Quantifying the Effects of Post-surgery Recovery Time on the Migration Dynamics and Survival Rates in the Wild of Acoustically Tagged Atlantic Salmon Salmo Salar Smolts

Jason Daniels (jdaniels@asf.ca)
Atlantic Salmon Federation, 15 Rankine Mill Road, Chamcook, NB, Canada. E5B 3A9
https://orcid.org/0000-0002-5234-3107

Eric B. Brunsdon
Atlantic Salmon Federation

Gerald Chaput
Fisheries and Oceans Canada

Heather Dixon
Wilfrid Laurier University

Holly Labadie
Miramichi Salmon Association

Jonathan W. Carr
Atlantic Salmon Federation

Research

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Posted Date: October 2nd, 2020

DOI: https://doi.org/10.21203/rs.3.rs-84100/v1

Version of Record: A version of this preprint was published on January 29th, 2021. See the published version at https://doi.org/10.1186/s40317-020-00228-6.

Quantifying the effects of post-surgery recovery time on the migration dynamics and survival rates in the wild of acoustically tagged Atlantic salmon *Salmo salar* smolts

J. Daniels[1*] (corresponding author): jdaniels@asf.ca, 506-466-8201

E. B. Brunsdon[1*]

G. Chaput[2]

H. J. Dixon[3]

H. Labadie[4]

J. W. Carr[1]

[1]Atlantic Salmon Federation, 15 Rankine Mill Road, Chamcook, NB, Canada. E5B 3A9

[2]Fisheries and Oceans Canada, 343 University Ave, Moncton, NB, Canada. E1C 9B6

[3]Wilfrid Laurier University, 75 University Avenue West, Waterloo, Ontario, Canada. N2L 3C5

[4]Miramichi Salmon Association, 485 Route 420, South Esk, NB, Canada. E1V 4L9

*Both authors contributed equally to the manuscript.

Abstract

Background: The experimental effects of surgically implanting fish with acoustic transmitters is likely to have negative effects on survival and behavior. Measuring the extent of these negative effects is important if we wish to extrapolate inferences from tagged animals to unmanipulated animals. In this study, we examine the effect of surgery and post-tagging recovery time on the survival and migration rate of acoustically tagged wild Atlantic Salmon (*Salmo salar)* smolts through freshwater, estuarine and ocean phases of migration. Four treatment groups were used: pre-smolt captured in the fall that overwintered in a hatchery and were tagged either 75 days prior to release (winter hatchery) or within 24 hours prior to release (spring hatchery) and smolt captured during the spring smolt run, tagged 24 hours prior to release and released during the day (day-released) or night (night-released).

Results: The spring hatchery treatment group served as a reference treatment group such that surgical (comparison to winter hatchery treatment) and hatchery effects (comparison to day-released and night-released treatments) could both be discerned. The hatchery effect increased migration rate whereas short recovery times and captivity in a hatchery negatively affected survival. These effects were most pronounced within the first 5 days and/or 48 km downstream post-release, however, the residual surgical effects appeared to persist during the transition from the estuary into salt water.

Conclusions: Even with smolts originating from the wild and spending relatively little time within the hatchery environment, post-release survival was still negatively affected. Migration speed was faster for hatchery smolts but is likely only due to their larger size. Surgical effects were most prominent during the initial migration period in freshwater and again in the transition from the estuary to saltwater which may be due to added stress during these transitional zones. As surgery related bias will likely never be completely removed from telemetry studies it is important to quantify and account for these effects *in situ* when making inferences on the unmanipulated component of the population.

Keywords: Acoustic telemetry, Experimental effects, Captivity effects, Tagging effects

Introduction

Acoustic telemetry has become a broadly applied technology for studying the migration dynamics and for estimating survival rates of many fish species, including juvenile stages of wild Atlantic salmon in both fresh and salt water [1-5]. The use of acoustic technologies generally involves the surgical implantation (hereafter “tagging”) of acoustic transmitters (hereafter “tags”) inside the abdominal cavity of fish which are released back to the wild and remotely detected when in range of receivers placed in the study area. The primary purpose of these studies is to draw inferences on the behaviour and survival of wild untagged animals which are otherwise difficult to observe and monitor.

In the case of such tracking studies, inferences are made based on a number of assumptions regarding the tags and the animals which carry them. Biased inferences of survival and behaviour can result if the tag stops functioning, if the tag is ejected from the tagged animal, if the tag animal is preyed upon and the functional tag is retained in the predator, or if the behaviour and survival of the tagged animal is affected by the handling and tagging procedure [6-12].

With the increasing application of acoustic telemetry in the study of survival and behavior of fish, it is important to quantify the impact of the experimental manipulation associated with capture and surgical implantation of acoustic transmitters in fish on the biological characteristics of interest. The effects of handling, surgeries, and of tags themselves on salmonid behaviour and survival have been extensively studied in laboratory settings [7, 8, 12-14], but there is limited in-situ research regarding the extent of these effects on tagged animals released to the wild and how long these effects may persist post-tagging. Generally, the release of Atlantic Salmon (*Salmo salar)* in acoustic telemetry studies has occurred within several hours post-tagging to days [2, 5, 15]. There has been limited research examining the consequences of increasing post-tagging release time [16] in order to minimize the negative effects of the surgical procedure on fish behaviour and survival. Panther et al. [17] recommended holding fish until the surgical incision from tagging is closed (28-70 days) thus reducing the negative effects and potential biases but this would preclude any research work on actively migrating wild fish such as smolts of Atlantic Salmon.

We examine the impact of handling and tagging with different recovery periods prior to release on the migration rate and inferred survival of acoustically tagged Atlantic Salmon smolts. A treatment group with a long recovery period post tagging (several months) was constructed by capturing wild Atlantic Salmon juveniles in the late fall, holding them in a captive environment, implanting a subset of these fish with tags during the winter and allowing a long post-surgery recovery period. The potential secondary effects of over-winter captivity on behaviour and survival post-release were also considered by holding a subset of the fall captured juveniles in the hatchery, but only tagging the fish prior to release with a very short recovery period in the spring. Both groups of captive juveniles were subsequently released at the same location and time as wild smolts which were collected and tagged during the spring smolt migration. The fish held in the hatchery and tagged in the spring (hereafter referred to as the spring hatchery treatment) were used as the reference treatment. Spring captured and tagged (i.e. spring wild) relative to spring hatchery was interpreted as the effect of hatchery holding, whereas the fish held in captivity and tagged in the winter (i.e. winter hatchery) relative to the spring hatchery was interpreted as the tagging effect. Our expectation was that the tagging manipulation and short recovery time would negatively affect survival and migration rate compared to fish with a long recovery time. We also expected that a hatchery holding effect would negatively impact survival and migration post-release relative to the wild capture treatment.

Another consideration in post-release strategies is related to the time of day when tagged fish are released. Vollset et al. [18] reported that acoustically tagged wild Atlantic Salmon smolts released in the evening had higher estimated survival rates in freshwater and in a fjord than tagged smolts released in the morning. The time of release of tagged and recovered Atlantic Salmon smolts is an important consideration given that during active migration, Atlantic Salmon smolts in freshwater generally move at night and rest or take shelter during the day [19-21] at least during the early stages of migration. This nocturnal migration of smolts has been interpreted to be a strategy for predator avoidance [20, 22]. As many of the predators of migrating salmon smolts including birds and fish are visual predators, releasing tagged smolts during the day may further increase their susceptibility to predation relative to wild untagged fish. Smolts released during the night after post-surgery recovery may also use this time to further recover from the stress of capture and handling [23]. We examined the effect of time of release by releasing the wild captured and tagged smolts either during the day following recovery or as an evening release. Our expectation was that releasing smolts in the evening at dusk would enhance their survival rates relative to tagged smolts released during the day. This effect was only examined for the wild smolt group captured in the spring.

Materials and methods

Study location and study species

The Northwest Miramichi River is the second largest branch of the Miramichi River in New Brunswick Canada (Figure 1). It drains a catchment area of 3,900 km^2 into the main stem of the

Miramichi where it continues into the Gulf of St Lawrence. Atlantic Salmon smolts are mostly comprised of 2 to 4-year-old juveniles with a fork length range of 11 to 17 cm, and a mean size of 13 to 14 cm [24]. Based on acoustic tracking studies, after smolts exit from the river, they migrate northward through the Gulf of St Lawrence and enter the Labrador Sea via the Strait of Belle Isle (SoBI; Figure 1; [5]).

Fall collection of Atlantic Salmon pre-smolt juveniles

A backpack electrofisher (Smith-Root; model LR24) was used to collect wild large juveniles (> 11 cm fork length), assumed to be potential smolt migrants the following spring. Juveniles were collected from two sites (Figure 1; Table 1): Miners Bridge on October 9, 2015 (n=31) and Trout Brook on October 13, 2015 (n=52). The fish were transported in oxygenated tanks to a salmonid hatchery located at the Miramichi Salmon Conservation Centre in South Esk, New Brunswick, Canada. Juvenile salmon were held in a 1.8 m circular fibreglass tank and maintained on flow-through well water at a temperature of approximately 7°C and natural photoperiod. Fish were fed a freeze-dried krill diet for the first week, then gradually transitioned to a semi-moist pellet diet, followed by a hard pellet diet (1.2 mm and 1.5 mm). Fish were fed two to three times per day to satiation throughout the period of captive rearing.

Survival rate in captivity was high; from the time of capture to March 6, 2016, 72 of the 83 juveniles were still alive, an 87% survival rate. For the first treatment (winter hatchery), 30 fish were randomly selected and taken off feed on March 6 (2016) and tagged on March 8 (72 days prior to release) and then placed in a separate holding tank from the untagged fish at which point feeding was resumed. One of the 30 tagged juveniles one died 26 days post-surgery. Eight fish were culled and sent to Department of Fisheries and Oceans Canada laboratory for disease screening/release approval. The tagged fish group and the untagged group were taken off feed on

May 15, four days before being transferred to oxygenated containers and transported by truck to the Miners Bridge release site in the Northwest Miramichi (Figure 1; Table 1), a trip which took approximately 45 minutes. Upon arrival at the release site, river water was gradually added to the transport containers for approximately 30 minutes for purposes of temperature and water chemistry acclimation. River water temperatures at the time of transfer ranged from 8.5 to 9.5°C. The winter tagged captive smolts were released as a group immediately following acclimation. The remaining 34 untagged captive smolts were transported to the release site where 29 were tagged for the second treatment group (spring hatchery), held for a minimum of one hour to allow restoration of equilibrium of the fish, then released (Table 1). The remaining 5 untagged captive smolts were released at the release site. Smolts from the two captive treatment groups were released on May 19, 2016.

Collection of wild Atlantic Salmon smolts for day and night releases

A total of 61 wild salmon smolts were selected during May 17 – 19 (2016) from catches in a rotary screw trap set at Trout Brook in the Northwest Miramichi (Figure 1; Table 1). Only smolts with a fork length ≥ 13 cm were selected for the experiment to accommodate the size of the acoustic tag. All smolts selected for tagging were held in in-stream tanks for 20 to 24 hours prior to tagging to allow for digestion of stomach contents. Smolts were then transported by truck in oxygenated tanks to the Miners Bridge release site, a trip which took approximately 15 minutes, where surgery and tagging were conducted. After surgery, smolts were held in plastic flow through stream side containers (length: 80 cm; depth: 35 cm; width: 50 cm) for a minimum of one hour after equilibrium had been restored before being released (Table 1). Collected smolts were divided daily into two treatment groups. The first treatment group, consisting of a total of 32 smolts, was tagged and released during the day (day-released). The second treatment group, consisting of 29 smolts, was tagged and released in the late evening at 2200 hours, approximately one-hour post-sunset (night-released). Wild tagged smolts from these treatment groups were released on May 18, 2016 (22 for day release), May 19, 2016 (9 and 19 for day and night released, respectively) and May 20, 2016 (one and 10 for day and night released, respectively; Table 1). The combination of both day-released and night-released treatments are referred to as a spring wild treatment.

