing rivers (Thorstad et al. 2008; Bendall et al. 2012). Additionally, adult salmon use olfactory cues generated by the chemical composition of natal river water and presence of conspecifics to navigate during in-river migration (Quinn et al. 1983; Bett and Hinch 2015); absence of such cues may affect salmon movements during reintroduction and colonization. Finally, characteristics that make pools suitable for holding by adult salmon during in-river migration are understudied, with references in the literature largely qualitative (Bardonnet and Bagliniere 2000). For example, carrying capacity for holding pools used by adult Atlantic Salmon has been related to proximity to spawning areas, depth, and presence of instream cover; however, characteristics that make a pool "suitable" for holding likely differ among river systems based on drainage size, hydrology, or temperature regimes (Hawkins and Smith 1986; Moreau and Moring 1993; Frechette et al. 2018).

The objective of our study was to examine migration patterns and habitat use by adult Atlantic Salmon *Salmo salar,* during the colonization of novel habitat in a free-flowing river in eastern Canada. The Atlantic Salmon is an iteroparous salmonid that historically ranged from southern New England (USA) to Ungava Bay (Canada) in North America and from Portugal to

Russia in Europe (Thorstad et al. 2011). Currently, many stocks are listed as endangered or extirpated (COSEWIC 2010; Thorstad et al. 2011). Atlantic Salmon exhibit premature migration, meaning they enter rivers many months before spawning (Power 1981; Jonsson et al. 1990; Fleming 1996; Quinn et al. 2015). In Eastern Canada, salmon enter rivers in an immature state between June and August. The maturation process occurs during the long in-river residence period, in preparation for spawning in October and November (Stabell 1984; Scott and Scott 1988). This extended in-river residence means that Atlantic Salmon colonizing novel habitat will be exposed to a wide range of environmental conditions that affect movement patterns and habitat use (Erkinaro et al. 1999; Økland et al. 2001; Karppinen et al. 2004; Quinn et al. 2015). Consequently, determining how biotic and abiotic factors affect movement patterns and habitat use during colonization is essential to the success of this and other reintroduction and assisted migration programs designed to enhance and protect Atlantic Salmon populations (Thorstad et al. 2008).

In this study, we linked Atlantic Salmon movement patterns and habitat use with intrinsic fish characteristics and extrinsic environmental conditions experienced during colonization of novel habitat. Our specific questions were two-fold. First, we asked: how do salmon movement patterns vary in response to environmental conditions (river temperature, river discharge, season, diel period) and fish characteristics (sex and size) during colonization? Second, we asked: what physical characteristics (e.g., surface area, depth) make a pool suitable for holding by adults during in-river residence and does the use of pools change as a function of environmental factors (e.g., river temperature and discharge). We addressed these questions using a combination of acoustic telemetry, remote sensing, ground surveys, and continuous records of river temperature and discharge. We applied generalized linear mixed modeling and machine learning to determine the key variables driving salmon movements in novel habitat and obtain a detailed picture of how adult Atlantic Salmon use habitat during colonization.

Methods

Study Area

The Rivière Sainte-Marguerite Nord-Est (hereafter, Nord-Est) is a designated salmon river in the province of Québec, Canada that drains a catchment of approximately 1000 km^2. It joins the Rivière Sainte-Marguerite 5 km upstream of its confluence with the Saguenay Fjord.

Prior to 1981, anadromous Atlantic Salmon had access to 7 km of river habitat before further upstream passage was blocked by an impassible waterfall (Chute Blanche). The installation of a fish ladder at Chute Blanche in 1981-1982 now allows returning adults to access an additional 18 km of river habitat (Figure 1). Further upstream passage is blocked by a pair of impassable waterfalls at river kilometer (rkm) 33.7 (Chute du 16 Miles) and rkm 36.2 (Chute du 18 Miles), where the 0-rkm point is set as the confluence with the Saguenay Fjord.

In 2014, a three-year program was initiated to capture a subset of the adult salmon returning to the Chute Blanche fish ladder for transport into the inaccessible habitat upstream of Chute du 18 Miles. The objective of this program was to increase the population productivity of the river by reducing density-dependent effects on juvenile growth and survival (Pess et al. 2011; Anderson et al. 2014). Transported adults would be able to access between 13 and 27.5 kilometers of river, depending on whether they could ascend the waterfalls Chute André and Chute du 30 Miles (Figure 1). The ultimate upstream end of the potential novel habitat is a large, impassible waterfall (Chute du 35 Miles).

Transport and tagging

Atlantic Salmon that entered the Chute Blanche fish ladder first arrived in a capture cage, which permitted an annual count and length estimates for all of returning adults. Of the returning adults, an annual target of 30 individuals were captured for transport into the novel habitat, either directly from the capture cage using a soft mesh net or via a retention cage installed in the fish ladder in 2015. The retention cage allowed salmon that entered the fish ladder in the evening (between 18:00 and 21:00) to be held overnight for transport the next morning. Salmon were held in the retention cage for no more than 12 hours and were transported within one hour of sunrise.

Salmon were transported by truck in a 1600-L tank supplied with recirculating water and an oxygen delivery system. Water temperature and dissolved oxygen in the tank were measured continuously during transport using an EcoSense DO200A probe (YSI Incorporated, Yellow Springs, Ohio). Oxygen delivery was adjusted if the oxygen saturation (% O_2) exceeded 150% or dropped below 80% and blocks of ice were added if tank temperature approached 20°C or if the temperature difference between the river and the tank was greater than 2°C upon departure from the fish ladder. No transports were conducted if water temperature exceeded 20°C and no more than four salmon were transported in a single trip.

We surgically implanted all transported salmon with an acoustic transmitter (Vemco V13–H, 13 mm diameter, 6 g in water) before release into the novel habitat. The average tag body burden of 0.24% (SD = 0.13%) was much less than the maximum recommended tag body burden of 2% (Winter 1983; Thorstad et al. 2000). We anesthetized individuals in a bath containing 30 mg of acetyleugenol/L of water. Dosage time increased with decreasing water temperature (mean = 267 sec; SD = 73 sec). Once a salmon was adequately anesthetized, (determined by gill respiration rate and strength of the reflex response), it was transferred to a V-shaped surgery table for tagging. We administered water and a maintenance dose of acetyleugenol (15 mg/L) over the gills during tagging via a custom-designed reservoir. The acoustic tag was inserted into the intraperitoneal cavity through an incision placed anterior to the pelvic girdle (lateral to the ventral midline). The incision was closed using three or four simple interrupted sutures and aseptic technique was followed throughout the tagging procedure.

We measured fish fork length (FL: distance from the snout to the end of the middle caudal fin rays) and mass while salmon were anesthetized. Salmon may return to the river after one winter at sea (termed one-sea-winter salmon, 1SW) or after multiple winters at sea (termed multi-sea-winter salmon, MSW salmon). The distinction between 1SW and MSW salmon is based on size: MSW salmon are those individuals with FL > 63 cm, whereas 1SW salmon have a FL < 63 cm (DFO Science 1998). We separated 1SW and MSW individuals when comparing fish size; however, we combined 1SW and MSW individuals and used FL as continuous explanatory variable in statistical analyses.

We visually determined sex in the field using morphological features (body depth, position of the maxillary relative to the eye, presence or absence of a kype or eggs in later-returning salmon). Sex identification was verified using measurements of maxillary length and published regressions relating fork length to maxillary length (Massie et al. 1988; Prevost et al. 1991). The established regression relationships did not apply to 1SW salmon; therefore, we assumed that all transported 1SW salmon were males because most had evidence of a prominent kype and males comprise nearly 95% of 1SW salmon in the province of Quebec (Dionne et al. 2015). We attempted to transport an equal number of males and females into the novel habitat to mimic sex ratios in Quebec salmon rivers and maximize effective population size (Foose et al. 1986; O'Reilly and Kozfkay 2014; Dionne et al. 2015).

Following tagging, salmon were transferred to a water-filled stretcher and moved to an in-river recovery cage. The recovery cage was equipped with a door that was opened once the fish was upright and swimming freely, allowing the fish to exit the cage volitionally. If salmon remained in the cage one hour after release, they were evaluated and either given more time for recovery or, more frequently, released by hand. All animal handling protocols were approved by the INRS Institutional Committee for the Protection of Animals (CIPA Protocol 1406-03).

Telemetry and Environmental Monitoring

We tracked movements of tagged salmon using an array of acoustic receivers (VR2W, Vemco, Halifax, NS) deployed in pools > 0.5 m depth (Figure 1). Range testing conducted during 2014 indicated that 95% of tag emissions were detected at a distance of 40 m, and 80% of tag emissions were detected at a distance of 200 m under calm conditions (Frechette et al. 2018). We observed a reduction in detection range when river discharge exceeded 60 m^3s^{-1} and during discrete rainfall events; however, redundancy produced by the combination of high frequency of signal transmission (every 30 to 90 sec) and long-term monitoring at fixed locations allowed us to successfully track salmon movements, even at the greatest river discharge recorded during the study (167 m^3s^{-1}).

The number of receivers in the array increased with each year of the study; however, a core network of eight receivers were deployed each year in the novel habitat, from which movement data were analysed. A receiver placed upstream of Chute du 30 Miles was used to determine whether salmon passed both Chute André and Chute du 30 Miles. We deployed a receiver upstream of Chute André to assess whether salmon passed this waterfall in 2015 only because access to this site was extremely challenging. Receivers were deployed before the first transport occurred each year and were recovered during the spawning season in October before snow and ice formation (October 23, 2014; October 20, 2015; and October 31, 2016). We extracted raw telemetry data from receivers using VUE software (Vemco, Halifax, NS) and processed it using the VTrack package for R (Campbell et al. 2012).

We obtained river temperature measurements from a temperature logger (HOBO UA-002-64, Onset, Bourne, MA) deployed by the RivTemp Network (Boyer et al. 2016) in a shallow, well-mixed area of the river downstream of Chute du 16 (T1, Figure 1). Logging station T1 provided the most complete temperature time series for the Nord-Est for the three study years. It was deemed to be an adequate representation of the thermal regime experienced by adults in the novel habitat, based on the fit of a linear regression between logger T1 and T2, a temperature logger deployed in the novel habitat (Adjusted $R^2 = 0.92$, $P < 0.01$). We obtained river discharge measurements from the Centre d'expertise hydrique du Québec (CEHQ) station 062803 (48.267962N, -69.908823W). River temperature and discharge were recorded at 15-min intervals throughout the study, from which we computed mean daily temperature (Tmean), mean daily discharge (Qmean), and the daily range in both temperature (Trange) and discharge (Qrange) for use in subsequent analyses.

Post-transport Movement Patterns

On a given day, salmon could either remain as a resident in a single telemetered pool, or they could move between pools (determined by detection on more than one receiver during a given day). We assessed the daily probability of movement relative to fish length, sex, Tmean, Trange, Qmean, Qrange, day of year, day length, season, and year using a binomial generalized linear mixed model (GLMM). Use of the mixed model structure allowed us to account for the fact that the response variable (move vs. no move) consisted of repeated measures on individual fish (Zuur et al. 2009). The variance associated with the random effect provided a measure of within-fish variability in the frequency of occurrence of movement types. We standardized continuous variables by subtracting the mean and dividing by the standard deviation. We fitted models using R version 3.4.2 (R Core Team 2017) using the glmer function (package: lme4; Bates et al. 2015). Given: 1) the large number of candidate models possible based on our use of 10 explanatory variables ($2^{10} = 1024$ possible models); and 2) that we did not know the relative importance of each explanatory variable, we used methods described by Venables and Ripley (2002) and Zhang (2016) to compare models sequentially. We used forward stepwise selection beginning with the null model. Variables were added sequentially, and compared against the model from the previous step using the Akaike Information Criterion (AIC, Akaike 1974). The model that received the lowest AIC score was retained and used as the basis for the candidate model in the next round of the selection. We considered that the selected model was better supported than the competing model when ΔAIC was ≥ 2 (Burnham & Anderson 2002). Given that data were recorded daily, we expected some degree of temporal autocorrelation, which is a problem common to studies of effects of environmental variables on fish migration (Trépanier et al. 1996). The glmer function does not allow for inclusion of autocorrelation structure in the model; therefore, we incorporated a first order autoregressive dependence structure to the model by using the function glmmPQL (package: MASS; Venables and Ripley 2002). We assessed model fit by computing the area under the receiver operating curve (Hosmer et al. 2013).