Tagging procedure

The tagging procedure was the same for all treatment groups and as previously described by Daniels et al. [10] and Chaput et al. [5]. Fish were anaesthetised using clove oil (40 mg/L concentration) until loss of equilibrium and very little operculum movement was observed (generally 3 - 5 minutes). All surgical tools and tags were disinfected in anhydrous ethyl alcohol and rinsed in distilled water. Wet weight (g) and fork length (mm) were taken before the fish was placed ventral side up on a v-shaped operating board lined with a chamois leather. An ≈11 mm incision was made along the mid-ventral line about 10 mm anterior to the pelvic girdle. Acoustic tags (Innovasea Marine Systems Canada, Inc., Halifax, NS; model V8; diameter=8 mm, length=20.5 mm, weight in air=2.0 g; output = 144 dB re 1uPa@1m, transmission cycle = random 25-55 s) were inserted into the body cavity of the fish via the incision. The fish's gills and body were continuously irrigated with anaesthetic or water during the surgery while avoiding the incision area. One suture per five mm of incision (typically two sutures) was used to close the incision and the fish was placed in a recovery bath, with aerated water, for observation. Two surgeons tagged the same number of smolts in each treatment. The acoustic tags for the winter tagged group were programmed for a delayed start on May 14, 2016.

Fish from all treatment groups were only weighed and measured at time of tagging. Winter tagged hatchery fish were weighed and measured at the time of surgery (March 8) but not at the time of release (May 19) as we did not want to introduce anaesthetic and handling effects immediately before release. The captive treatment group tagged in the winter was of intermediate size at time of tagging (median fork length 149 mm) to captive fish tagged in the spring (median FL = 172 mm) and to wild smolts captured and tagged in the spring (median FL = 138 mm; Figure 2).

Receiver deployment

Arrays of acoustic receivers (Innovasea Marine Systems Canada, Inc., Halifax, NS; model VR2W) were deployed within the Miramichi River and bay and at the Strait of Belle Isle northern exit of the Gulf of St. Lawrence (Figure 1). All receivers were attached to moorings consisting of varying weight anchors (depending on current and water surface conditions), line and surface floats. Receivers within the river were suspended approximately 4 m below the surface floats whereas receivers at the SoBI were suspended 20 m below the surface. Sinking line was used from the surface floats to a nylon swivel located below the receiver, which in turn was attached to the anchor with floating line. At the SoBI a second gate was deployed 3.5 km north of the first gate to allow the estimation of detection probabilities and survival to the primary SoBI array (see statistical methodology). The number of receivers used at each gate was based on manufacturer recommendations of 400 m detection ranges for V8 tags; receivers were spaced approximately 800 m apart and 400 m from each side of the shoreline. There was a total of 16 gates between the release location to SoBI (Figure 1). Survival and timing were estimated at a subset of receiver gates located at the head of tide (HoT), Nelson, Inner Bay, Outer Bay and SoBI, situated 48.8, 70, 87.3, 114.3, and 899.3 km from the release site respectively (for additional details on receiver deployments and retrieval see [10, 5]; supplementary material).

Statistical analyses

Smolt size

Similarities among the treatment groups for length and tag burden (tag weight as % of smolt weight in air) at tagging were examined with a one-way ANOVA and post-hoc pairwise t-test comparisons with the Holm correction [25] to control for Type I errors.

Survival and probability of detection model

Sequential survival rates of tagged smolts from release to the SoBI line were estimated using a state-space formulation of a Cormack-Jolly-Seber (CJS) model [26, 27]. The state-space parameterization of the CJS model constructs distinct processes for the unobserved survival (ϕ) and the observed detections (p). We refer to survival as the joint probability of a tagged fish surviving to pass a receiver array and of the tag being detected at that array. The unobserved survival process (Eq. 1) is modeled as random draws from a Bernoulli distribution where $z(i, j)$ is conditional on $z(i, j-1)$, whether fish i is alive (1) or dead (0) at the previous detection point:

$$z(i,j) \mid z(i,j-1), \emptyset_j \sim Bernoulli(z(i,j-1)\emptyset_j) \qquad (1)$$

with parameter $\emptyset_j$ the probability of survival within the zone defined by detection arrays j-1 to j and j corresponding to the sequence of post-release detection points.

The detections ($y(i,j)$) are modelled as independent Bernoulli random variables, conditional on the $z(i,j)$'s and the probability of detection (p_j):

$$y(i,j) \mid z(i,j), p_j \sim Bernoulli(z(i,j)p_j) \qquad (2)$$

with parameter p_j the probability of detection at array j.

The parameters p and ϕ are proportions bounded on the range [0, 1] but are logit-transformed for flexibility in parameterization of survival factors and to improve model convergence.

It was assumed that the probabilities of detection of individual tags (i) at each array line (j) were similar across treatments (i|t) but could differ among arrays and these were given uninformative priors ($p_{i|t,j} \sim Beta(a_j, b_j)\ with\ a_j = b_j = 1$). To determine if there were differences in survival rates by zone and treatment (winter hatchery, spring hatchery, spring wild), we modelled the survival process using a fixed effects model:

$$y_{i|t,j} \sim Bern(\emptyset_{i|t,j})$$

$$logit(\emptyset_{i|t,j}) = \mu_j + \alpha_j * T_{i|1} + \beta_j * T_{i|2} \qquad (3)$$

with μ_j the average logit survival of fish of the reference treatment group in zone j;

α_j the difference from the reference treatment group in logit survival of fish in treatment 1 ($T_{i|1}$) in zone j;

$T_{i|1}$ an indicator variable that equals 1 if the fish is of treatment 1 and 0 otherwise;

β_j the difference from the reference treatment group in logit survival of fish in treatment 2 ($T_{i|2}$) in zone j;

$T_{i|2}$ an indicator variable that equals 1 if the fish is of treatment 2 and 0 otherwise.

Note that the fish in the reference treatment have $T_{i|1}$ = 0 and $T_{i|2}$ = 0 hence logit survival of the reference group in zone j = μ_j. We set the spring hatchery tagging group as the reference treatment because we were interested in estimating the expected survival rate of wild captured smolts with minimal tagging effect (i.e. long recovery time). However, to do so, we also had to account for the effect of captive holding of fish for several months. Spring wild (Treatment 1) relative to spring hatchery represents the hatchery holding effect (α), whereas Winter hatchery (Treatment 2) relative to the spring hatchery represents the tagging effect (β). From equation 3, the adjusted logit survival rate of wild captured smolts with a long recovery time is the sum of the posterior distributions of $\mu_{j,}$ α_j and β_j. The odds ratio of survival among treatment groups is used to make inference on the effect of captivity in the hatchery (wild spring tagged relative to spring hatchery tagged) and the effect of recovery period (captive winter tagged relative to captive spring tagged and to wild spring tagged).

Several model structures for survival were examined and the final model retained for assessing treatment effects modelled the survival rates through the Gulf of St. Lawrence zone, between the Outer Bay and the Strait of Belle Isle array, as similar across treatments. In this way, we limited our analysis of treatment dependent survival rates by zone from the point of release to detection at the Outer Bay arrays. Noninformative priors, on the logit scale, were assumed for the survival parameters by zone $(\mu_j, \alpha_j, \beta_j)\ as$:

$$\mu_j, \alpha_j, \beta_j \sim Normal(0, \sigma^2)\ with\ \sigma^{-2} = 0.368\ [28].$$

Details of a similar CJS model to the one used in this study are found in Chaput et al. [5].

The model was coded in OpenBUGS (version 3.2.3) and run with two chains of 15,000 iterations with a burn-in of 10,000 and thinned by 10 to produce 10,000 MCMC values for summaries of the posterior distributions. Model convergence was assessed visually through examining trace plots of each Markov chain as well as ensuring Gelman Rubin statistics were <1.1 for the estimated parameters.

Migration speed to gates

Migration speed to each gate was calculated as the distance (km) divided by the time between first detections from the current and preceding gate. Speed was not standardized by body lengths due to the uncertainty of size for the winter hatchery treatment at the time of migration. A mixed effects ANOVA was performed with smolt ID nested in gate as random effects to account for individual smolt having repeated migration speeds to multiple gates. AIC scores were examined for competing models for all combinations that included fixed effects of treatment, gate, fork length, and all two-way interactions. Post-hoc pairwise comparisons were conducted using least squared means and resulting p-values were Holm's adjusted.

Potential source of predation induced survival and migration rate bias

In the NW Miramichi River, concurrent intra-species acoustic telemetry studies involving Atlantic Salmon smolts and Striped Bass (*Morone saxatilis)* demonstrated considerable spatial and temporal overlap, the occurrence of predation of acoustically tagged salmon smolts, with resultant predation bias potential for survival and migration rate estimates [10, 11]. Daniels et al [11] suggested migration rates based on the first detections at arrays presented the least amount of predation induced bias; this is the timing methodology we used. With respect to survival estimates, predation induced bias is introduced when a tagged smolt is consumed by a predator and the tag is detected further along the migration route from within the predator's gastrointestinal tract. Based on detection patterns at the full set of receivers in the river and bay, tags implanted in smolts were subjectively classified into one of two categories; 1) pattern consistent with smolt behaviour and, 2) pattern consistent with striped bass behaviour and presents predation induced bias. Predation induced bias in the context of the model structure used here is introduced when a tagged animal is preyed upon and the functional tag within the predator is detected downstream of the predation event. Therefore, the number of tags including predation induced bias and the number of tagged smolts predated are not synonymous. Subjective assignments were made based on expert opinion by interpreting sequential detection patterns of smolts detected at the Strait of Belle Isle and acoustically tagged Striped Bass monitored within the same study site and year (see Daniels et al. [10] for details and examples).

CJS models were run with and without total unique tags inferred to introduce predation induced bias to explore potential interactions between predation induced bias and tagging induced bias. It should be noted, however, that an increased rate of predation and therefore, the potential rate of predation induced bias, could be an indirect result of tagging effects.

Results

Smolts size

Overall, there was a significant difference in fork length ($F=43.24$; $df=3$; $p<0.0001$) between treatment groups. Post-hoc treatment comparisons showed only spring hatchery smolts to be significantly longer than all other treatments (Table 1; Figure 2). Tag burden also differed significantly between treatment groups ($F=59.73$; $df=3$; $p<0.0001$). Post-hoc comparisons showed that spring hatchery smolts tag burdens were smaller than all other treatment groups while winter hatchery smolts had smaller tag burdens compared to day- and night-released wild smolts (Table 1). Day-released and night-released wild spring smolt groups had similar tag burdens.

Day-release vs night-release

There were no significant differences in the apparent survival and migration rate to arrays of day-released compared to night-released wild smolts (Table 2). Therefore, day-released and night-released treatments were combined for comparisons to the captive treatments.

Observed detections

Observed detections of tagged smolts varied between zones and treatments. Of the 61, 29, and 29 tagged smolts released for the spring wild, winter hatchery, and spring hatchery treatments, 50 (82%), 25 (86%), and 13 (45%) smolts, respectively, were subsequently detected at downstream receivers. Only 13 of 29 tags (45%) of the spring hatchery treatment were detected at the HoT array, much lower than the 79% of tags from the winter hatchery treatment and the spring wild treatment detected at the HoT array (Figure 3). The relative reduction in detections between the HoT and the outer bay array was similar for the spring wild treatment and the spring hatchery treatment (-61%) in contrast to the relatively lower reduction in tags detected for the hatchery winter treatment (-52%). There was no evidence of size selection in survival between receiver arrays and within treatments.

Predation induced bias

Based on the interpretation of detection patterns, 8 of 61 tags from spring wild tagging, 2 of 29 tags from spring hatchery tagging, and 4 of 29 tags from winter hatchery tagging were inferred to have been predated by Striped Bass and introduce predation bias (Table 1). This represents 13% of tags of the spring wild release group (95% Confidence Interval range, 5% - 20%), 7% (95% C.I. 1% - 17%) of the spring hatchery release group, and 14% (95% C.I. 3% - 26%) of the winter hatchery release group. Based on tags detected post-release, the number of tags with detections consistent with Striped Bass movement and inducing predation bias was similar among treatments; 17% (95% C.I. 6% - 24%) of the spring wild group, 15% (95% C.I. 2% - 34%) of the spring hatchery group, and 17% (95% C.I. 4% - 30%) for the winter hatchery group. As there was no evidence of differential rates of predation induced bias between treatments, CJS model results including total unique tags are presented and discussed.

Smolt survival and probability of detection

The mean probabilities of detection at the arrays within the river and estuary were generally high, ranging from 0.914 to 0.984. The outer bay and SoBI arrays, however, were estimated to have lower detection probabilities, with mean values of 0.731 and 0.702, respectively (Figure 4), consistent with previous analyses [5].

Evidence of statistically significant negative hatchery and tagging effects were present from release to the HoT array (Figure 5). There was no evidence of hatchery or tagging effects present through the estuary (HoT to inner bay). A potentially significant ($p = 0.06$) negative tagging effect was noted between the inner and outer Miramichi bay whereas there was no evidence of a hatchery effect in this zone (Figure 5).

Results suggest that the winter hatchery treatment group may have had slightly improved survival through the bay in comparison to the other treatments, however, small sample sizes preclude firm conclusions (Figure 4). Throughout all regions survival odds generally favored the winter hatchery treatment (Figure 4; Table 3). An extended recovery period prior to release improved the odds of survival post-release (winter hatchery treatment) with survival odds of just under 2.53; this is due to the poor survival immediately post release of the spring hatchery treatment (Figure 5; Table 3). The survival odds of a long recovery period were also improved relative to wild spring tagged smolts, with a median value of 1.38 favouring the survival of the long recovery treatment. After the initial mortalities in the freshwater portion of the river, above the HoT, the survival odds still favoured the long recovery period treatment, 1.34 to 1.47 relative to the short recovery treatments, however the statistical evidence for this was weaker (p-values 0.11 to 0.14) because of small sample sizes. A hatchery effect was noted for the initial survival odds, favouring by a factor of 1.83 the survival of spring wild smolts relative to the spring hatchery treatment (Table 3). After the initial triage of compromised fish from the spring hatchery treatment, the odds of survival through the estuary and bay were similar (1.1, $p = 0.39$) for spring wild and spring hatchery fish (Table 3).

The expected survival after controlling for both tagging and hatchery effects suggests that survival for untagged fish could be much higher than inferred from tagged animals during the initial phase of the migration through freshwater. Due to subsequent decreases in sample size throughout the remainder of the migration a great deal of uncertainty prohibits clear expectations. Despite this uncertainty, there was a reasonable increase in expected survival (median 28%) in comparison to the spring wild treatment between the inner and outer bay (Figure 6).

Migration rates

The best fitting model according to AIC scores included treatment, gate, and the interaction of treatment and gate as fixed effects. Mixed effects ANOVA showed significant differences between treatments ($F = 5.85$; $p < 0.01$), gates ($F = 42.21$; $p < 0.01$), and the interaction of treatment and gate ($F = 3.44$; $p < 0.01$). Pairwise comparisons between treatment group migration speeds showed spring wild smolts had significantly slower migration speeds compared to winter hatchery ($t = 5.54$; $p \leq 0.01$) and spring hatchery ($t = 3.06$; $p < 0.01$) smolts between release to HoT (Figure 7). From release to HoT, spring hatchery and winter hatchery smolt migration speeds did not differ ($t = 1.32$; $p = 0.19$). There were no other differences between treatment migration speed comparisons between any of the other gates ($t \leq 1.27$; $p \geq 0.62$). On average, smolts in the winter hatchery and spring hatchery treatments migrated to the HoT gate between two to three days, whereas the spring wild treatment took over five days.

The mean expected migration speed increased from the point of release to the inner bay along with variability of the estimates and then decreased between inner bay to the SoBI. The mean expected migration speed estimates were similar to the those of the spring wild treatment between all zones.

Discussion

We report on a field experiment to assess the effects of handling/tagging on migrating Atlantic Salmon smolts and on inferences of survival and migration rates using acoustic technologies. In particular, we assess the extent to which recovery time post-surgery can affect those common metrics and the inferences which could be made from such studies relative to migration and survival of untagged smolts. The results suggest that there is a detectable negative effect on survival and migration rates when fish are only allowed short recovery times post-surgery before release. We found that in this first experiment, capturing juveniles in the fall, holding them in captivity over the winter and releasing back to the river in the spring immediately after a tagging intervention imparted a very strong compromise on survival immediately post release. Although we might suspect the manipulation, transport, and short period of acclimation prior to release would be stressful to all fish, immediate short-term survival was not compromised in the winter hatchery treatment subjected to the same handling procedures, absent the tagging.

In comparison to the other treatment groups, it is unclear why the spring hatchery smolts experienced such low short-term survival post release. Both hatchery treatments underwent the same transportation to and release protocols at the release site. As well, the wild spring smolts were also manipulated, transported for a shorter distance and time, and held in stream-side containers post tagging. Surgery and handling protocols were identical between the spring wild and spring hatchery treatments, but these groups had very different estimated survivals to HoT from the release site. Therefore, it seems unlikely that solely transportation or surgery and handling protocols resulted in the high early mortality observed for the spring hatchery treatment. The most likely explanation for the high rate of early mortality of spring hatchery smolts is the result of cumulative stress from transportation and acclimation immediately followed by surgery. There is evidence that cumulative stress results in higher than expected mortality. For example, Handeland et al. [29] found that the interaction between osmotic stress and predator induced stress resulted in higher rates of predation than the combined effects of predation and osmotic stress solely. Similarly, Dietrich et al. [30] present evidence which suggests sublethal doses of organophosphates increase mortality rate of Chinook salmon in the presence of thermal stress. We suggest that the unexpectedly high mortality may have been due to the cumulative impacts of hatchery transport, surgery, and release to the wild following a short recovery period.

Tagging effects on migration speed and survival

While there was no statistical difference in migration rates between the winter and spring hatchery treatments, there was a slightly faster mean migration speed for winter hatchery smolts between release and HoT. This was unexpected as the size of the spring hatchery treatment appeared to be much larger based on visual inspection pre-release and larger fish tend to have faster swimming speeds [6, 8]. While small sample size prohibits any definitive conclusions, the slight difference could be indicative of a tagging effect and short recovery period on the migration speed.

There was a noticeable tagging effect on apparent survival from release to HoT. Although, tag burden is most often viewed as the leading cause for reduced survival the results from this study imply surgery may be the larger effect. Compared to the spring hatchery treatment, the winter hatchery group had higher tag burdens but assumingly without the tagging effects and they presented a higher survival rate. It is important to note, however, that we did not measure size of the winter hatchery group at time of release and their tag burdens were likely to have been exaggerated in relation to what would have been experienced at the time of release. Other studies have also drawn similar conclusions that surgery has a larger effect than tag burden. Studies have found no difference in mortality rates between tagged smolts and sham treatments (ie. received surgery, yet no tag was implanted) also suggesting that surgery related mortality may be more important than the size of the tag [9, 12].

Determining when and where mortality occurs is a key question however, experimental manipulations such as those considered here can affect the conclusions from the interpretation of acoustic telemetry data [31]. For example, a study presented by Chaput et al. [5] involved a fourteen-year multi-stock inference on the survival and migration of Atlantic Salmon smolts and post-smolts which suggested that differences between stocks migrating through a shared environment may be indicative of post-surgery acclimation factors. They also suggest that mortality associated with migration duration could be enhanced as a result of direct tagging effects and/or vulnerability to predation that occurred within the first 8 to 12 days of migration. While field-based studies and analysis of telemetry detections provide some information on survival and behaviour of tagged fish, they generally are inadequate to ascribe causal factors of mortality. Laboratory-based studies report similar time frames of surgery related mortality as found in this study. Brunsdon et al. [12] found that the majority of the mortality of tagged Atlantic Salmon juveniles occurred within the first 10 days after surgery using the same tags used in this study (Vemco V8) and did not find any difference in survival rates between tagged smolts and a sham treatment. Ammann et al. [9] also found no difference in mortality rates between acoustically tagged individuals and a sham treatment. These results suggest that for smolts of the size used in these laboratory studies and in this experiment, mortality may be more likely a consequence of surgery related effects as opposed to effects related to tag burden.

Hatchery effects on migration speed and survival

The juvenile salmon held in the hatchery were collected from the wild and held in captivity for a period of less than six months. Despite this relatively short-term holding period we did note an effect on migration rates associated with captivity through the freshwater zone of migration. The larger size of the hatchery held smolts in comparison to spring wild smolts may partially explain the faster migration speed observed. Many studies have found a positive relationship between fork length and speed of Atlantic salmon [22, 32, 33] and fish with higher tag burdens tend to have slower swimming speeds [6, 8]. However, the difference in migration speed was only noted for survivors from release to HoT (<5 days). This suggests that migration rate in freshwater to the estuary may be related to fork length, whereas, migration rate through the estuary is conditioned by other factors such as variation in smoltification stage and acclimation to saltwater [34].

In general, wild smolt survival rates tend to be higher than for hatchery-reared smolts, interpreted to be a consequence of poorer foraging and predator avoidance abilities of hatchery reared smolts [35-38]. The effect of the hatchery holding (i.e. the spring wild relative to the spring hatchery treatment) appeared to negatively impact survival within the same zone of the river in which migration speed appeared to have been affected, between release and HoT. Jokikokko et al. [39] reported that survival of wild smolt and hatchery reared Atlantic Salmon released as parr was twice that of hatchery reared Atlantic Salmon released as smolts. Thorstad et al. [40] found that hatchery released smolts suffered approximately 50 percent mortality near the transition from fresh to salt water and imply that hatchery rearing of these fish may have resulted in poor predator avoidance as the vast majority of mortality in their study was likely due to piscine predators.

Most of the comparisons of wild versus hatchery survivals and behaviour are from studies in which the hatchery reared smolts originated from spawning, hatching and rearing in the hatchery environment. We found no information regarding the impacts of short-term captive holding of wild fish on their subsequent behavior and survival once released back into their natal river. There is however evidence from this study that some effects of captivity may manifest themselves even for relatively short periods of captivity.

Expected survival

The effect of the tagging procedure on survival after controlling for a hatchery effect is quite apparent in the very early stages of the migration, between release and HoT and to a lesser and more uncertain degree between the inner and outer bay zone. Our results suggest that smolt survival could have been greater than 95% and nearly 90% through the freshwater and bay regions of the migration, respectively. The uncertainty in these estimates primarily resulting from higher than expected spring hatchery mortality limits our ability to suggest these effects are short-lived, however, we have presented information from both field and laboratory settings which suggests that direct and indirect tagging related mortality is temporally short-lived or a result of increased stress when transitioning through different environments.