To examine patterns in fish movement, we characterized daily movements using four metrics (Roy et al. 2013): 1) number of movements per day (total number of times a fish moved between receivers each day); 2) number of sites visited per day (number of receivers where a fish was detected each day); 3) distance travelled per day (sum of the distance between successively visited receivers); and 4) daily extent (distance between the two most distant receivers). The number of movements and the number of sites provide measures of how frequently fish moved, (i.e., they indicate overall activity levels). The total distance travelled represents the minimum distance moved by an individual on a given day, as fish may have moved downstream or upstream of a given receiver, but returned before entering the detection range of another receiver. Extent provides a measure of the total river length explored by a given fish on a single day.

Initial plots of movement patterns by day of the year indicated a potentially strong seasonal component, where the number of movements, number of sites visited, distance traveled, and extent all increased dramatically in mid-September (Supplementary Table S.2 available in the online version of this article). We fitted a piecewise linear model to the relationship between day of year and each movement metric to identify the threshold day at which the slope changed, using the segmented package for R (Muggeo 2008; Muggeo 2017). This threshold (i.e., breakpoint) was used to divide each study year into two seasons, summer and autumn. The breakpoints occurred on Day 255 (number of movements), Day 248 (number of sites), Day 255 (distance), and Day 253 (extent). Among the four metrics, the mean breakpoint occurred on Day 253. Consequently, we assigned all days up to Day 253 (September 10) as “summer” and from Day 254 to the end of the study as “autumn”, which we used as an explanatory variable in our analyses of salmon movement patterns.

We identified movement types by applying principal component analysis (PCA) and k-means clustering to the four daily movement metrics. Movement metrics were centered and standardized (log + 1) before use in the PCA and cluster analysis. We obtained the most parsimonious number of groups (i.e., movement types) for use in the k-means clustering by comparing three methods. First, we used the NbClust package in R, which varies the number of clusters, clustering methods, and distance measures to determine the optimal number of clusters that is best supported by 30 different indices (Charrad et al. 2014). We then compared the number of clusters produced by NbClust with a plot of the within groups sum of squares (Everitt and Hothorn 2009). Finally, we examined the silhouette width for the range of the number of clusters deemed most likely from the previous two methods using the cluster package for R, where silhouette values ≥ 0.51 indicate a reasonable clustering structure (Maechler et al. 2018).

We used the results of the k-means clustering to assign a movement type to each individual on each day that it exhibited movement and computed the frequency of occurrence of each movement type. We again used binomial GLMM to model the daily frequency of occurrence of each movement type as a function of fish length, sex, Tmean, Trange, Qmean, Qrange, day of year, day length, season, and year. We again employed the sequential model selection described previously to compare models, with minimization of AIC used to retain or reject explanatory variables (Venables and Ripley 2002; Zhang 2016). We compared among-fish variability in the frequency of occurrence of movement types using descriptive statistics (mean and SD). The variance associated with the random effect provided measure of within-fish variability in the frequency of occurrence of movement types.

We tested the hypothesis that salmon would exhibit a crepuscular movement pattern by calculating the number of movements initiated at dawn, during daylight hours, at dusk, and at night for comparison to an expected distribution. We used the time that a fish left a given receiver as the initiation of movement. To account for the loss of daylight as the year progressed from summer to autumn, we obtained sunrise and sunset times from the 'suncalc' package (version 0.4) for R (Agafonkin and Thieurmel 2018) using the coordinates 48.467N, -69.939W. We defined dawn as the period spanning from two hours before sunrise to one hour after sunrise and dusk as the period spanning from one hour before sunset to two hours after sunset. This accounts for the amount of time that the sun is below the mountains bordering the river after sunrise and before sunset (approximately 1 h). Consequently, the number of dawn/dusk hours was constant throughout the study, whereas the number of hours during the day and night changed as a function of the day of the year. We summed the number of hours occurring in each time period within and across study years to obtain the total number and proportion of hours occurring within each period, which we used to calculate the expected frequency of movements initiated at dawn, during the day, at dusk, and during the night.

Habitat Use

We obtained measurements of physical characteristics of all pools containing acoustic receivers via remote sensing or ground surveys. We used GIS to extract measurements of maximum pool width, channel width (calculated as the mean of three bank-to-bank measures of river width immediately upstream of the pool), and surface area from aerial images (30 cm resolution) of the river obtained from the Ministère des Forêts, de la Faune et des Parcs du Québec. We also calculated the expansion factor for each pool, which was simply the ratio between maximum pool width and the channel width upstream of the pool. We obtained measurements of maximum pool depth on July 25, 2016 at a river discharge of 26 m^3s-^{1} using a single beam echo sounder (Hydroball, CIDCO, Rimouski, QC). The presence or absence of a cold thermal refuge was identified from thermal infrared (TIR) images obtained from a helicopter survey conducted August 25, 2014 (see Frechette et al. 2018 for methods) and from a bottom survey conducted August 24, 2017. The TIR images permitted us to identify cold seeps that extended to the river surface, whereas the ground survey allowed us to identify sub-surface seeps that did not extend to the river surface and would have been missed using TIR imagery alone. We conducted the ground survey by dragging the weighted probe of an EcoSense DO200A (YSI Incorporated, Yellow Springs, Ohio) along the bottom of each pool. Before surveying each pool, we measured the temperature at the surface and the bottom of the river at the inflow (when working upstream to downstream) or outflow of each pool (when working downstream to upstream). Identical temperature at the surface and bottom indicated that the river was well mixed, and was used as the reference river temperature. We traversed pools in a series of transects with the YSI probe suspended ≤ 10 cm above the substrate. Pool temperatures ≥ 0.5°C cooler than the reference river temperature were classified as a cool patch (Dugdale et al.

2013; Frechette et al. 2018). We identified the locations of spawning areas during surveys conducted via canoe and snorkel during the spawning period in 2015 and 2016 (Frechette 2019).

We used a random forest approach to identify the importance of physical characteristics of pools and environmental conditions in influencing pool use by adult salmon. The random forest approach is a machine learning extension to the accepted use of classification trees for analyzing ecological data. This method improves classification accuracy by generating and combining the predictions from a large number of classification trees (Breiman 2001; Cutler et al. 2007). The random forest approach avoids overfitting, and unlike many commonly applied parametric methods used in ecology, does not rely on assumptions regarding the underlying distribution of the data, so it can be used in cases (like ours) where relationships between dependent and independent variables are highly non-linear (Dahl 2001; Cutler et al. 2007). Additional advantages of the random forest approach for our application are 1) the ability to include categorical and continuous predictor variables, 2) insensitivity to different units, and 3) the potential to retain correlated predictor variables that are ecologically important (Breiman 2001; Cutler et al. 2007).

We implemented the random forest approach using the package ‘randomForest’ in R (Liaw and Weiner 2002). The number of variables randomly sampled as candidates at each split was optimized using the function train within the R package ‘caret’ (version 6.0-80), where the optimal number of variables minimized the RMSE (Kuhn 2008). Variables included in the analysis were mean daily river temperature and mean daily river discharge, three measures of pool size (maximum depth, surface area, and expansion factor), presence or absence of a cool thermal refuge, and mean distance to all documented spawning areas. We also included day of year to assess how pool use changed over time.

Results

Transport and tagging

We released 68 tagged salmon into the novel habitat during the three years of the study (30F, 38M). Conditions experienced by salmon during transport are described in detail by Frechette et al. (2019). Briefly, mean transit time between the fish ladder and the release site was 52.1 min (range: 40-75 min). All transport occurred when water temperature was less than 20.5˚C (mean = 17.4˚C; SD = 1.4˚C). The mean difference between the river temperature at the fish ladder and the temperature in the transport tank was 0.46˚C (SD = 0.38˚C). The mean difference between the tank temperature at departure from the fish ladder and arrival at the release site was 0.1˚C (SD = 0.2˚C).

Each year, a subset of salmon exhibited fallback, (i.e., they swam back downstream over the impassible falls), generally within 7 days of release (Frechette et al. 2019). Post-transport fallback rates were 42% during 2014 (5 of 12), 28% during 2015 (7 of 25), and 32% during 2016 (10 of 31). A detailed analysis of fish characteristics and environmental conditions contributing to fallback was published by Frechette et al. (2019). Given that the objective of the present study was to examine how colonizing salmon used habitat, we excluded individuals that exhibited post-transport fallback, as well as salmon that either died or lost their transmitter following release from analysis of movement patterns and habitat use. Death or tag loss was assigned if a tag failed to move from a location for the duration of the study year. It was not possible to distinguish between a lost tag and the death of an individual. Four salmon either lost tags or died (Table S.1). Our analyses of movement patterns and habitat use were thus restricted to 42 salmon (15F, 27M) that remained alive and with functioning tags in the novel habitat from release until the onset of the spawning season in October (Table S.1).

There was no significant difference in fork length between MSW females ($\bar{x}$ = 77.4 cm; N = 15, SE = 1.6) and MSW males ($\bar{x}$ = 77.2 cm; N = 12; SE = 1.8; OLS regression, t = -0.093; P = 0.927). There was no significant difference in mass between MSW females ($\bar{x}$ = 4.2 kg; N = 14, SE = 0.3) and males ($\bar{x}$ = 3.9 kg; N = 9; SE = 0.3; OLS regression, t = -0.530; P = 0.602). By definition, 1SW males were substantially smaller in fork length and mass than MSW males and females (Figure 2).

Telemetry and Environmental Monitoring

Of the 42 salmon that remained upstream alive and with functioning transmitters after transport, 32 individuals were detected for the first time by the receiver in the pool immediately downstream (<50 m) of the release site (pool U3), while the remaining 10 individuals were first detected by the receiver 697 m upstream of the release site (pool U4). The initial direction of movement, defined as the direction of travel between the first receiver of detection (pool U3 or U4) to the second receiver of detection, was predominantly upstream: 69% of individuals (29 of 42) initially moved 0.7 to 2.5 km upstream, whereas 31% of individuals (13 of 42) made an initial downstream movement of 1.2 km to pool U2 (Figure 3). Of the 22 individuals that exhibited fallback (thus were excluded from subsequent analyses of habitat use and movements), only three initially moved in an upstream direction, while the remainder moved downstream either 1.5 km from pool U3 to U2 (18 individuals) or 2.6 km from pool U3 to U1 (1 individual). No salmon were detected upstream of Chute du 30 Miles during any of the three study years and no salmon were detected by the receiver deployed upstream of Chute André during 2015, the only year that a receiver was deployed between Chute André and Chute du 30 Miles.

In general, post-transport migration by large, MSW-salmon could be divided into three "phases". The first phase was characterized by directed, step-wise movements in the upstream direction, which was occasionally preceded by several upstream and downstream movements after release. The second phase consisted of holding in one pool for an extended period of time, often punctuated by movements into pools immediately upstream or downstream of the holding pool. The third phase was characterized by extensive upstream and downstream movements that began in mid- to late-September (Figure 3). This "search" behaviour was centered on what were subsequently identified as spawning sites (Frechette 2019). Smaller, 1SW-salmon generally exhibited more extensive upstream and downstream movements. However, some 1SW salmon also exhibited the clear, three-phase migration described for MSW salmon and some MSW salmon had movement patterns that more closely resembled the extensive movements observed in 1SW-salmon (Figure 3).

The years 2014 and 2016 were characterized by relatively dry summers, with low base-flow punctuated by increases in discharge following rain events (Figure 4). Discharge was consistently greater during 2015; however, the maximum mean daily discharge was greater in 2014 and 2016 than 2015 (Table S.2), due to high flow events that occurred during autumn (Figure 4). River temperature exceeded 20°C during August in all years, which is within the range considered stressful for adult Atlantic Salmon (Breau 2013, Frechette et al. 2018). The greatest number of days with mean daily temperature ≥ 20°C occurred during 2014 (7.4% of days, or 7 of 94). Mean daily temperature exceeded 20°C on 4.4% of days during 2015 (5 of 113) and 4.8% of days during 2016 (6 of 125).