The effect of the tag burden on the survival and behavior of smolts was not quantified in this study. Tag burden has been extensively investigated and results have shown mortality increases with tag burden while swimming speed and predator avoidance decrease [6-8, 41]. Studies have also reported that larger tagged smolts have greater survival during the early stages of migration compared to smaller counterparts [5]. However, this study found the larger spring hatchery smolts had lower survival compared to the smaller spring wild and winter hatchery treatments but hatchery and tagging effects, respectively, likely influenced results. Furthermore, there was also no evidence that larger smolts within each treatment had higher survival rates (see Supplementary materials). Nevertheless, the much higher mortality of the spring hatchery treatment was surprising as larger smolts were expected to have greater survival due to a reduced vulnerability to predators and a reduced tag burden [5, 36, 42].

Vollset et al. [18] reported that acoustically tagged wild Atlantic Salmon smolts released in the evening had higher estimated survival rates in freshwater and in a fjord than tagged smolts released in the morning. We examined and did not find any evidence of differences in inferred survival rates of smolts released during the day or the late evening. This lack of effect may be due to the majority of the current study site being within the estuary and ocean which corresponds to areas where daytime migration patterns tend to dominate [19, 20, 43]. Day versus night release effects may be important in areas where visual predators are in closer proximity to the release sites or where there is a substantial freshwater migration phase which tends to be nocturnal for salmon smolts.

Conclusion

The objective of most acoustic telemetry studies is to quantify survival and behavior of tagged individuals and to use these to infer survival and behaviour of untagged and un-manipulated animals [22]. In this experiment, we examined the effects of the length of post-recovery period on the migratory behaviour and inferred survivals of tagged animals post-release. We found that allowing for a long post-surgery recovery period can improve the survival rates of tagged smolts relative to smolts with only a short recovery time post-surgery. There is evidence of an immediate short-term improvement in survival as well as a later benefit as smolts moved from brackish water into a more saline environment, a stressful environmental transitional zone. In order to have a treatment group with a long recovery period, we captured juveniles from the wild and held them in captivity for a relatively short overwinter period. This may have introduced unintended and undesired effects on behaviour and survival of individuals post release. However, the results from this one-year study suggest that the effects of captivity if present are minor compared to the effects related to surgery and short recovery times. An alternate experimental design that would provide a long recovery period without captivity would involve capturing, tagging and releasing in the late fall salmon juveniles of an appropriate size to accommodate the acoustic tags and that would be indicative of a high likelihood of becoming a smolt the following spring. The long recovery treatment group would then consist of those fall-tagged juveniles which survived and became smolts and were detected at a key receiver array in freshwater. This treatment group could be monitored in concert with the reference treatment involving capture, tagging and releasing actively migrating smolts but with a short recovery period. This type of study was conducted and reported by Gregory et al. [44] on salmon juveniles which were tagged with small passively induced transponder tags in the fall prior to smolt emigration and tracked using instream antennas and loggers as they migrated in the spring and returned as adult salmon one and two years later. Furthermore, different sized tags could also be incorporated into the proposed study designs to examine the effects of tag burden in addition to the tagging (i.e. surgical) effects.

Acoustic telemetry studies of wild fish will always introduce a certain degree of bias as they involve the manipulation of animals. Provided the bias is consistent over time, which requires establishing and respecting standardized experimental procedures and protocols, long-term multi-stock telemetry studies such as that presented by Chaput et al. [5], may provide relevant and applicable relative trends in population and life history rates which can be inferred to be representative of characteristics of un-manipulated populations. However, quantifying the bias introduced through manipulation is most important in short term and/or single stock studies and experiments, such as the one reported here.

Declarations

Ethics approval and consent to participate

All methodologies used during this study were approved by an animal care committee and followed the Canadian Council of Animal Care guidelines.

Consent for publication

Not applicable

Availability of data and materials

Data will be made available upon request.

Competing interests

The authors state that there are no competing interests.

Funding

Funding for the purchase of acoustic tags was provided by the Atlantic Salmon Federation and Fisheries and Oceans Canada.

Authors' contributions

JD, JC, and GC conceived the project and created the project design. EBB, JD and HD wrote the manuscript. JD, EBB, and GC performed statistical analyses. All authors revised the manuscript and provided comments on design for publication.

Acknowledgements

We would like to thank Miramichi Salmon Association for their contribution to the collection of pre-smolt juveniles and smolts as well as the captive rearing at the hatchery. We would also like to thank Atlantic Salmon Federation staff for assistance in the tagging of smolts and deployment of acoustic receivers.

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Table 1. Experimental details and observed detections of smolts per receiver array. For the detections, the values in parentheses are the number of tags detected at each array inferred to be of a smolt tag ingested by a predator which induced predation bias rather than of a free-swimming smolt relative to the total number of unique tags which were inferred to have been ingested by a predator and induced predation bias over the whole migration period.

	Day-released	Night-released	Spring hatchery	Winter hatchery
Dates of collection (n)	May 17 (22); May 18 (9); May 19 (1)	May 18 (19); May 19 (10)	Oct 9, 2015 (31) from Miner's Bridge; Oct 13, 2015 (52) from Trout Brook	
Dates taken off feed (n)	May 17 (22); May 18 (9); May 19 (1)	May 18 (19); May 19 (10)	May 15	March 6 – March 8; May 15
Dates of tagging (n)	May 18 (22); May 19 (9); May 20 (1)	May 19 (19); May 20 (10)	May 19 (29)	March 8 (30)
Dates of release (n)	May 18 (22); May 19 (9); May 20 (1)	May 19 (19); May 20 (10)	May 19 (29)	May 19 (29)
Post-surgical recovery time (mean days ± SD)	0.17±0.06	0.42±0.08	0.27±0.06	71.43±0.01
Size at tagging (min; median; max)				
Fork length (mm)	(129; 136; 182)	(130; 141; 169)	(131; 172; 202)	(130; 149; 163)
Mass (g)	(17.3; 23.9; 54.6)	(19.8; 26.1; 43.9)	(31.1; 45.6; 67.5)	(24.7; 37.0; 50.1)
Tag burden (%)	(3.66, 8.38; 11.56)	(4.56; 7.66; 10.10)	(2.96; 4.38; 6.43)	(3.99; 5.41; 8.10)
Number of individual fish detected (detections inferred from a predator fish inducing bias in relation to total tags inferred ingested by a predator and inducing bias)				
At release	32	29	29	29
At Cassilis	26 (0 of 4)	22 (0 of 4)	13 (0 of 2)	23 (0 of 4)
At Nelson	20 (2 of 4)	17 (3 of 4)	10 (1 of 2)	18 (2 of 4)
At Loggieville	16 (4 of 4)	16 (4 of 4)	10 (2 of 2)	17 (4 of 4)
At Outer Bay	8 (1 of 4)	9 (1 of 4)	4 (0 of 2)	10 (0 of 4)
At Strait of Belle Isle	3 (0 of 4)	5 (0 of 4)	1 (0 of 2)	6 (0 of 4)
At Strait of Belle Isle North	1 (0 of 4)	3 (0 of 4)	1 (0 of 2)	7 (0 of 4)

Table 2. The probability of survival and migration speed (Km/day) of day- and night-released treatments between each gate (head of tide= HoT; the intersection of the Northwest Miramichi River and the main stem of the Miramichi River= Nelson; the entrance into the Miramichi Bay= Inner Bay; the exit of the Miramichi Bay= Outer Bay; Strait of Belle Isle= SoBI) and cumulative survival from release to SoBI.

		Survival (mean; 95% CI)		Migration speed (mean±SD; n)	
Gate	Distance (km)	Day-released	Night-released	Day-released	Night-released
Release-HoT	48.8	0.817; 0.660-0.940	0.759; 0.579-0.906	9.96±3.03; 22	11.63±4.86; 18
HoT-Nelson	21.2	0.668; 0.470-0.838	0.654; 0.440-0.838	21.68±12.00; 15	15.30±11.83; 12
Nelson-Inner Bay	17.3	0.910; 0.734-0.996	0.931; 0.766-0.998	39.95±31.78; 13	51.82±37.01; 13
Inner Bay-Outer Bay	27	0.592; 0.327-0.867	0.666; 0.393-0.923	24.61±12.16; 6	28.89±12.59; 8
Outer Bay-SoBI	785	0.566; 0.217-0.937	0.646; 0.302-0.960	16.26±0.86; 3	16.37±1.13; 5
Release-SoBI	899.3	0.164; 0.054-0.326	0.197; 0.074-0.366	NA	NA

Table 3. Survival odds ratio of tagged Atlantic Salmon smolts from release to exit of Miramichi Bay and from the head of tide (HoT) area to exit of Miramichi Bay for three treatments.

		Odds ratio of survival	
Experimental effect	Treatment comparison	Release to Outer Bay median; (5^{th} to 95^{th} percentile); prob. <= 1)	HoT to Outer Bay median; (5^{th} to 95^{th} percentile); prob. <= 1)
	Winter hatchery tagged relative to spring wild tagged	1.38; (0.86 to 2.18); p = 0.13	1.34 (0.85 to 2.06) p = 0.14
Tagging effect	Winter hatchery tagged relative to spring hatchery tagged	2.53 (1.39 to 5.13) p = 0.01	1.47 (0.89 to 2.79) p = 0.11
Hatchery effect	Spring wild tagged relative to spring hatchery tagged	1.83 (1.01 to 3.71) p = 0.05	1.10 (0.66 to 2.08) p = 0.39