Post-transport Movement Patterns

In assessing the probability of moving versus residing in a pool on a given day, the selected model included the covariates season, Qmean, Tmean, and interactions between sex and Tmean and between sex and Qmean as explanatory variables (Table 1). Using the methods of Royston and Altman (1994), we determined that a linear function was appropriate to define the relationship between the response variable and both temperature and discharge. The area under the receiver operating curve (ROC) was 0.86, indicative of "excellent" model discrimination according to the criteria of Hosmer et al. (2013). Correlation between observations made one day apart was 0.73; however, temporal autocorrelation was considered to break down quickly enough so as to not be problematic.

The significant, negative slope for the effect of season indicates that salmon were less likely to move on or before September 10 (Figure 5). The significant sex by Qmean interaction indicates that females were more likely to move at high discharge (slope = 0.79) but males were not (slope = 0.02). The non-significant slope for Tmean indicates that temperature did not affect the probability of moving for females; however, the significant sex by Tmean interaction indicates that males were less likely to move at high temperature (slope=0.8). The variance attributable to the random effect of individual was low (1.94).

All movement variables (number of movements, number of sites, total distance, and extent) were negatively correlated with the first principal axis (PCA1), representing a movement pattern characterized by a greater number of movements between many sites. The number of movements was strongly negatively correlated with the second principal axis (PCA2) and extent was strongly positively correlated with PCA2, representing a movement pattern consisting of fewer movements but greater extent. In total, the first two principal axes accounted for 93% of the variability in the data (Table 2).

There was consensus among the three methods applied to determine the number of clusters included in the k-means analysis (within-groups sum of squares, the NbClust function in

R, and silhouette analysis). Examination of a plot of the within-group sum of squares by number of clusters indicated that either two or three clusters minimized the within-group sum of squares (Everitt 2005; Everitt & Hothorn 2010). Using the NbClust function in R, the greatest number of indices (10 of 30) proposed two clusters as the best solution, whereas only two indices proposed three clusters as the best solution. A comparison of silhouette values provided further support for the two-cluster solution (mean silhouette width = 0.53) relative to the three-cluster solution (mean silhouette width = 0.45).

The first cluster defined a movement type characterized by relatively low mobility, hereafter referred to as sedentary (*sensu* Roy et al. 2013). Sedentary behavior was characterized by a lesser number of movements and sites visited, and shorter distance and extent travelled (Table 3). The second cluster defines a high-mobility movement type, hereafter referred to as "exploratory", characterized by a greater number of movements, sites visited, distance travelled and extent (Table 3). Rate of movement was significantly greater during exploratory ($\bar{x}$ = 0.29 m/s) than during sedentary movements ($\bar{x}$ = 0.16 m/s; OLS Regression, t = 16.232; $P < 2e^{-16}$). During sedentary movements, males had a significantly greater rate of movement (0.18 m/s) than females (0.12 m/s; OSL Regression, t = 5.578; $P = 3.4e^{-8}$). Males also had a greater rate of movement during exploratory movements (0.30 m/s) than females (0.25 m/s; OLS Regression, t = 4.202; $P = 3.09e^{-5}$).

The frequency of occurrence (FOC) for the sedentary movement type (expressed as a percentage of the total number of days) was 60% (both sexes combined) and the variation among individuals was reasonably high (SD = 18%). This frequency was 68% for females and 56% for males, and females had less among-individual variation in the FOC of each movement type (SD = 14%) than males (SD = 19%).

The covariates retained in the selected model were Tmean, Qmean, and the interactions between sex and Tmean and sex and Qmean (Table 4). Using the methods of Royston and Altman (1994), we determined that a linear function was appropriate to define the relationship between the response variable and both temperature and discharge. The area under the ROC was 0.72, indicative of acceptable discrimination (Hosmer et al. 2013) Correlation between observations made one-day apart was very low (0.26), thus temporal autocorrelation was not considered to be problematic. Neither temperature nor discharge influenced the probability that a female was sedentary. The significant sex by discharge and sex by temperature interactions indicate that males were more likely to be sedentary at high temperature and high discharge. The variance attributed to the random effect of individual was very low (0.39).

Salmon exhibited a predominantly crepuscular movement pattern. The number of movements initiated during dawn and dusk was greater than expected and the number of movements initiated during daylight hours was less than expected for both males ($X^2 = 479$, df = 3, $P = 0.01$) and females ($X^2 = 536$, df = 3, $P = 0.01$). Males initiated more movements at night than expected, whereas females initiated slightly fewer movements at night than expected.

Habitat Use

Pools in the novel habitat ranged substantially in size and forms (Table S3). They consisted as either channel constriction pools (pools U1 & U3), tributary confluence scour pool (U7); meander bends lateral scour pools (U4, U5, U6 & U8), or bedrock trench pools (U2). The smallest pool (U8) had a surface area of 1176 m^2 and maximum depth of 2.9 m at median flow (26 m^3s-^{1}). The smallest pool (U8) had a surface area of 1176 m^2 and maximum depth of 2.9 m. The shallowest pool (U1) had a maximum depth of 1.25 m, but was the third largest in terms of surface area (8714.03 m^2). Expansion factor ranged from 0.54 (pool U1) to 3.48 (pool U7). Pool U7 was the most frequently used pool, with 867 residences that were ≥ 1 h in duration (representing 55% of the total hours that fish were resident in pools; Table S.3), whereas pool U1 was least frequently used (only 7 residences ≥ 1 h in duration). The total number of hours that all fish were present in pools (residences ≥ 1 h in duration) ranged from 27.7 (U1) to 15201.5 (U7). Sub-surface cold seeps were identified in three pools during the August 2017 ground survey (pools U3, U6, and U7). Surface-intersecting cold water patches were previously identified by Frechette et al. (2018) in these three pools by thermal infrared imagery, in which pool U6 (this study) was referred to as pool U7 and pool U7 (this study) was referred to as U8 by Frechette et al. (2018).

With the optimal number of variables randomly sampled as candidates at each split set to 5, (the value which minimized RMSE), the random forest regression (500 trees) explained 53.3% of the variance in the frequency of pool use. Mean daily discharge was associated with the greatest increase in percent mean squared error (%MSE), indicating that this variable had the greatest importance in predicting pool use, followed by day of year and mean daily temperature

(Table 5). Examination of partial dependence plots indicate that pool use was greatest at river discharge less than 10 m^3s^{-1} and stabilized at discharges greater than 20 m^3s^{-1} (Figure 7). Pool use increased steadily until mid-September and decreased as the spawning season approached. Pools were used less frequently when river temperature was less than 11°C and most frequently at the highest river temperatures (≥ 20°C).

For the periods when tagged salmon were available in the novel habitat, discharge ≥ 20 m^3s^{-1} was recorded primarily during the autumn spawning period and following isolated summer rainfall events, except in 2015, when discharge was ≥ 20 m^3s^{-1} throughout much of the summer (Figure 4). During 2015, mean daily discharge was ≤ 20 m^3s^{-1} on 43% of days when fish were available for tracking (48 of 113), whereas mean discharge was ≤ 20 m^3s^{-1} on 62% of days during 2014 (58 of 94 days) and 2016 (78 of 125 days). High temperature events (≥ 20°C) were restricted to August (Figure 4), and corresponded to periods when salmon were not moving (Figure 5) or were engaged in sedentary behavior (Figure 6). River temperature did not drop below 11°C until after September 10 during all years.

Surface area was the physical pool characteristic associated with the greatest increase in %MSE (Table 5), followed by maximum depth. Specifically, pools with surface areas < 15000 m^2 or maximum depth < 4 m were used less than pools exceeding these size thresholds (Figure 7). Expansion factor (EF) was associated with a relatively low increase in %MSE and the partial dependence plot demonstrated a step-wise form: pools with EF <1 were rarely used and pools with EF > 2.5 were most frequently used, whereas pools with intermediate EF values (1.5 - 2.5) had moderate use. The presence of a cold refuge was associated with an increase in %MSE of only 6.28; however, pools with cold refuges were more frequently used than pools without cold refuges. The least important variable was the proximity to spawning sites. Pools that were < 3 km from spawning sites were used more than pools that were further away; however, there was an increase in use of pools that were ≥ 5 km away from pools, relative to those that were at intermediate distances to spawning sites.

Discussion

Use of acoustic telemetry combined with both direct and remote sensing measurements of habitat characteristics allowed us to obtain a holistic view of how adult Atlantic Salmon use the riverscape during the colonization of novel habitat in a pristine, free-flowing river. Salmon movements and use of holding pools were influenced by temperature, discharge, fish sex, timing within the pre-spawn period, and pool size. Of particular note was the interaction between river temperature and discharge on modifying salmon movements. Integrating multiple daily movement metrics (number, sites visited, distance, and extent) into discrete movement patterns allowed us to maximize the information used to examine effects of river conditions and fish characteristics on salmon movements. Broader use of the type of discrete movement patterns based on multi-dimensional measures such as we developed here may improve among-river comparisons of how salmon respond to environmental conditions relative to comparisons based solely on movement rates or plots of migratory tracks.

Previous telemetry studies have produced conflicting results regarding the relationship between environmental conditions (e.g., temperature or discharge) and upstream migration by salmon. Most studies used either migration speed or movement rate as the response variable describing salmon movement. Migration speed has been observed to increase, stop, or show no response to increasing discharge (Hawkins and Smith 1986; Hawkins 1989; Erkinaro et al. 1999; Karppinen et al. 2004). Movement rates have been shown to both increase and decrease with increasing temperature, or be greatest at intermediate temperatures (Alabaster 1990; Erkinaro et al. 1999; Karppinen et al. 2004; Hasler et al. 2012; Strange 2012). Recently, Martin et al. (2015) used a novel application of exercise physiology to demonstrate that differences among studies in the response of salmon movement rates to temperature and discharge was context-specific and resulted from the way each variable modified the effect of the other. That is, migration speed was driven by temperature at low water velocities, but discharge became more important at high water velocities (Martin et al. 2015).

In general, male salmon moved more and engaged in more exploratory behavior than females. However, males moved less (i.e., the probability of movement was lower and the probability of being sedentary was greater) as river temperature increased. Increased pool use by males at elevated temperatures was further reflected in the random forest analysis of habitat use: pool use was greatest when river temperature exceeded 20°C, temperatures considered stressful for Atlantic Salmon (Shepard 1995; Breau 2013; Frechette et al. 2018). Although temperatures rarely exceeded 20˚C, temperatures as low as 17˚C induced behavioral thermoregulation by Atlantic Salmon in this river (Frechette et al. 2018). Because metabolism increases with river temperature in salmon, exposure to stressful temperature can reduce energy reserves available for spawning and can even result in death if salmon are unable to access holding areas with a source of cool water (Elliott and Elliott 2010; Hasler et al. 2012; Martin et al. 2015). The energy expenditure by male and female Atlantic Salmon during migration and spawning are similar (c. 59% of total energy reserves); however, males are less likely than females to survive spawning, possibly because of intense male-male competition (Fleming 1998). It should be evolutionally beneficial for males to maximize their within-season (as opposed to among-season) reproductive success by spawning with multiple females (Hawkins and Smith 1986; Fleming 1996). Consequently, holding in pools during stressful summer heat events combined with the greater incidence of exploratory behavior should allow males to maximize survival, energy stores available for spawning activities, mating opportunities, and ultimately, reproductive success.