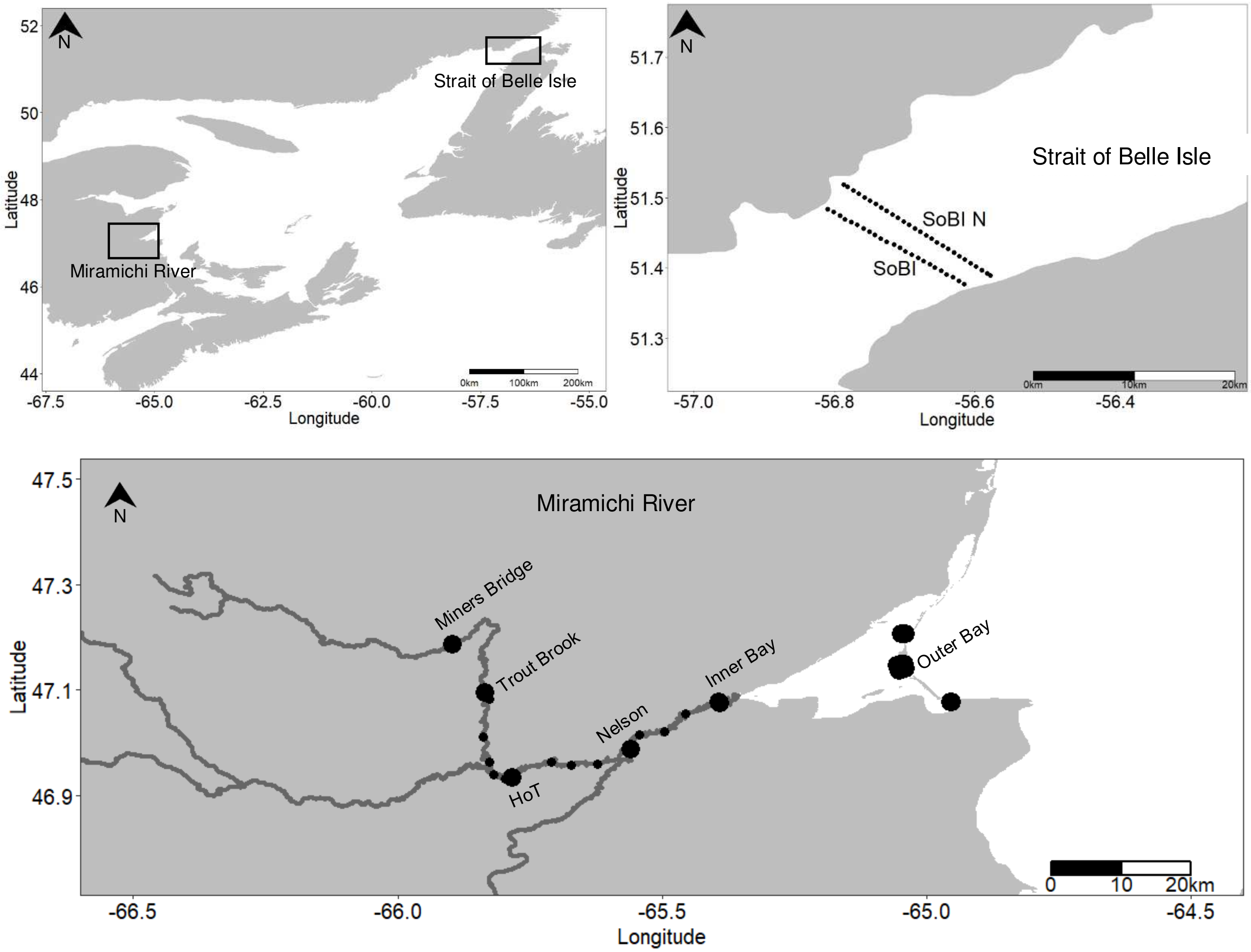


Figure 1. Map of capture/release sites and receiver gate locations in the Northwest Miramichi River, the Miramichi River and Bay, and the Strait of Belle Isle. The capture of pre-smolt occurred at both Miners Bridge and Trout Brook, whereas smolt capture in the spring only occurred at Trout Brook. All fish were released at Miners Bridge. Receiver gates were placed at the head of tide (HoT), the intersection of the Northwest Miramichi River and the main stem of the Miramichi River (Nelson), the entrance into the Miramichi Bay (Inner Bay), the exit of the Miramichi Bay (Outer Bay), and the Strait of Belle Isle (SoBI and SoBI N). Smaller circles in

the Miramichi River denote receiver locations where survival was not quantified but were used to discern between Striped Bass and smolt movement patterns.

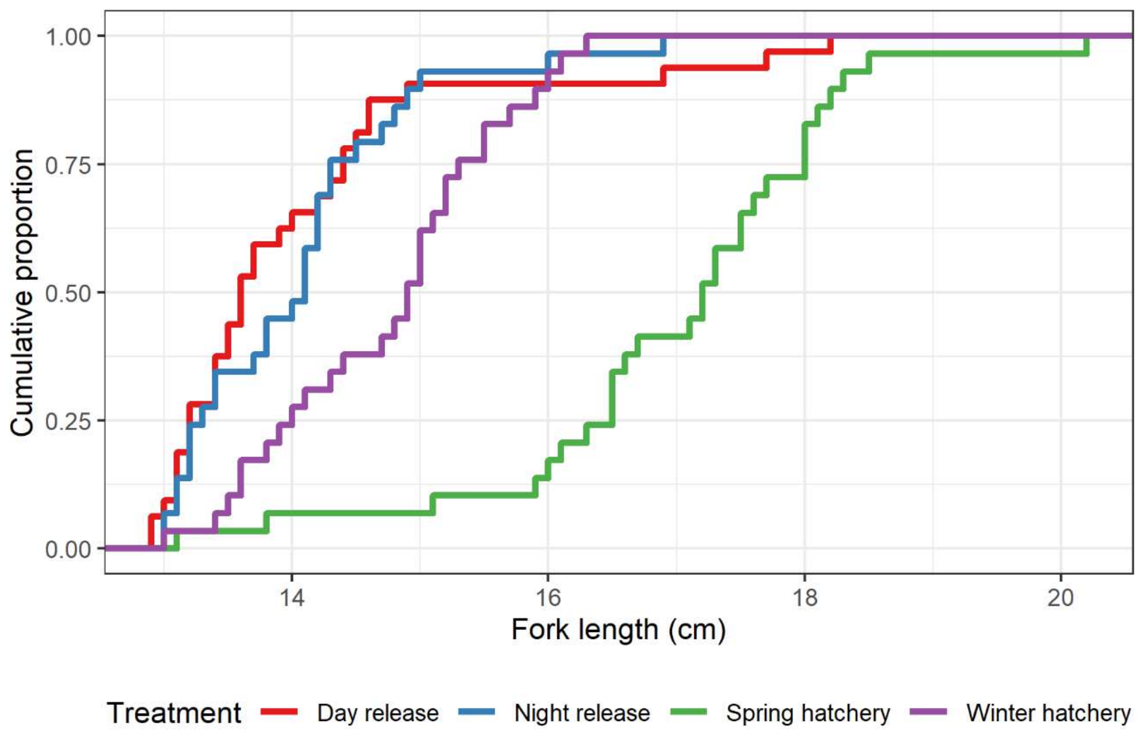


Figure 2. Cumulative distribution of Atlantic Salmon smolt fork lengths (cm) at time of tagging for the three treatment groups. Day release and night release represent the wild spring tagging group.

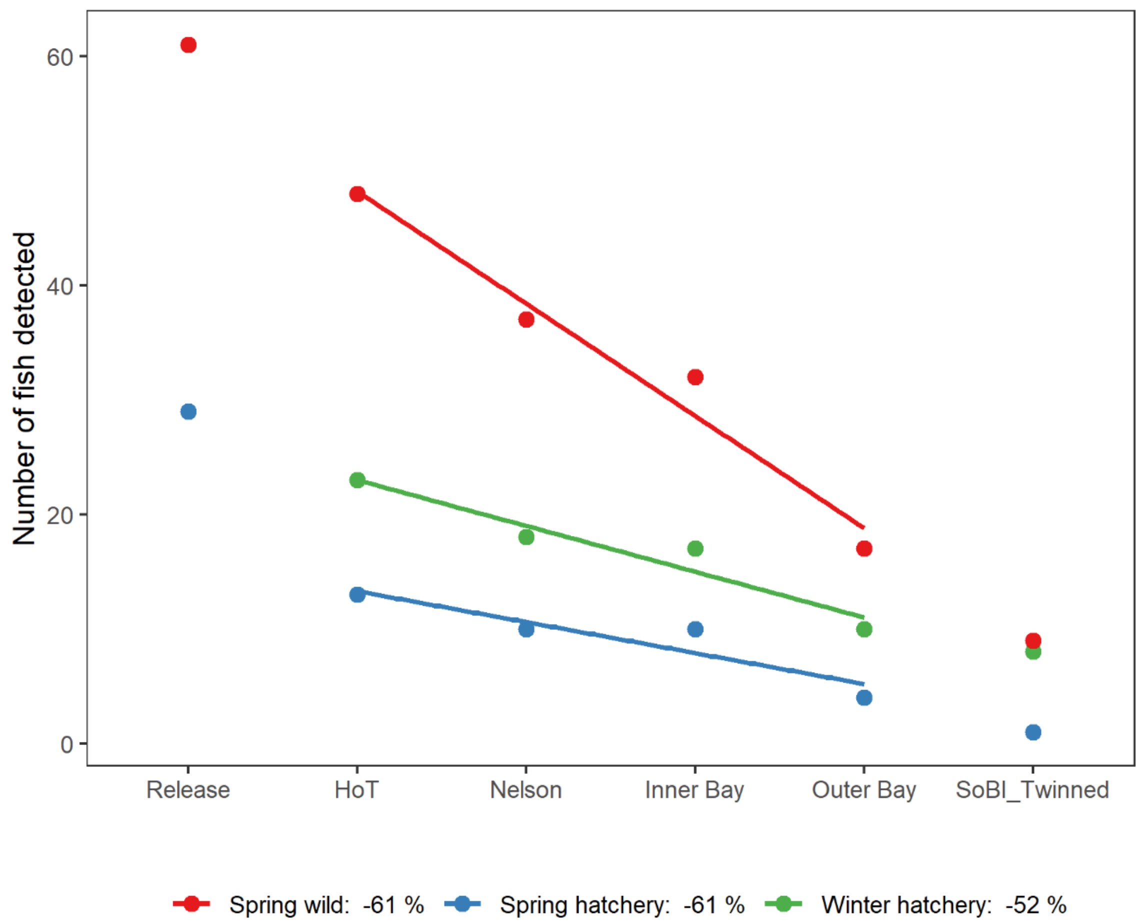


Figure 3. Detections of individual unique tags by receiver gate and treatment. The linear trend line of tag detections is shown for the zone from the head of tide (HoT) to the outer bay array and the percent change in detections between the HoT and outer bay array by treatment is shown in the legend. SoBI_Twinned refers to the number of unique tags detected at the combined Southern and Northern SoBI receiver gate.

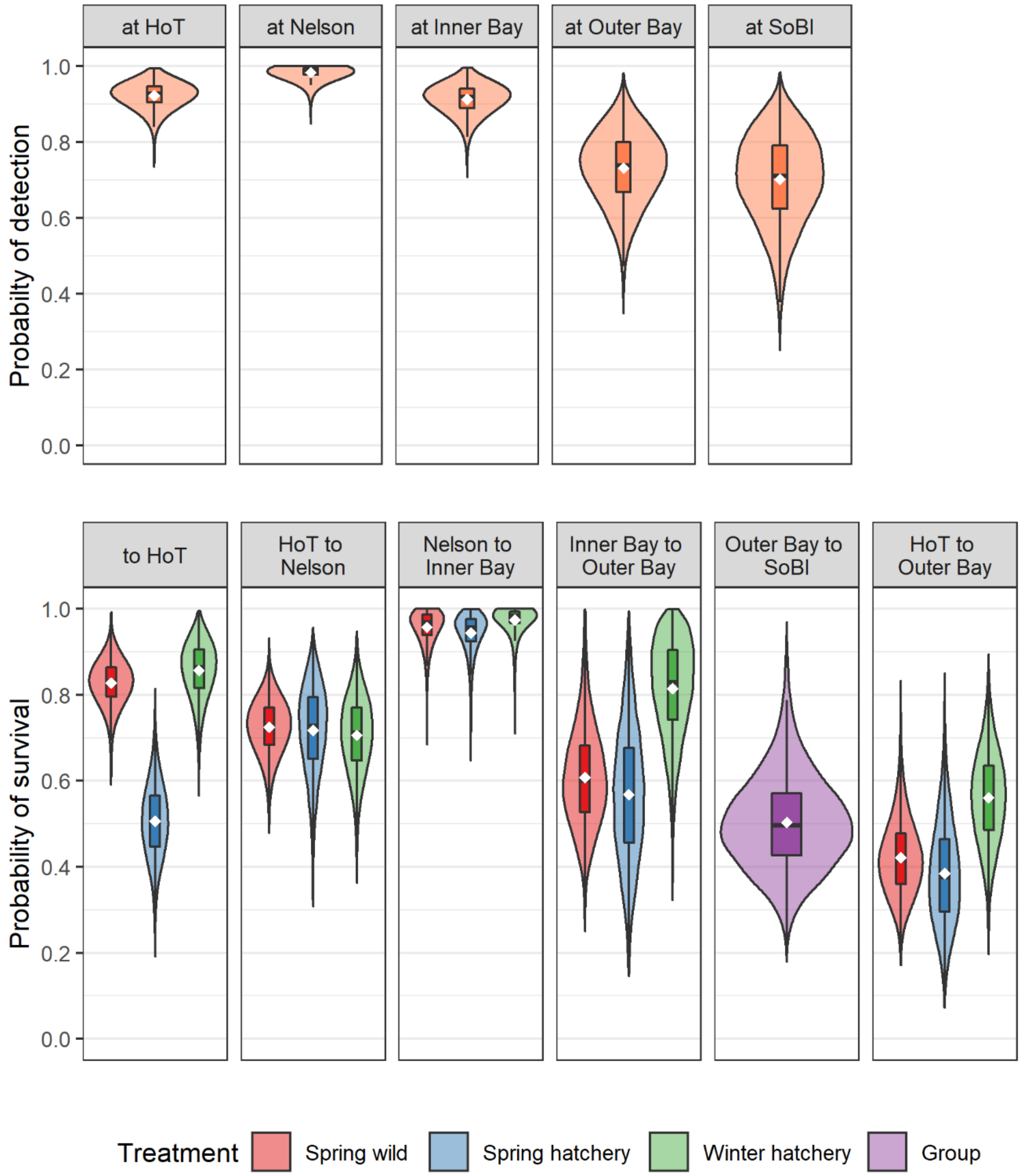


Figure 4. Posterior distributions of probability of detection at (top row) and probability of survival between (bottom row) gates and cumulative survival through the estuary and bay (HoT to Outer Bay). White symbols in the violin plots are the mean whereas the internal rectangle and dash are the interquartile range and median, respectively.