Females exhibited more sedentary than exploratory movements, regardless of river temperature and discharge. Their probability of movement, however, increased within increasing discharge, which was further reflected in the random forest analysis: pool use was greatest at low discharge (c. 10 m^3s^{-1}). Low discharge can limit the ability of salmon (especially large individuals) to access holding and spawning areas (Mitchell and Cunjak 2007). The greatest discharge events occurred during the spawning season, thus the increased probability of movement exhibited by females likely indicates movement to and from redd sites during the spawning season. Baglinière et al. (1990) also observed that an increase in discharge triggered movement of female salmon to spawning grounds in the Selune River system (France). Female Atlantic Salmon produce a finite number of eggs each year and have a greater probability of repeat-spawning than males (Fleming 1996, 1998). High movement rates can reduce energy stores needed for egg development, redd digging, and egg laying or by increasing post-spawning mortality that prevents females from spawning during subsequent years (Thorstad et al. 2008). It may be evolutionarily more advantageous for females to move less during the pre-spawning period (even at lower temperatures) to conserve energy. This would increase both within-season reproductive effort and the chance of repeat spawning, thereby increasing life-time reproductive success (Hawkins and Smith 1986, Fleming 1996, 1998).

Interestingly, although plots of post-transport migration revealed that many 1SW males made numerous upstream and downstream movements, fish size was not retained in either the model for the probability of movement or the model of movement type. Smaller (1SW) males are less capable of defending mates and so may move more extensively among different spawning grounds to find mates and increase spawning success (Fleming 1996). In the Selune River (France), 1SW males moved more than larger MSW males and female size was inversely correlated with daily distance travelled (Baglinière et al. 1990, 1991). Our sample size was relatively small and 1SW salmon comprised only one-third of the tagged individuals (N = 15), which may have reduced our ability to resolve any size-based differences in movement patterns.

Previous studies indicate that Atlantic salmon migrate predominantly from dusk until dawn, although passage of obstacles may be concentrated during the day (Hawkins and Smith 1986; Jonsson 1991; Thorstad et al. 2008). Movement between dusk and dawn is considered an evolutionarily adaptive mechanism to avoid visual predators that are active predominantly during the day (Hansen and Jonsson 1986; Thorstad et al. 2008). Daytime passage of obstacles may represent a tradeoff between the need for light to visually navigate obstacles and use of dark for predator avoidance (Thorstad et al. 2008). The colonization habitat is free of obstacles to migration, so we expected that individuals would be least active during daylight hours. The salmon translocated into novel habitat did not deviate from this expectation. Use of low light conditions to avoid visual predators may be so well conserved a trait that salmon exhibit crepuscular and nocturnal behavior even in systems like the Nord-Est where species large enough to prey on adult salmon are rare. Given that water temperature was generally coolest during the night and early morning (Frechette et al. 2018), movement between dawn and dusk could alternatively be explained by use of cooler water temperatures to reduce the energetic costs of swimming.

Of the physical features measured, pool size was the most important habitat feature defining a suitable holding pool, with larger and deeper pools being used more often.
The only pool that was consistently used for long-term holding during the three years of this study (U7) was the largest pool in the novel habitat in terms of surface area and depth (Supplementary Figure S.1 available in the online version of this article). This pool also contained a consistent cold seep and was thermally stratified during summer months (Frechette et al. 2018). Depth and temperature and have previously been identified as influencing carrying

capacity of holding pools (Moreau and Moring 1993). Larger pools have greater carrying capacity for serving as hydraulic and thermal refuges during the summer in-river residence (Gendron 2013; Frechette et al. 2018). In addition to over-summer refuge habitat, salmon also require pools to rest between spawning attempts (Bardonnet and Bagliniere 2000). Our results suggest that as discharge increased and temperature decreased, pools that were not suitable for holding during the warm, dry summer months became suitable for resting during the spawning season, allowing salmon to use pools closer to spawning sites.

It should be noted that we did not observe adult salmon holding in other types of habitat (runs, glides, or tributary confluence plumes) via active telemetry surveys that were periodically conducted. Habitat features that have been identified as suitable holding habitat in other types of river systems (e.g., large woody debris, instream cover, boulders in runs or glides) are not present in the Nord-Est (Hawkins and Smith 1986; Bardonnet and Bagliniere 2000; D. Frechette *personal observation*). Large wood gets blown out during ice breakup in the spring and large boulders are only present in pools or rapids. Tributary confluence plumes in the Nord-Est are considered too shallow (< 0.5 m) for long-term holding by large adult salmon (Moreau and Moring 1993; Frechette et al. 2018). We suggest, therefore, that suitable holding pools are scarce in the Nord-Est, a condition that is likely common to shallow, gravel-bed rivers in Quebec and may play a role in influencing in-river pre-spawning migration by Atlantic Salmon (Richard et al. 2014).

During colonization in the Nord-Est, the majority of MSW salmon and some 1SW salmon exhibited a three-phase migratory pattern consisting of directed, stepwise upstream migration (migratory phase), followed by a holding period, then a “search” phase with movements centered on spawning areas. This pattern differs from that observed in the freely-flowing Tana and Lærdalselva rivers of Norway, where the migratory phase was followed by the search phase, (in which salmon made erratic movements around future spawning areas), then the “holding” phase lasted until the onset of spawning (Økland et al. 2001; Finstad et al. 2005). The pattern described in the Tana and Lærdalselva rivers has come to be considered the “normal” migration pattern for Atlantic Salmon in unregulated rivers; deviations from this pattern have been classified as aberrant behavior associated with stress from handling fish during catch and release (C&R) or tagging (Thorstad et al. 2003; Havn et al. 2015). It could be argued that the migratory pattern observed in the Nord-Est could be attributed to transport and handling effects. However, in the Escoumins River of Quebec, (located c. 50 km northeast of the Nord-Est), salmon that experienced C&R (i.e, subjected to more handling) and control fish that did not experience C&R (i.e., subjected to less handling) exhibited the same migratory pattern that we observed in the Nord-Est (Richard et al. 2014).

Richard et al. (2014) hypothesized that suitable holding pools may be scarce in small rivers like the Escoumins relative to larger rivers like the Tana, causing fish to seek out over-summering habitat before searching for spawning areas. The Lærdalselva River is smaller than the Escoumins River, so availability of holding pools alone may not explain the difference in migration patterns. The Tana and Lærdalselva are subarctic rivers where temperatures do not become stressful to adult Atlantic Salmon, (i.e., temperature remains < 20˚C). Water temperature in the Tana River was 9-13˚C during in-river migration (Økland et al. 2001), whereas temperatures ranged from 14-23˚C in the Escoumins (Richard et al. 2014) and Nord-Est (this study). A wider range of pools may be suitable for over-summer holding in the cooler rivers like the Tana and Lærdalselva, which would allow salmon to search for holding pools near spawning sites before entering the holding phase of the migration. Further, the migratory pattern observed in the Nord-Est and Escoumins rivers has also been observed in rivers of the United Kingdom, France, and New Brunswick, Canada (Hawkins and Smith 1986; Bardonnet and Bagliniere 2000; Mitchell and Cunjak 2007). These rivers span a range of catchment size and discharge regimes; however, they are all warmer than the Tana and Lærdalselva rivers. We suggest, therefore, that the pattern of directed migration-holding-search should be considered representative of Atlantic Salmon migratory patterns in warmer, temperate rivers where locating suitable holding pools to conserve energy during summer high temperature/low discharge events is more important than searching for spawning areas to maximize reproductive success.

These results support the ‘best of a bad situation’ hypothesis proposed by Quinn et al. (2015) for explaining premature migration in salmonids. Salmon fast while in freshwater; therefore, there must be an adaptive advantage to premature migration that outweighs additional foraging opportunities that would have occurred if salmon remained in the ocean until closer to the onset of spawning (Fleming 1996; Thorstad et al. 2008; Quinn et al. 2015). Under the ‘best of a bad situation’ hypothesis, premature migration results from the tradeoff between greater marine growth (and increased fecundity) and the need to reach suitable spawning habitat at the correct time to maximize offspring survival and reproductive fitness (Quinn et al. 2015). In rivers like the Nord-Est, where summer high temperature and low discharge events co-occur, premature migration would allow salmon to reach suitable holding areas before the onset of high temperature and low discharge conditions prevent upstream passage and increase mortality. As climate change causes river temperatures to rise in northern latitude rivers within the range of Atlantic Salmon, ensuring that salmon have access to suitable holding pools and thermal refuges during their long in-river summer residence is likely to become even more important for population persistence (Ferrari et al. 2007; Webb and Nobilis 2007; van Vliet et al. 2013).

By furthering our understanding how Atlantic Salmon colonize novel habitat, the results of this study will be a direct asset for optimizing future reintroduction and assisted migration programs to ensure that programs meet desired outcomes with respect to salmon productivity or recovery criteria. Because the direction of initial movements post-transport was linked with fallback (Frechette et al. of 2019), releasing salmon nearer the upstream extent of the target habitat may have reduced fallback. However, since at total of 31 of the transported individuals (18 of which ultimately fallback) made an initial movement of 1.5 km downstream, we recommend ensuring that the release locations be at least 2 km upstream of barriers denoting the downstream end of habitat targeted for colonization. Our findings also provide support for the importance of pools where salmon can rest during upstream migration (Økland et al. 2001; Finstad et al. 2005; Richard et al. 2014). Surface area and depth were the most important characteristics influencing pool use; therefore, drainages or river reaches selected for colonization or reintroduction programs should that contain an adequate number of large pools to support the number of Atlantic Salmon adults to be introduced. In temperate rivers where summertime temperatures exceed the tolerance range, release of adults should occur in systems or river reaches containing thermal refuge habitat within adequately-sized pools. If thermal refuge habitat is lacking, release of adults should occur later in the season, when the risk of exposure to high heat events is reduced. Because the ability for salmon to ascend challenging obstacles is limited at low temperatures (Gerlier and Roche 1998), release should also occur before temperatures drop too low to allow salmon to reach spawning areas. Timing of release must also take local discharge regimes into consideration, as release when river discharge is too low could prevent salmon from accessing thermal refuges or spawning habitat. Finally, use of the riverscape was consistent with previous studies of upstream migration by Atlantic Salmon in temperate rivers, despite the fact that salmon were captured, transported via truck, surgically tagged, and released into novel habitat where they had no prior experience. Our findings, therefore, may be more broadly applicable to understanding the ecology the species as a whole.

Acknowledgements

Funding for this work was provided by the Programme de mise en valeur des habitats du saumon de la Côte-Nord of the Fédération Québécoise du Saumon Atlantique, and the Atlantic Salmon Conservation Foundation. Financial support for D. Frechette was provided by the Fonds de recherche du Québec - Nature et technologies (FRQNT) Merit Scholarship Program for Foreign Students. We would like to thank the Ministère de la Faune, des Forêt, et des Parcs du Québec, the Association de la Rivière Sainte-Marguerite, and the Corporation de Pêche Ste-Marguerite for their vital collaboration and support of this research. We thank Gaétan Daigle (Université Laval) for invaluable statistical advice and editing for the movement analyses, and Jon Lefcheck for statistical advice for the random forest analysis. S. Dugdale provided graphical support and R. Saunders provided feedback on an earlier draft. Finally, this research program could not have been accomplished without an army of individuals who helped get this program up and running, deployed and recovered acoustic receivers, and safely transported and tagged salmon. In particular, we wish to thank the following people for their invaluable field and logistical support: A. Boivin, V. Maltais, F. Caron, M. Valentine, V. Cauchon, S. Gravel, M. Murdock, R. Gagnon, J.B. Toteroto, J. Isabelle, J. Carrier, M. St-Amour, I. Bergeron, and T. Suskiewicz.

Literature Cited

Agafonkin, V., and Thieurmel, B. (2018). suncalc: Compute Sun Position, Sunlight Phases, Moon Position and Lunar Phase. R package version 0.4. CRAN.R-project.org/package=suncalc

Akaike, H. 1974. A new look at the statistical model identification. IEEE Transactions on Automatic Control 19:716–723.

Alabaster, J. S. 1990. The temperature requirements of adult Atlantic Salmon, *Salmo salar* L., during their upstream migration in the River Dee. Journal of Fish Biology 37:659–661.

Anderson, J. H., G. R. Pess, R. W. Carmichael, M. J. Ford, T. D. Cooney, C. M. Baldwin, and M. M. McClure. 2014. Planning Pacific salmon and steelhead reintroductions aimed at long-term viability and recovery. North American Journal of Fisheries Management 34:72–93.

Askling, O. 2015. A telemetry study for reintroducing wild Atlantic Salmon (*Salmo salar* L.) in the Daugava and Ogre Rivers, Latvia. M.S. Karlstad University, Karlstad, Sweden.

Baglinière, J. L., G. Maisse, and A. Nihouarn. 1990. Migratory and reproductive behaviour of female adult Atlantic Salmon, *Salmo salar* L., in a spawning stream. Journal of Fish Biology 36:511–520.

Baglinière, J. L., G. Maisse, and A. Nihouarn. 1991. Radio-tracking of male adult Atlantic salmon, *Salmo salar* L., during the last phase of spawning migration in a spawning stream (Brittany, France). Aquatic Living Resources 4:161–167.

Bardonnet, A., and J. L. Baglinière. 2000. Freshwater habitat of Atlantic Salmon (Salmo salar). Canadian Journal of Fisheries and Aquatic Sciences 57:497–506.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software 67:1–48.

Bendall, B., A. Moore, D. Maxwell, P. Davison, N. Edmonds, D. Archer, D. Solomon, V. Greest, R. Wyatt, and K. Broad. 2012. Modelling the migratory behaviour of salmonids in relation to environmental and physiological parameters using telemetry data. Fisheries Management and Ecology 19:475–483.

Bett, N. N., and S. G. Hinch. 2015. Attraction of migrating adult sockeye salmon to conspecifics in the absence of natal chemical cues. Behavioral Ecology 26:1180–1187.

Boyer, C., St-Hilaire, A., Bergeron, N. E., Daigle, A., Curry, R. A., and D. Caissie. 2016. RivTemp: A water temperature network for Atlantic Salmon rivers in eastern Canada. Water News 35: 10–15.

Breau, C. 2013. Knowledge of fish physiology used to set water temperature thresholds for in-season closures of Atlantic Salmon (Salmo salar) recreational fisheries. DFO Can. Sci. Advis. Sec. Res. Doc. 2012/163. iii + 24 p.

Breiman, L. 2001. Random Forests. Machine Learning, 45:5–32.

Bryant, M. D., B. J. Frenette, and S. J. McCurdy. 1999. Colonization of a watershed by anadromous salmonids following the installation of a fish ladder in Margaret Creek, Southeast Alaska. North American Journal of Fisheries Management 19:1129-1136.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodal inference: A practical information-theoretic approach. Second Edition. Springer-Verlag, New York, NY.

Campbell, H. A., Watts, M.E., Dwyer, R.G., Franklin, C.E. 2012. V-Track: software for analysing and visualising animal movement from acoustic telemetry detections. Marine and Freshwater Research 63:815–820.

Charrad, M., N. Ghazzali, V. Boiteau, and A. Niknafs. 2014. NbClust: An R Package for Determining the Relevant Number of Clusters in a Data Set. Journal of Statistical Software 61:1–36.

COSEWIC. 2010. COSEWIC assessment and status report on the Atlantic Salmon Salmo salar (Nunavik population, Labrador population, Northeast Newfoundland population, South Newfoundland population, Southwest Newfoundland population, Northwest Newfoundland population, Quebec Eastern North Shore population, Quebec Western North Shore population, Anticosti Island population, Inner St. Lawrence population, Lake Ontario population, Gaspé-Southern Gulf of St. Lawrence population, Eastern Cape Breton population, Nova Scotia Southern Upland population, Inner Bay of Fundy population, Outer Bay of Fundy population) in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. xlvii + 136 pp.

Cutler, D. R., T. C. Edwards Jr., Thomas, K. H. Beard, A. Cutler, K. T. Hess, J. Gibson, and J. J. Lawler. 2007. Random Forests for Classification in Ecology. Ecology 88: 2783–2792.

Dahl, J., J. Dannewitz, L. Karlsson, E. Petersson, A. Löf, and B. Ragnarsson. 2004. The timing of spawning migration: implications of environmental variation, life history, and sex. Canadian Journal of Zoology 82:1864–1870.

DFO Science. 1998. Atlantic Salmon Eastern Canada Overview 1998. Stock Status Report D0-01. Department of Fisheries and Oceans. Ottawa, Ontario.

Dugdale, S. J., N. E. Bergeron, and A. St-Hilaire. 2013. Temporal variability of thermal refuges and water temperature patterns in an Atlantic Salmon river. Remote Sensing of Environment 136:358–373. doi:10.1016/j.rse.2013.05.018.

Dunham, J., K. Gallo, D. Shively, C. Allen, and B. Goehring. 2011. Assessing the feasibility of native fish reintroductions: a framework applied to threatened Bull trout. North American Journal of Fisheries Management 31:106–115.

Elliott, J. M., and J.A. Elliott. 2010. Temperature requirements of Atlantic Salmon *Salmo salar*, brown trout *Salmo trutta* and Arctic charr *Salvelinus alpinus*: predicting the effects of climate change. Journal of Fish Biology 77:1793–1817.

Erkinaro, J., F. Okland, K. Moen, E. Niemelä, and M. Rahiala. 1999. Return migration of Atlantic Salmon in the River Tana: the role of environmental factors. Journal of Fish Biology 55:506–516.

Everitt, B. S. 2005. An R and S-PLUS® Companion to Multivariate Analysis. Springer Texts in Statistics. Springer-Verlag, London, UK.

Everitt, B. S., and T. Hothorn. 2009. A Handbook of Statistical Analyses Using R, Second Edition. Chapman & Hall/CRC, Boca Raton, FL.

Finstad, A. G., F. Økland, E. B. Thorstad, and T. C. Heggberget. 2005. Comparing upriver spawning migration of Atlantic Salmon Salmo salar and sea trout Salmo trutta. Journal of Fish Biology 67:919–930.

Fisch, K. M., C. C. Kozfkay, J. A. Ivy, O. A. Ryder, and R. S. Waples. 2015. Fish hatchery genetic management techniques: integrating theory with implementation. North American Journal of Aquaculture 77:343–357.

Fleming, I. A. 1996. Reproductive strategies of Atlantic Salmon: ecology and evolution. Reviews in Fish Biology and Fisheries 6:379-416.

Fleming, I. A. 1998. Pattern and variability in the breeding system of Atlantic Salmon (*Salmo salar*), with comparisons to other salmonids. Canadian Journal of Fisheries and Aquatic Sciences 55:59–76.

Frechette, D. M., S. J. Dugdale, J. J. Dodson, and N. E. Bergeron. 2018. Understanding summertime thermal refuge use by adult Atlantic Salmon using remote sensing, river temperature monitoring, and acoustic telemetry. Canadian Journal of Fisheries and Aquatic Sciences 75:1999–2010.

Frechette, D. M., E. Goerig, and N. E. Bergeron. 2019. Factors influencing fallback by adult Atlantic salmon following transport into a novel river reach. Fisheries Ecology and Management.

Gerlier, M., and P. Roche. 1998. A radio telemetry study of the migration of Atlantic Salmon (*Salmo salar* L.) and sea trout (*Salmo trutta trutta* L.) in the upper Rhine. Hydrobiologia 371/372:283–293.

Gustafson, R. G., R. S. Waples, J. M. Myers, L. A. Weitkamp, G. J. Bryant, O. W. Johnson, and J. J. Hard. 2007. Pacific salmon extinctions: quantifying lost and remaining diversity. Conservation Biology 21:1009–1020.

Hasler, C. T., B. Mossop, D. A. Patterson, S. G. Hinch, and S. J. Cooke. 2012. Swimming activity of migrating Chinook salmon in a regulated river. Aquatic Biology 17:47–56.

Hawkins, A. D., and G. W. Smith. 1986. Radio-tracking observations on Atlantic Salmon ascending the Aberdeenshire Dee. Scottish Fisheries Research Report 36:1–24.

Hewitt, N., N. Klenk, A. L. Smith, D. R. Bazely, N. Yan, S. Wood, J. I. MacLellan, C. Lipsig-Mumme, and I. Henriques. 2011. Taking stock of the assisted migration debate. Biological Conservation 144:2560–2572.

Hosmer Jr., D. W., S. Lemeshow, and R. X. Sturdivant. 2013. Applied Logistic Regression, Third Edition. John Wiley & Sons, Inc, Hoboken, New Jersey.

ICES. 2018. Report of the Working Group on North Atlantic Salmon (WGNAS), 4–13 April 2018, Woods Hole, MA, USA. ICES CM 2018/ACOM:21. 386 pp.

Izzo, L. K., G. A. Maynard, and J. Zydlewski. 2016. Upstream movements of Atlantic salmon in the lower Penobscot River, Maine following two dam removals and fish passage modifications. Marine and Coastal Fisheries 8:448–461.

Jonsson, B., and N. Jonsson. 2011. Ecology of Atlantic salmon and brown trout: habitat as a template for life histories. Springer, New York, NY.

Jonsson B., N. Jonsson, and L. P. Hansen, 1990. Does juvenile experience affect migration and spawning of adult Atlantic Salmon? Behavioral Ecology and Sociobiology 26:225–230.

Jonsson, N. 1991. Influence of water flow, water temperature and light on fish migration in rivers. Nordic Journal of Freshwater Research 66:20–35.

Karppinen, P., J. Erkinaro, E. Niemelä, K. Moen, and F. Okland. 2004. Return migration of one-sea-winter Atlantic Salmon in the River Tana. Journal of Fish Biology 64:1179–1192.

Klemetsen, A., P.-A. Amundsen, J. B. Dempson, B. Jonsson, N. Jonsson, M. F. O’Connell, and

E. Mortensen. 2003. Atlantic Salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories. Ecology of Freshwater Fish 12:1–59.

Kostow, K. 2009. Factors that contribute to the ecological risks of salmon and steelhead hatchery programs and some mitigating strategies. Reviews in Fish Biology and Fisheries 19:9–31.

Kuhn, M. 2008. Caret package. Journal of Statistical Software 28:1–26.

Liaw, A., and M. Wiener. 2002. Classification and Regression by randomForest. R News 2:18–22.

Maechler, M., P. Rousseeuw, A. Struyf, M. Hubert, and K. Hornik. 2018. cluster: Cluster analysis basics and extensions. R package version 2.0.7-1.

Martin, B. T., R. M. Nisbet, A. Pike, C. J. Michel, and E. M. Danner. 2015. Sport science for salmon and other species: ecological consequences of metabolic power constraints. Ecology Letters 18:535–544.

Milner, N. J., D. J. Solomon, and G. W. Smith. 2012. The role of river flow in the migration of adult Atlantic Salmon, *Salmo salar,* through estuaries and rivers. Fisheries Management and Ecology 19:537–547.

Mitchell, S. C., and R. A. Cunjak. 2007. Relationship of upstream migrating adult Atlantic salmon (*Salmo salar*) and stream discharge within Catamaran Brook, New Brunswick. Canadian Journal of Fisheries and Aquatic Sciences 64:563–573.

National Research Council. 1996. Upstream: salmon and society in the Pacific Northwest. National Academy Press, Washington, D.C.

Økland, F., J. Erkinaro, K. Moen, E. Niemelä, P. Fiske, R. S. McKinley, and E. B. Thorstad. 2001. Return migration of Atlantic Salmon in the River Tana: phases of migratory behaviour. Journal of Fish Biology 59:862–874.

Okland, F., T. C. Heggberget, and B. Jonsson. 1995. Migratory behaviour of wild and farmed Atlantic Salmon (*Salmo salar*) during spawning. Journal of Fish Biology 46:1–7.

Pess, G. R., R. Hilborn, K. Kloehn, T. P. Quinn, and M. Bradford. 2012. The influence of population dynamics and environmental conditions on pink salmon (*Oncorhynchus gorbuscha*) recolonization after barrier removal in the Fraser River, British Columbia, Canada. Canadian Journal of Fisheries and Aquatic Sciences 69:970–982.

Pess, G. R., P. M. Kiffney, M. C. Liermann, T. R. Bennett, J. H. Anderson, and T. P. Quinn.

2011. The influences of body size, habitat quality, and competition on the movement and survival of juvenile coho salmon during the early stages of stream recolonization. Transactions of the American Fisheries Society 140:883–897.