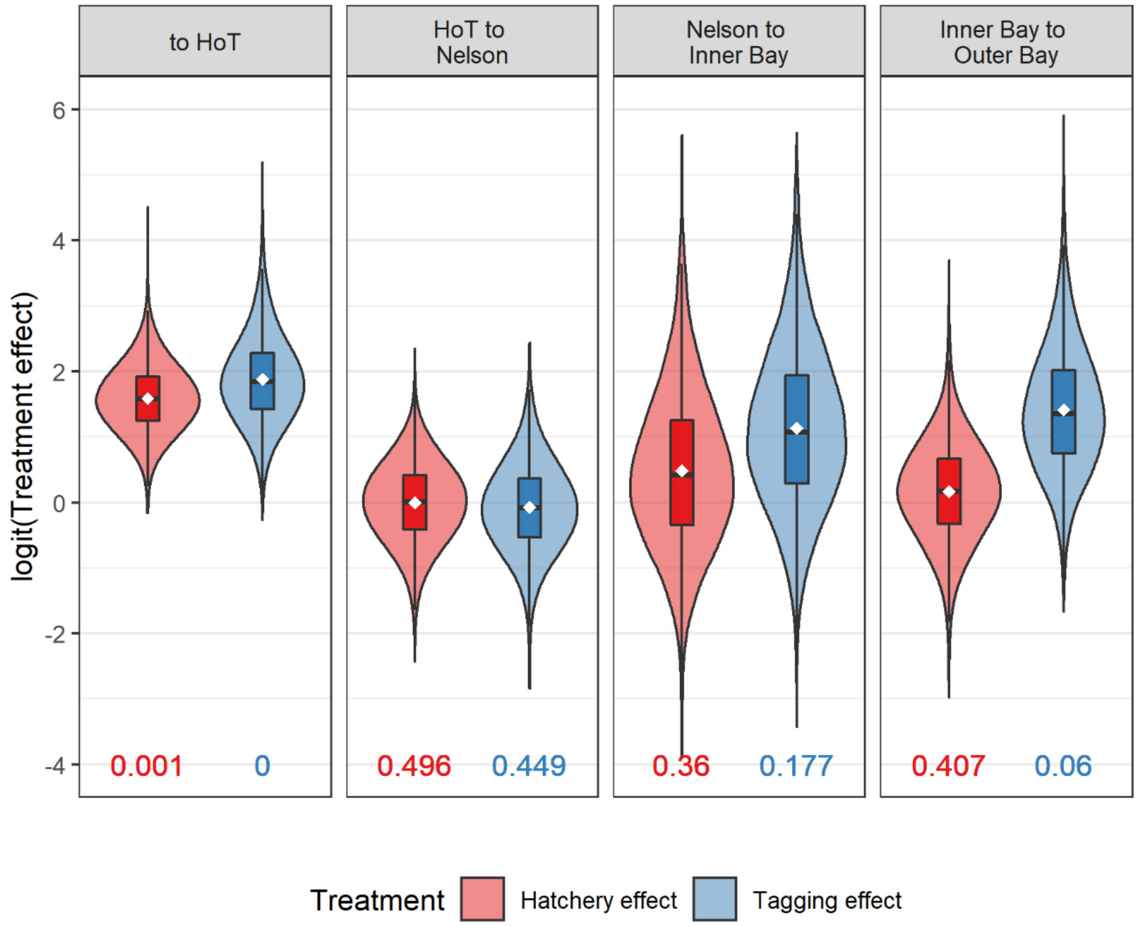


Figure 5. Inferred effect size on the logit scale of differences in survival rates relative to the reference treatment (spring hatchery) for spring wild tagged and winter hatchery tagged smolts by zone within the Miramichi River and bay. Violin plots are interpreted as in Figure 4. The p-values for the treatment effect by zone are shown under each violin plot.

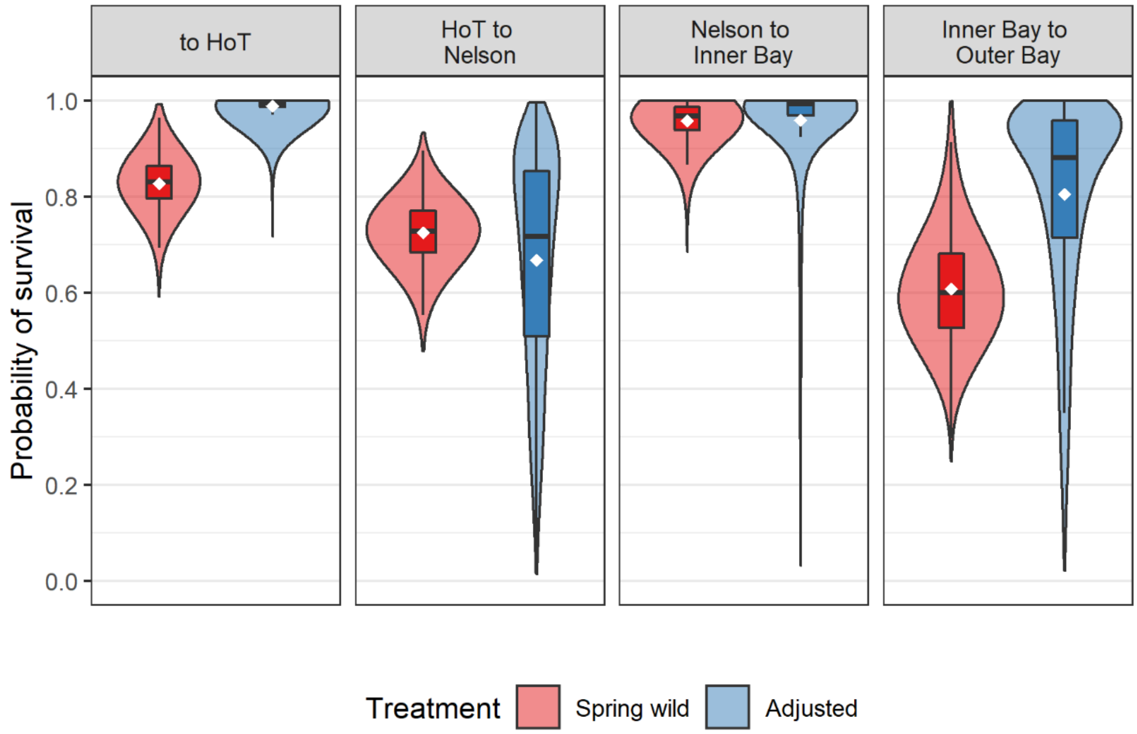


Figure 6. Posterior distributions of estimated probability of survival between gates for the spring wild treatment and the adjusted survival of spring wild treatment after correcting for hatchery and post recovery time effects. Violin plots are interpreted as in Figure 4.

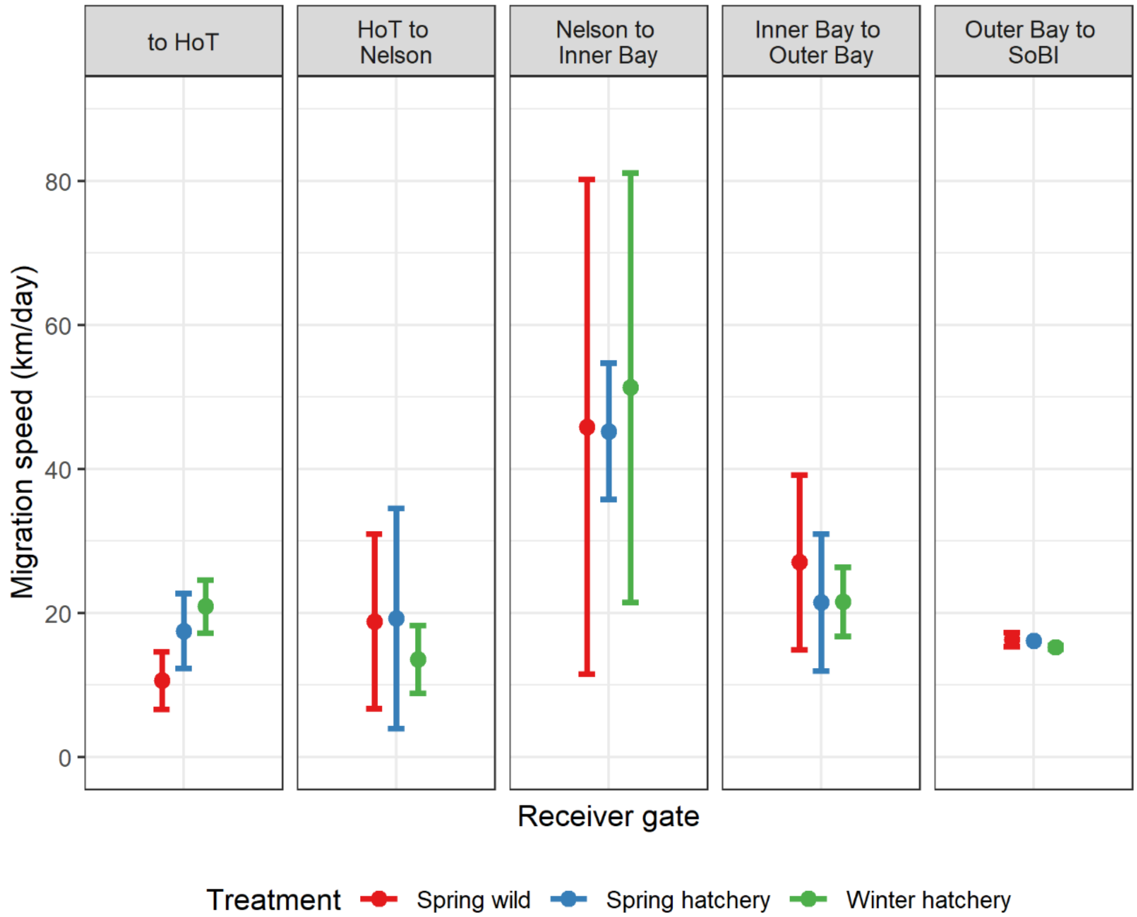


Figure 7. Mean and standard deviation of migration speed (km per day) of Atlantic Salmon smolts in three treatment groups between five receiver gates