Power, G. 1981. Stock Characteristics and Catches of Atlantic Salmon (*Salmo salar*) in Quebec, and Newfoundland and Labrador in relation to environmental variables. Canadian Journal of Fisheries and Aquatic Sciences 38:1601–1611.

Quinn T. P., E. L. Brannon, and R. P. Whitman RP. 1983. Pheromones and the water source preferences of adult coho salmon *Oncorhynchus kisutch* Walbaum. Journal of Fish Biology 22:677–684.

T. P. Quinn, P. McGinnity, T. E. Reed, and M. Bradford. The paradox of “premature migration” by adult anadromous salmonid fishes: patterns and hypotheses. Canadian Journal of Fisheries and Aquatic Sciences 73(7): 1015–1030.

Richard, A., L. Bernatchez, E. Valiquette, M. Dionne, and B. Jonsson. 2014. Telemetry reveals how catch and release affects prespawning migration in Atlantic Salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences 71:1730–1739.

Roy, M. L., A. G. Roy, J. W. A. Grant, N. E. Bergeron, and I. Fleming. 2013. Individual variability in the movement behaviour of juvenile Atlantic Salmon. Canadian Journal of Fisheries and Aquatic Sciences 70:339–347.

Royston, P., and D. G. Altman. 1994. Regression Using Fractional Polynomials of Continuous Covariates: Parsimonious Parametric Modelling. Journal of the Royal Statistical Society. Series C (Applied Statistics) 43:429–467.

Schoen, E. R., M. S. Wipfli, E. J. Trammell, D. J. Rinella, A. L. Floyd, J. Grunblatt, M. D. McCarthy, B. E. Meyer, J. M. Morton, J. E. Powell, A. Prakash, M. N. Reimer, S. L. Stuefer, H. Toniolo, B. M. Wells, and F. D. W. Witmer. 2017. Future of Pacific salmon in the face of environmental change: lessons from one of the world's remaining productive salmon regions. Fisheries 42:538–553.

Scott, W.B and M. G. Scott. 1988. Atlantic fishes of Canada. Canadian Bulletin of Fisheries and Aquatic Sciences. 219:731 p.

Seddon, P. J., D. P. Armstrong, and R. F. Maloney. 2007. Developing the science of reintroduction biology. Conservation Biology 21:303–312.

Stabell O. B. 1984. Homing and olfaction in salmonids: a critical review with special references to the Atlantic Salmon. Biological Review 59:333–388.

Thomas, C. D. 2011. Translocation of species, climate change, and the end of trying to recreate past ecological communities. Trends Ecology and Evolution 26:216–221.

Thorstad, E. B., P. Fiske, K. Aarestrup, N. A. Hvidsten, T. G. Hårsaker, T. C. Heggberget, and F. Okland. 2003. Upstream migration of Atlantic Salmon in three regulated rivers. Pages 111–121 in Aquatic telemetry: advances and applications. FAO/COISPA, Ustica, Italy.

Thorstad, E. B., F. Økland, K. Aarestrup, and T. G. Heggberget. 2008. Factors affecting the within-river spawning migration of Atlantic Salmon, with emphasis on human impacts. Reviews in Fish Biology and Fisheries 18:345–371.

Thorstad, E. B., F. Okland, and A. G. Finstad. 2000. Effects of telemetry transmitters on swimming performance of adult Atlantic Salmon. Journal of Fish Biology 57:531–535.

Thorstad, E. B., F. Whoriskey, A. H. Rikardsen, and K. Aarestrup. 2011. Aquatic Nomads: The Life and Migrations of the Atlantic Salmon. Pages 1-23 in O. Aas, E. S., A. Klemesten, and J. Skurdal, editors. Atlantic Salmon Ecology. John Wiley & Sons Ltd, Chichester, West Sussex, PO19 8SQ, United Kingdom.

Trépanier, S., M. A. Rodriguez, and P. Magnan. 1996. Spawning migrations in landlocked Atlantic Salmon: time series modelling of river discharge and water temperature effects. Journal of Fish Biology 48:925–936.

Venables, W. N., and B. D. Ripley. 2002. Modern Applied Statistics with S. Fourth Edition. Springer, New York.

Wolf, C. M., B. Griffith, C. Reed, and S. A. Temple. 1996. Avian and mammalian translocations: update and reanalysis of 1987 survey data. Conservation Biology 10: 1142–1154.

Zhongheng Zhang (2016). Variable selection with stepwise and best subset approaches. Annals of Translational Medicine 4(7): 136. doi: 10.21037/atm.2016.03.35

Zuur, A. F., A. A. Saveliev, E. N. Ieno, and G. M. Smith. 2009. Mixed effects models and extensions in ecology with R. Springer, New York, NY.

Table 1. Estimated model coefficients predicting probability of movement where Qmean = standardized mean daily discharge and Tmean = standardized mean daily temperature.

Fixed effects	Estimate	Std. Error	z value	Pr(>|z|)
Intercept	1.17	0.40	2.91	0.0036
Season (S)	-1.47	0.27	-5.38	< 0.0001
Qmean	0.79	0.19	4.17	< 0.0001
Tmean	-0.14	0.18	-0.81	0.4155
SexM	1.37	0.49	2.82	0.0049
Qmean:SexM	-0.77	0.23	-3.39	0.0007
Tmean:SexM	-0.66	0.18	-3.64	0.0003

Random effect	Variance	Std.Dev.
Fish ID	1.94	1.39

Table 2. Pearson correlation coefficients for PCA loadings and explained variance.

	PC1	PC2	PC3	PC4
No. of movements	-0.49	-0.73	0.06	0.47
No. of sites	-0.50	0.15	0.77	-0.37
Total distance	-0.51	-0.08	-0.61	-0.60
Extent	-0.50	0.66	-0.20	0.53
Proportion of Variance	0.86	0.08	0.06	0.00
Cumulative Proportion	0.86	0.94	1.00	1.00

Table 3. Daily salmon movement metrics (mean) and frequency of occurrence (FOC) by movement type and sex.

	Movement Type	
	Sedentary	Exploratory
n	752	539
No. of movements	1.4	4.3
No. of sites	2.0	3.7
Total distance	1.5	5.6
Extent	1.2	5.6
% FOC - Total	**60 (18)**	**40 (18)**
% FOC - Females	68 (14)	32 (14)
% FOC - Males	56 (19)	44 (19)

Table 4. Estimated model coefficients predicting probability of sedentary movement type where Qmean = standardized mean daily discharge and Tmean = standardized mean daily temperature

Fixed effects	Estimate	Std. Error	z value	Pr(>|z|)
Intercept	0.86	0.21	4.08	< 0.0001
Tmean	0.06	0.11	0.56	0.58
Qmean	-0.13	0.13	-1.04	0.30
SexM	-0.56	0.26	-2.17	0.03
Tmean:SexM	0.54	0.14	3.87	0.00
Qmean:SexM	0.41	0.15	2.74	0.01

Random effect	Variance	Std.Dev.
Fish ID	0.39	0.62

Table 5. Importance of pool characteristics generated via random forest analysis. Expansion factor is the ratio between maximum pool width and the channel width upstream of the pool, where channel width was calculated as the mean of three bank-to-bank measures of river width.

Variable	% Increase in MSE	Increase in node purity
Mean daily discharge	37.07	1461.84
Day of year	29.68	1283.65
Mean daily temperature	25.86	1224.12
Surface area	21.14	442.39
Maximum depth	15.44	328.96
Expansion Factor	10.88	173.55
Presence of cold refuge	6.28	22.35
Mean distance to spawning sites	5.25	50.51

Figure Legends

Figure 1. Map of the study area. Impassable waterfalls are denoted with an X, temperature monitoring locations are denoted with a solid black circle, acoustic receivers are denoted by solid grey circles, and the release site is marked with an arrow. The inset map shows the location of the study area (dark grey circle), with Quebec City indicated (black star) for reference.

Figure 2. Distribution of fish size (fork length, and mass) by adult age class and sex. Multi-sea-winter salmon (MSW) are > 63 cm fork length and one-sea-winter salmon (1SW) are < 63 cm fork length.

Figure 3. Representative movement patterns for male and female multi-sea-winter (MSW) and one-sea-winter (1SW) salmon. 1SW salmon are denoted by an asterisk. Fish identity matches the data in Table S.1. Day of year is on the x-axis, and receiver number (corresponding to Figure 1) are on the y-axis. Distance between receivers is to scale. Black points represent the detection of an individual fish by a receiver on a given day. Fish were often detected by multiple receivers on the same day. Vertical grey dashed lines indicate the three-phase migratory pattern (directed migration, DM; holding, H; search, S) for one individual per panel.

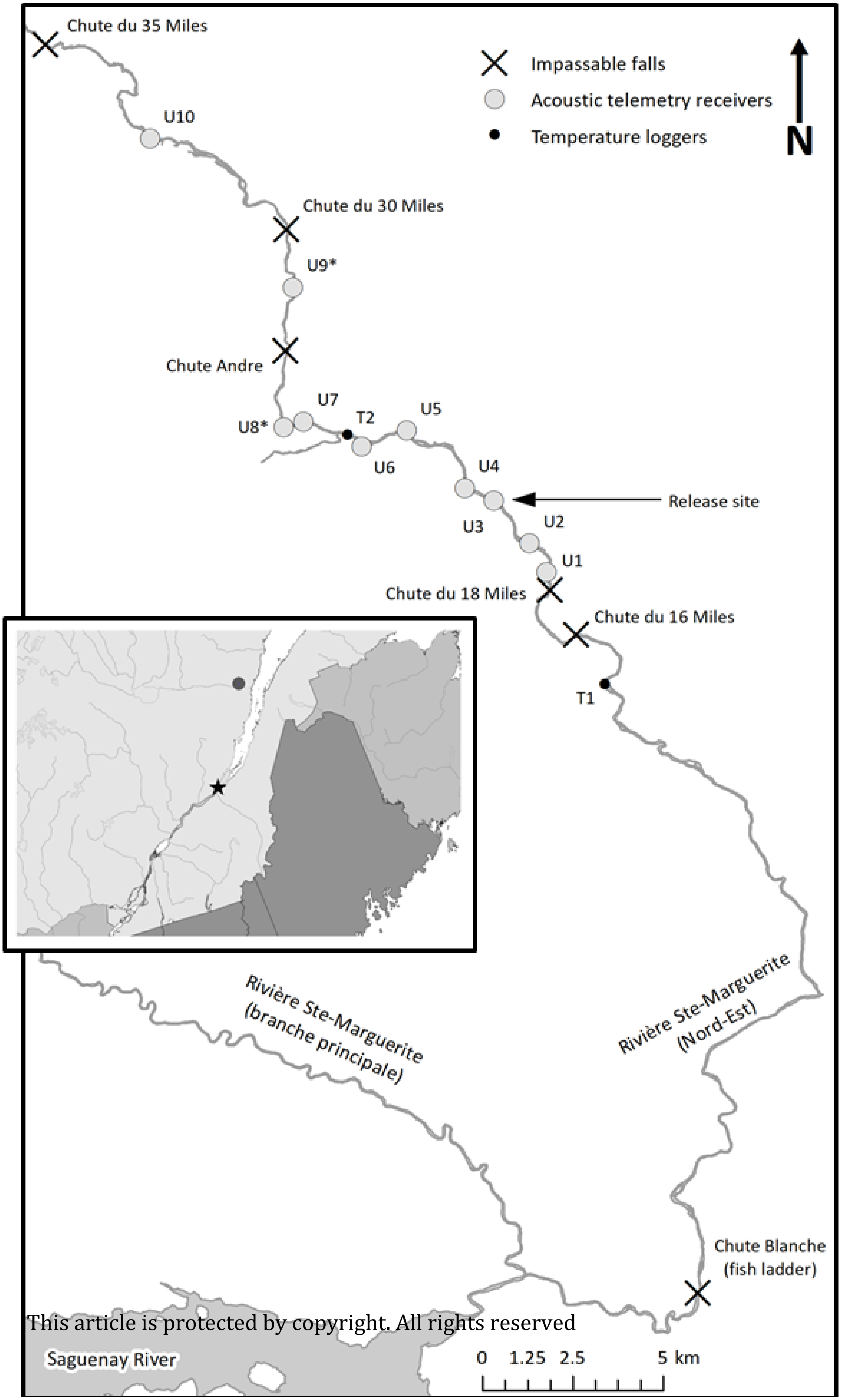
Figure 4. River temperature (black line, left y-axis) and discharge (grey line, right y-axis) for 2014-216. Dashed, black vertical lines indicate the date the first and last salmon was tagged in each year. The horizontal dotted black line denotes 20˚C and the horizontal dashed grey line indicates river discharge of 20 m^3s^{-1}.