Supplementary Material

<u>Additional details on receiver deployment and retrieval</u>

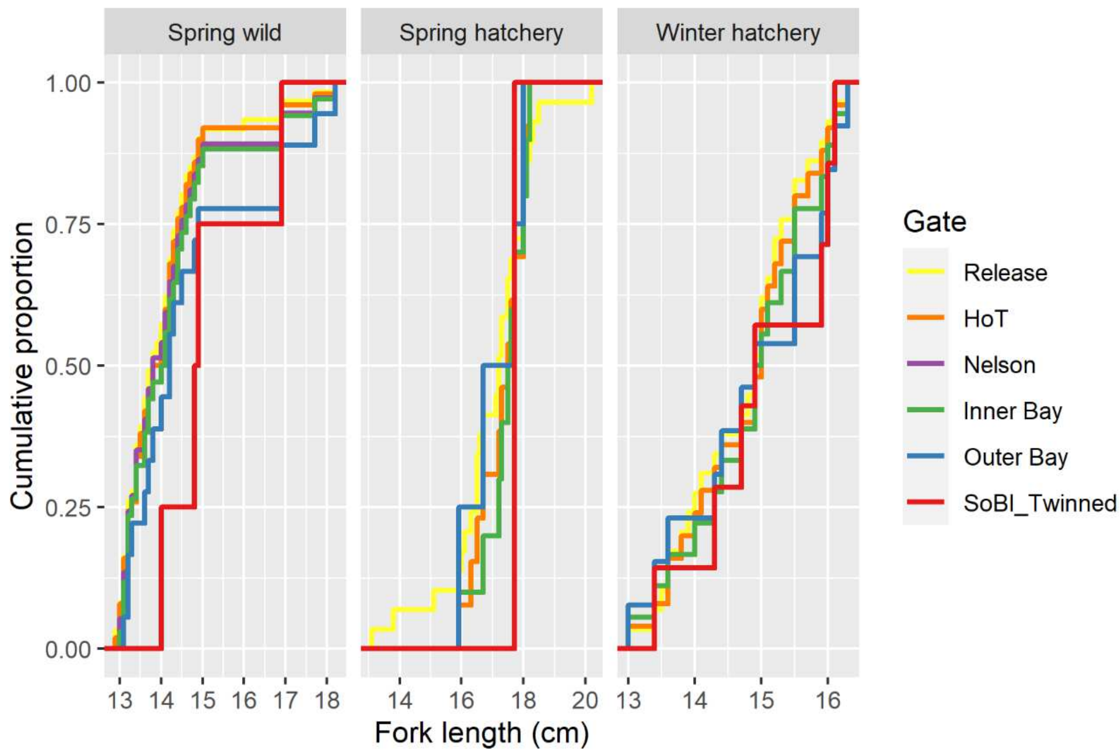
Receivers were attached to moorings consisting of varying anchor weights, line and surface floats depending on current and possible surface conditions. Sinking line was used from the surface floats to a nylon swivel located below the receiver, which in turn was attached to the anchor with floating line. In shallow reaches, receivers were attached $\approx$ 1 m below the surface floats whereas moorings in deeper sections of river had receivers attached $\approx$ 4 m below the surface floats. Both SoBI and SoBI N receivers were attached 10 m below the surface floats.

HoT, Nelson and Inner Bay gates were deployed on April 25 to 26, 2016, the Outer Bay gate on May 1, 2016 and SoBI on June 16, 2016. To ensure no data loss, receiver data were downloaded at HoT, Nelson and Inner Bay gates on June 22, 2016 and the Outer Bay gate on June 23, 2016. No mid-season download was undertaken for SoBI or SoBI N gates. Receivers were recovered in August and September, 2016 once the migration was completed.

A total of seven receivers were never recovered, three within the Outer Bay gate, two within the SoBI gate and two within the SoBI N gate. The three lost receivers within the Outer Bay were downloaded on June 23, 2016 and since the last smolt to pass any Outer Bay receiver occurred on June 5, 2016, it is likely that no smolt were undetected due to the unrecovered receivers. However, the SoBI and SoBI N missing receivers were never downloaded mid-season and therefore smolt were more likely to have passed undetected, and thus, lowered the probability of detection for these gates (see “Statistical analyses”).

Effect of size of smolts at tagging on subsequent detections.

The figure shows the cumulative distribution, based on fork length at time of tagging, of detected tags at each of the receiver lines. There is evidence of a size bias for the spring hatchery tag group with the few smolts less than 16 cm not detected post release and only smolts generally > 17 cm being detected at other downstream estuary arrays.



Figures

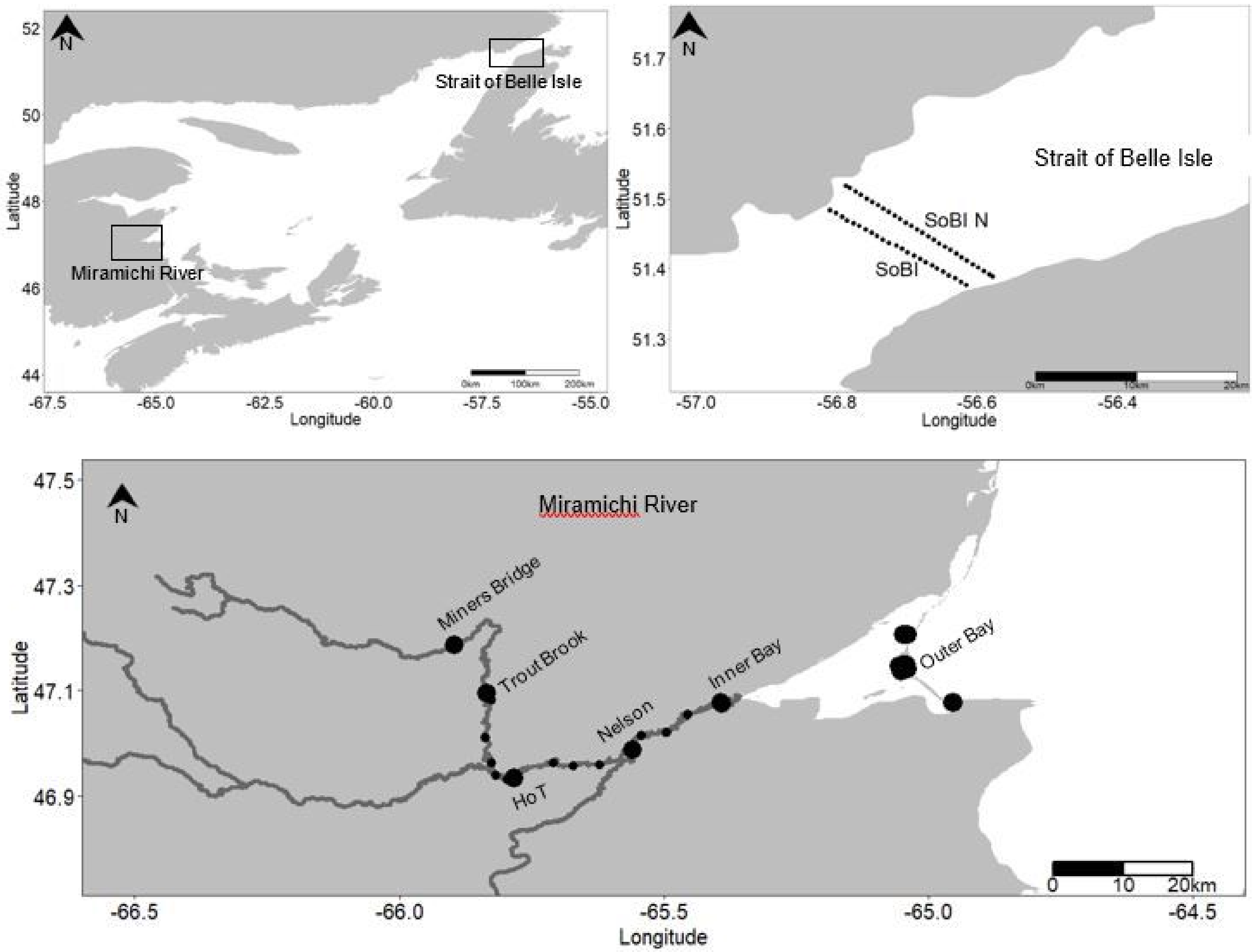


Figure 1

Map of capture/release sites and receiver gate locations in the Northwest Miramichi River, the Miramichi River and Bay, and the Strait of Belle Isle. The capture of pre-smolt occurred at both Miners Bridge and Trout Brook, whereas smolt capture in the spring only occurred at Trout Brook. All fish were released at Miners Bridge. Receiver gates were placed at the head of tide (HoT), the intersection of the Northwest Miramichi River and the main stem of the Miramichi River (Nelson), the entrance into the Miramichi Bay (Inner Bay), the exit of the Miramichi Bay (Outer Bay), and the Strait of Belle Isle (SoBI and SoBI N). Smaller circles in the Miramichi River denote receiver locations where survival was not quantified but were used to discern between Striped Bass and smolt movement patterns. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

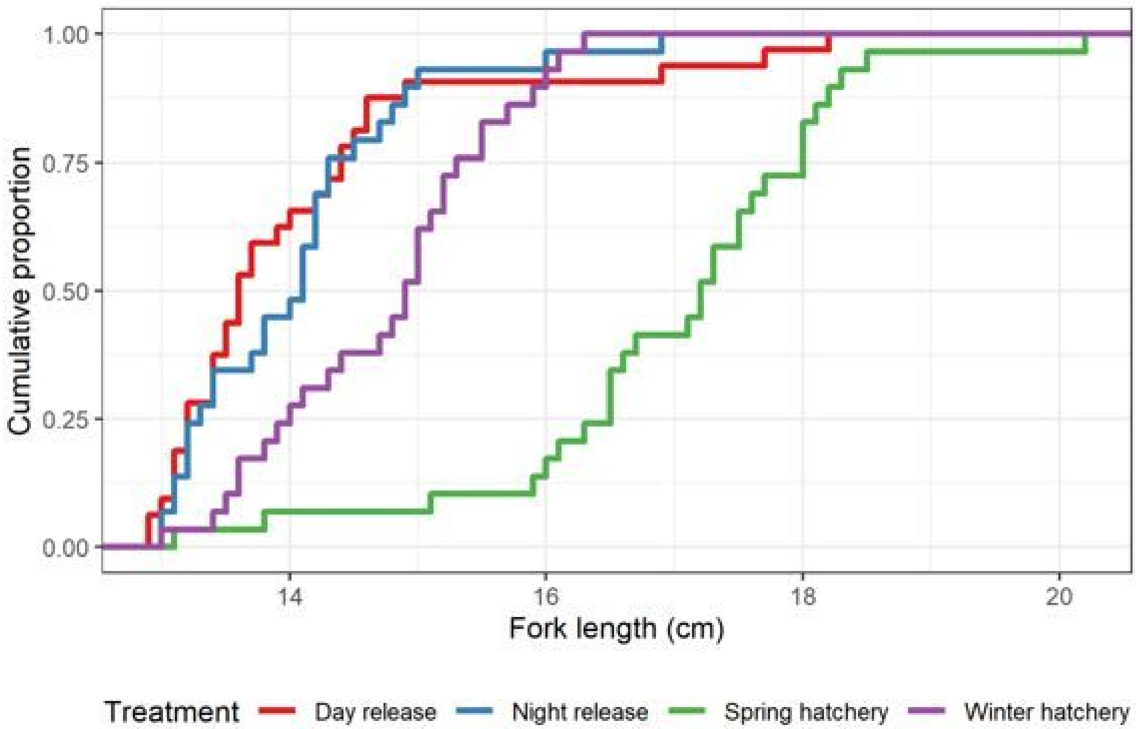


Figure 2

Cumulative distribution of Atlantic Salmon smolt fork lengths (cm) at time of tagging for the three treatment groups. Day release and night release represent the wild spring tagging group.