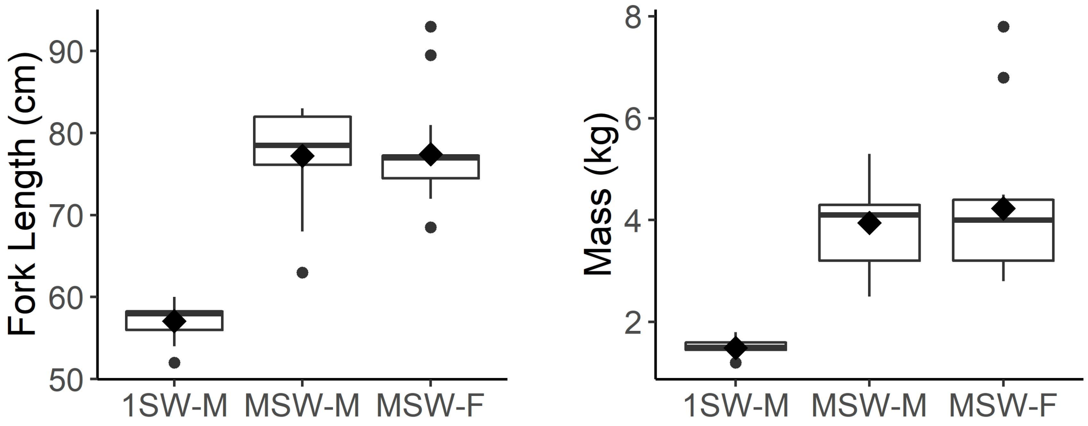
Figure 5. Number of females (upper panel) and males (lower panel) that moved ("move") or did not move ("stay") on each day for 2014, 2015, and 2016 combined. Dashed vertical lines are

included for reference and indicate 1 August and 10 September, where 10 September represents the breakpoint between “summer” and “autumn” seasons.

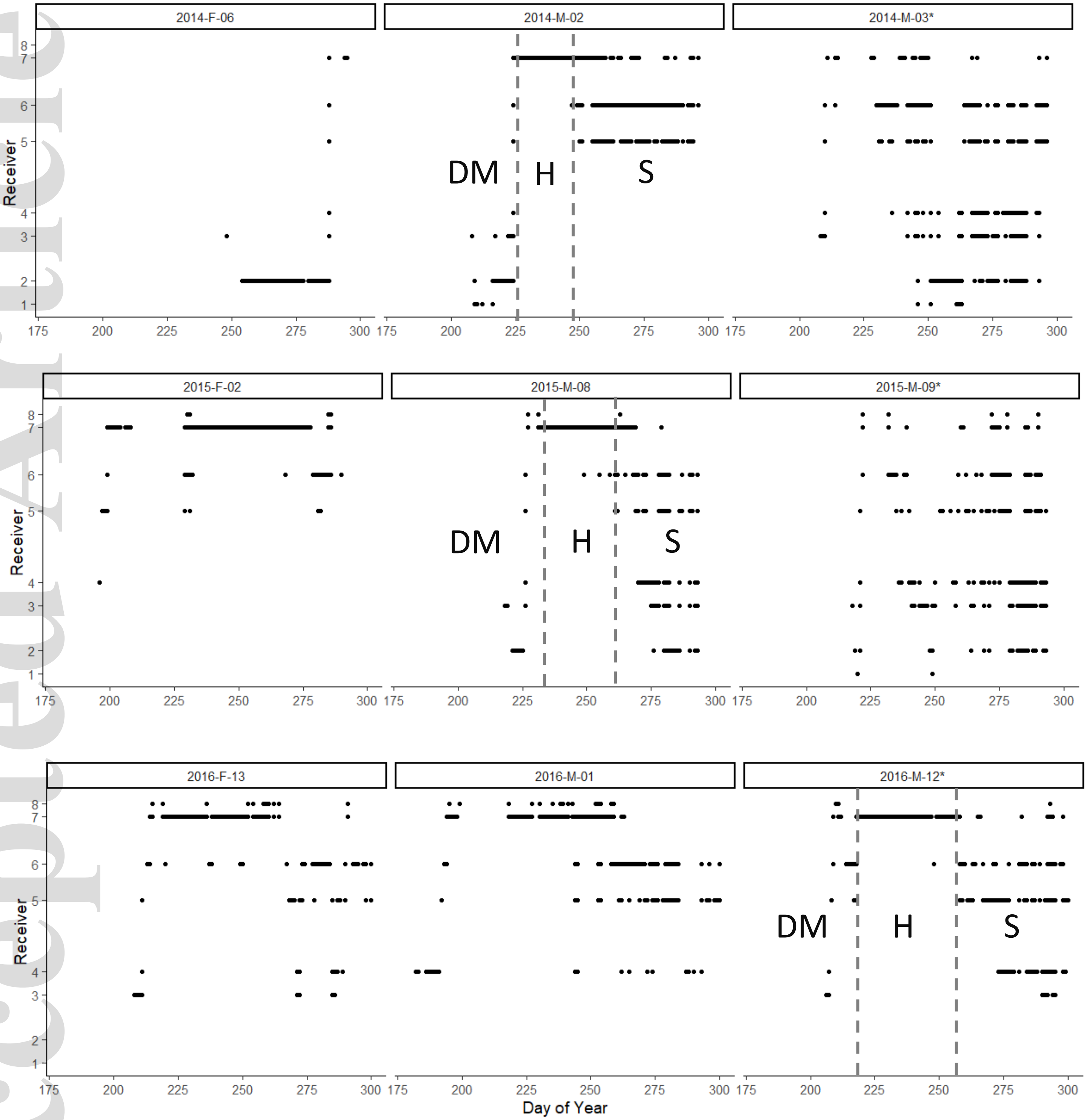
Figure 6. Number of females (upper panel) and males (lower panel) that exhibited exploratory or sedentary movement patterns each day for 2014, 2015, and 2016 combined. Dashed vertical lines are included for reference and indicate 1 August and 10 September, where 10 September represents the breakpoint between “summer” and “autumn” seasons.

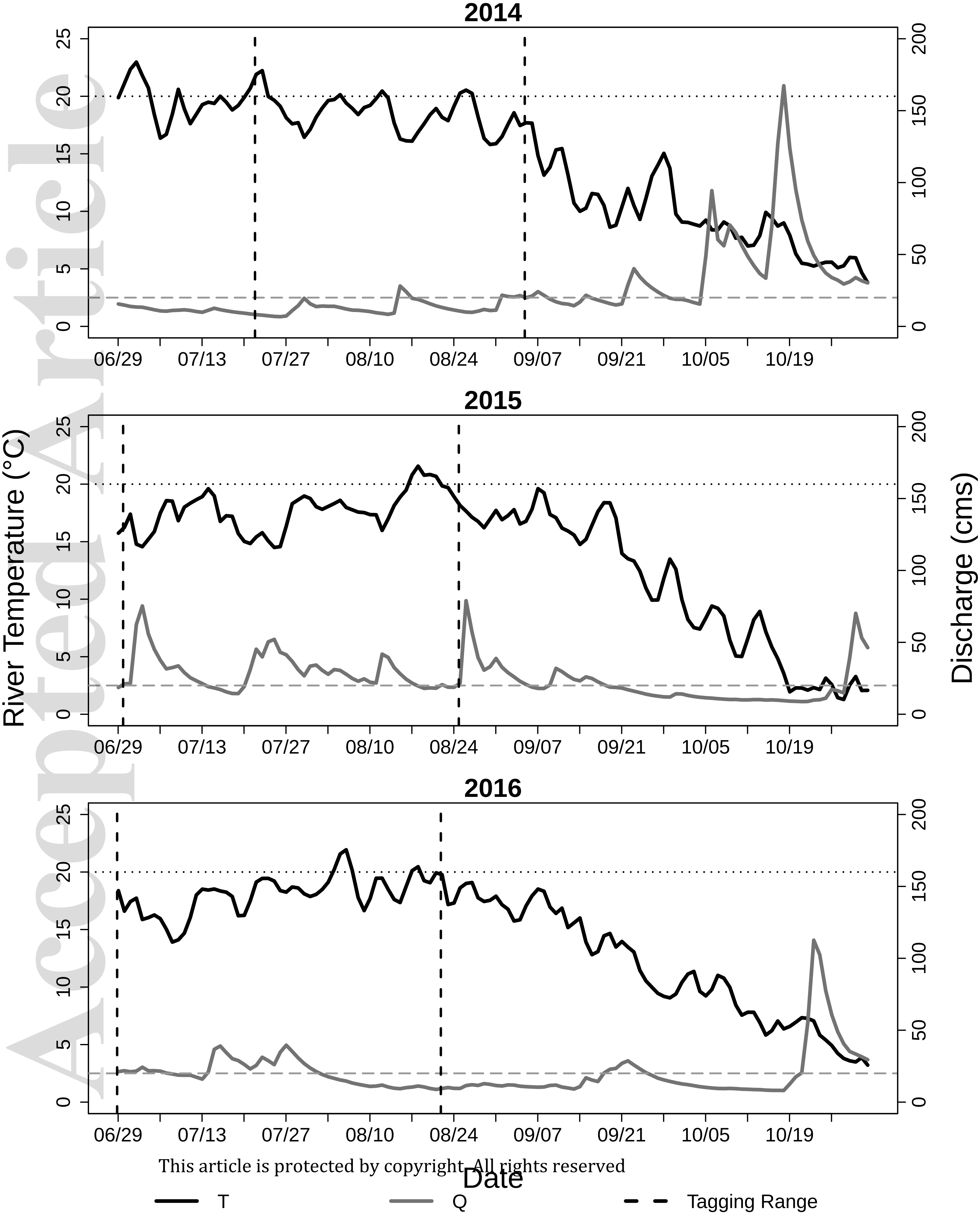
Figure 7. Partial dependence plots for the relationship between the logit of the probability of pool use and each variable included in the random forest analysis.


Chute du 35 Miles
Impassable falls
Acoustic telemetry receivers
Temperature loggers
N
U10
Chute du 30 Miles
U9*
Chute Andre
U7
T2
U5
U8*
U6
U4
Release site
U3
U2
U1
Chute du 18 Miles
Chute du 16 Miles
T1
Rivière Ste-Marguerite (branche principale)
Rivière Ste-Marguerite (Nord-Est)
Chute Blanche (fish ladder)
Saguenay River
0 1.25 2.5 5 km

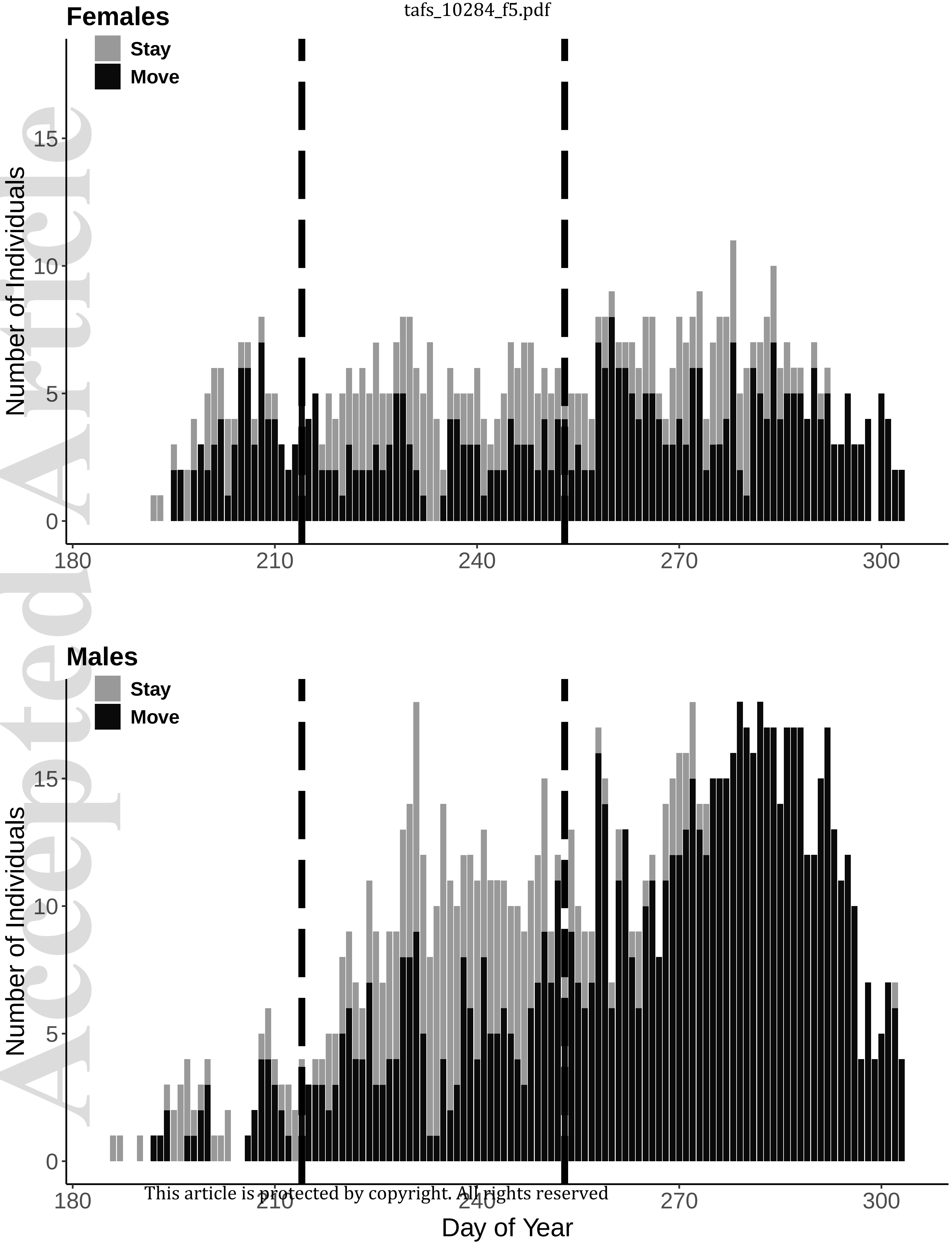


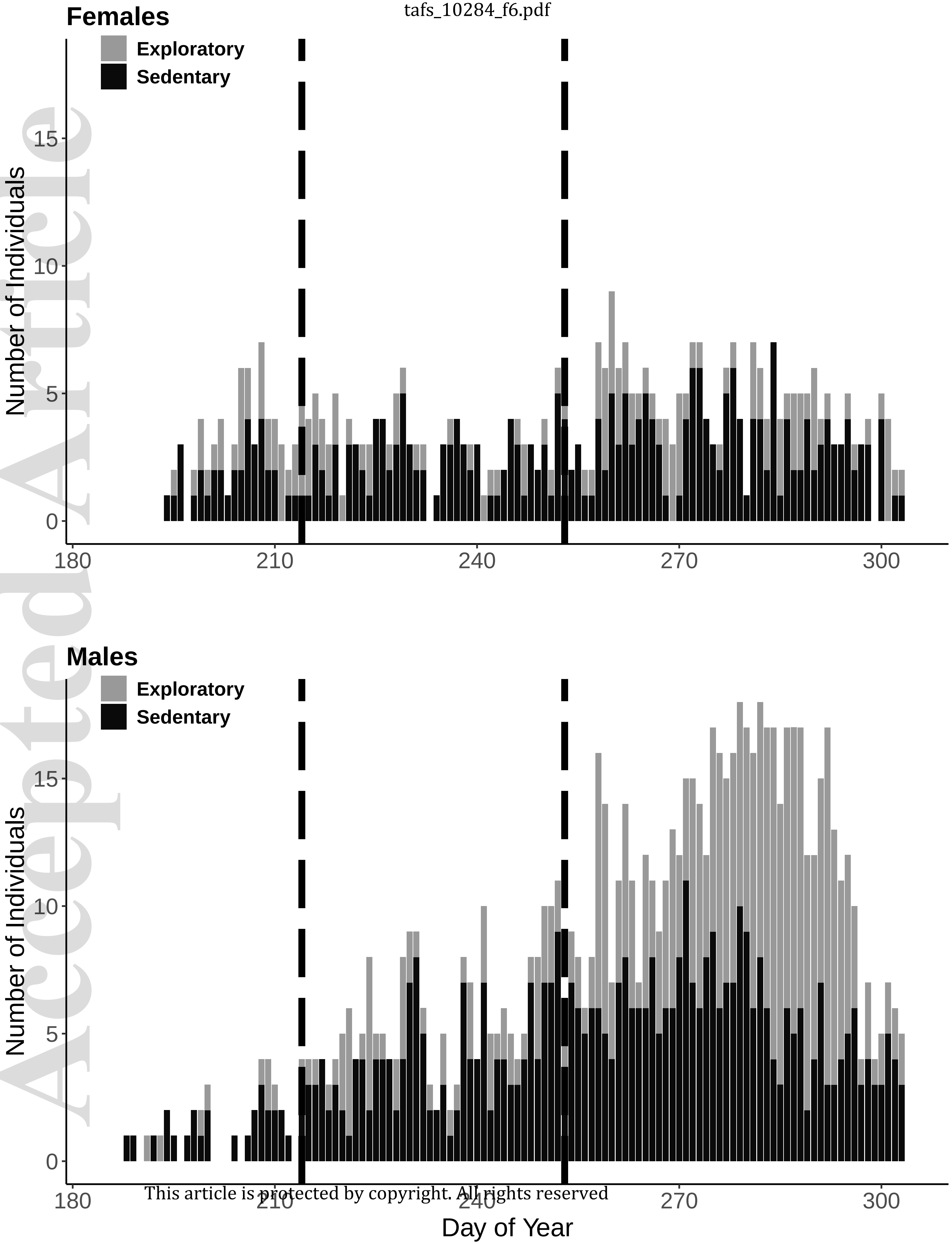
tafs_10284_f2.jpeg

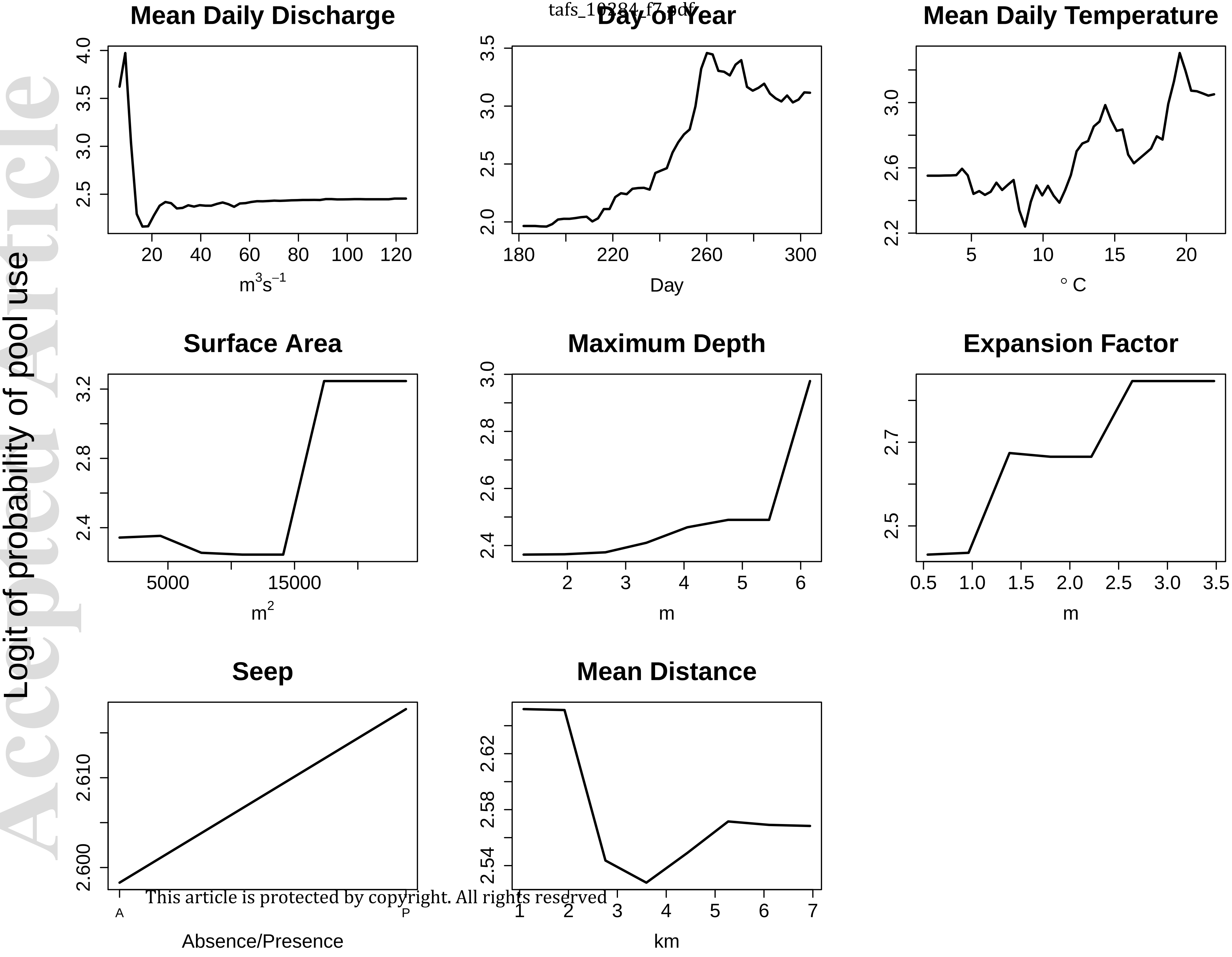

2014-F-06
2014-M-02
2014-M-03*
2015-F-02
2015-M-08
2015-M-09*
2016-F-13
2016-M-01
2016-M-12*
Receiver
1
2
3
4
5
6
7
8
DM
H
S
175
200
225
250
275
300
Day of Year



2014
2015
2016
River Temperature (°C)
Discharge (cms)
0
5
10
15
20
25
0
50
100
150
200
06/29
07/13
07/27
08/10
08/24
09/07
09/21
10/05
10/19
Date
T
Q
Tagging Range


Females
Stay
Move
Number of Individuals
15
10
5
0
180
210
240
270
300
Males
Stay
Move
Number of Individuals
15
10
5
0
180
210
240
270
300
Day of Year


Females
Exploratory
Sedentary
Number of Individuals
0
5
10
15
180
210
240
270
300
Males
Exploratory
Sedentary
Number of Individuals
0
5
10
15
180
210
240
270
300
Day of Year


Logit of probability of pool use
Mean Daily Discharge
2.5
3.0
3.5
4.0
20
40
60
80
100
120
m^3s^{-1}
Day of Year
2.0
2.5
3.0
3.5
180
220
260
300
Day
Mean Daily Temperature
2.2
2.6
3.0
5
10
15
20
° C
Surface Area
2.4
2.8
3.2
5000
15000
m^2
Maximum Depth
2.4
2.6
2.8
3.0
2
3
4
5
6
m
Expansion Factor
2.5
2.7
0.5
1.0
1.5
2.0
2.5
3.0
3.5
m
Seep
2.600
2.610
A
P
Absence/Presence
Mean Distance
2.54
2.58
2.62
1
2
3
4
5
6
7
km