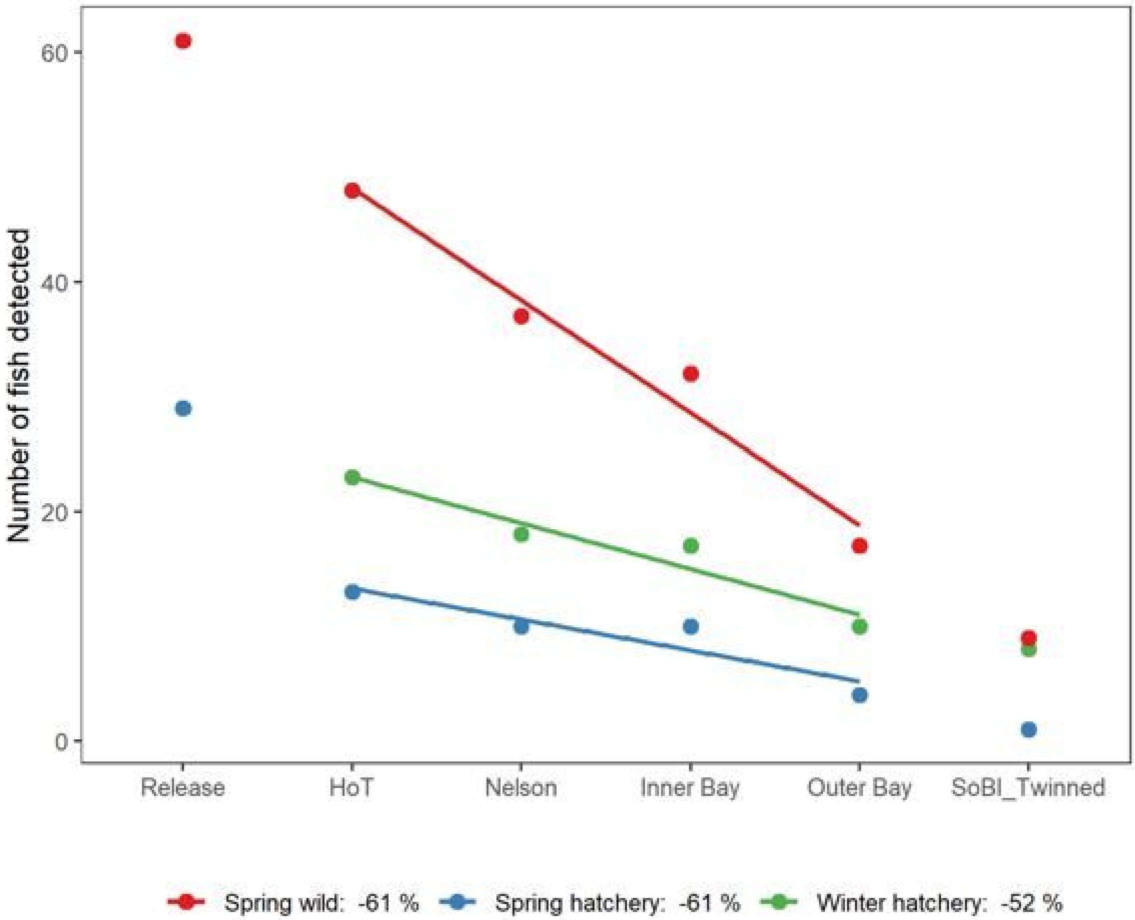


Figure 3

Detections of individual unique tags by receiver gate and treatment. The linear trend line of tag detections is shown for the zone from the head of tide (HoT) to the outer bay array and the percent change in detections between the HoT and outer bay array by treatment is shown in the legend. SoBI_Twinned refers to the number of unique tags detected at the combined Southern and Northern SoBI receiver gate.

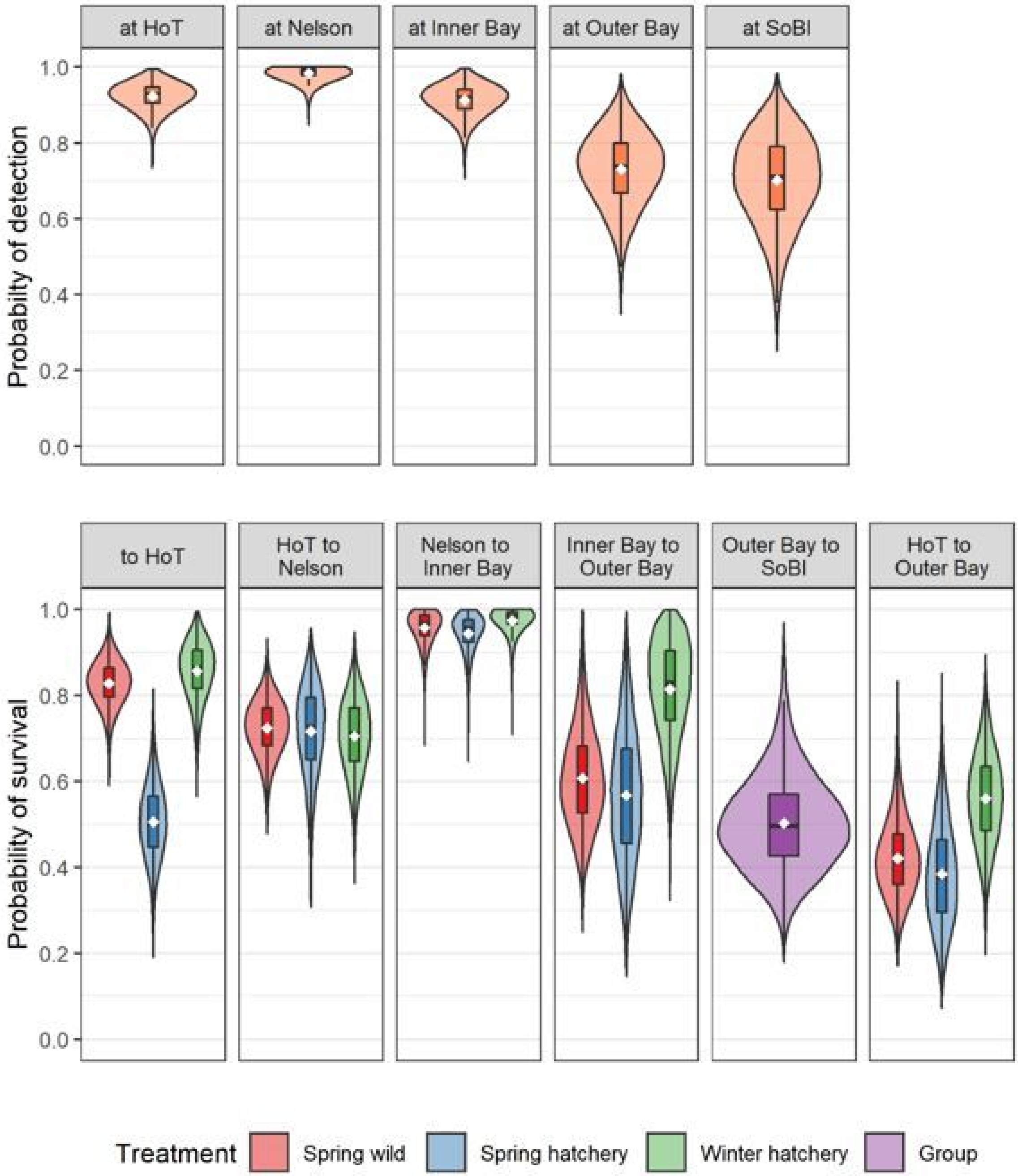


Figure 4

Posterior distributions of probability of detection at (top row) and probability of survival between (bottom row) gates and cumulative survival through the estuary and bay (HoT to Outer Bay). White symbols in the violin plots are the mean whereas the internal rectangle and dash are the interquartile range and median, respectively.

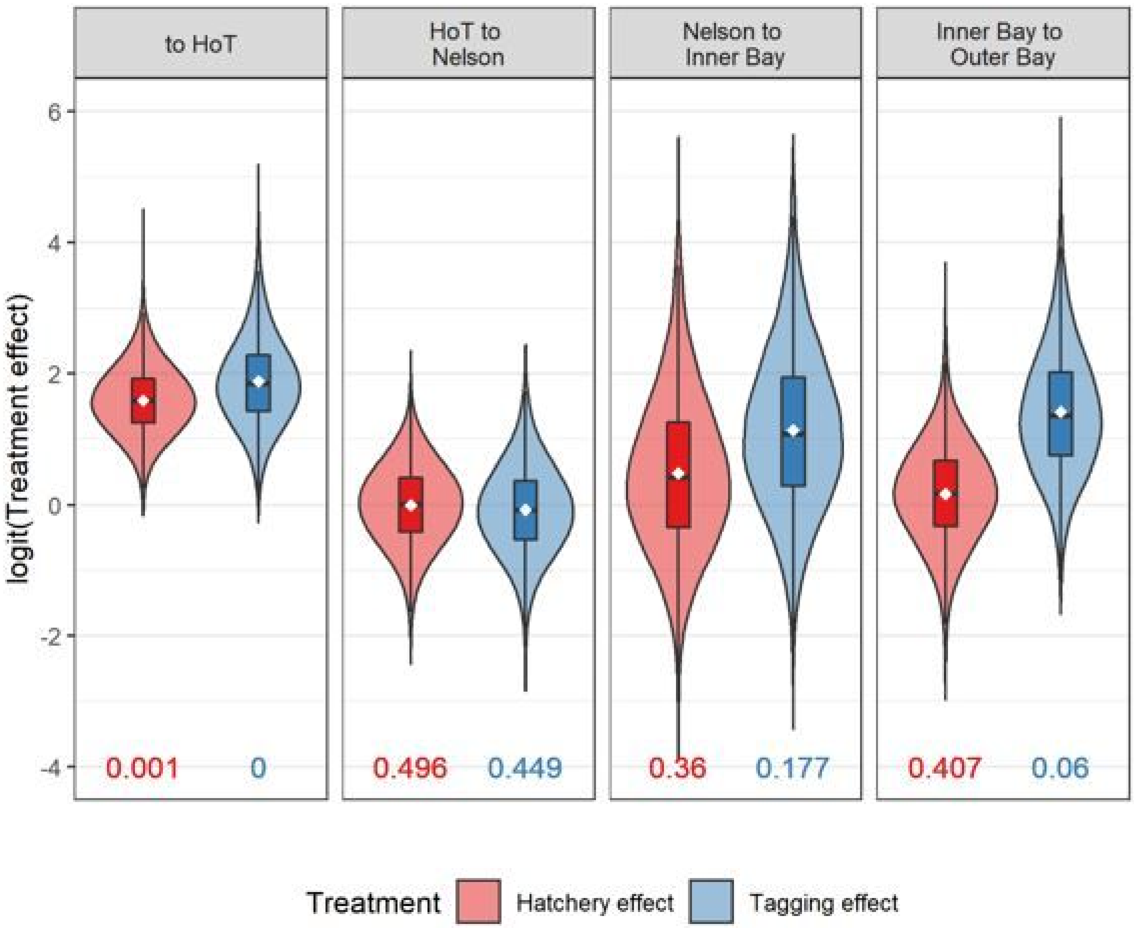


Figure 5

Inferred effect size on the logit scale of differences in survival rates relative to the reference treatment (spring hatchery) for spring wild tagged and winter hatchery tagged smolts by zone within the Miramichi River and bay. Violin plots are interpreted as in Figure 4. The p-values for the treatment effect by zone are shown under each violin plot.

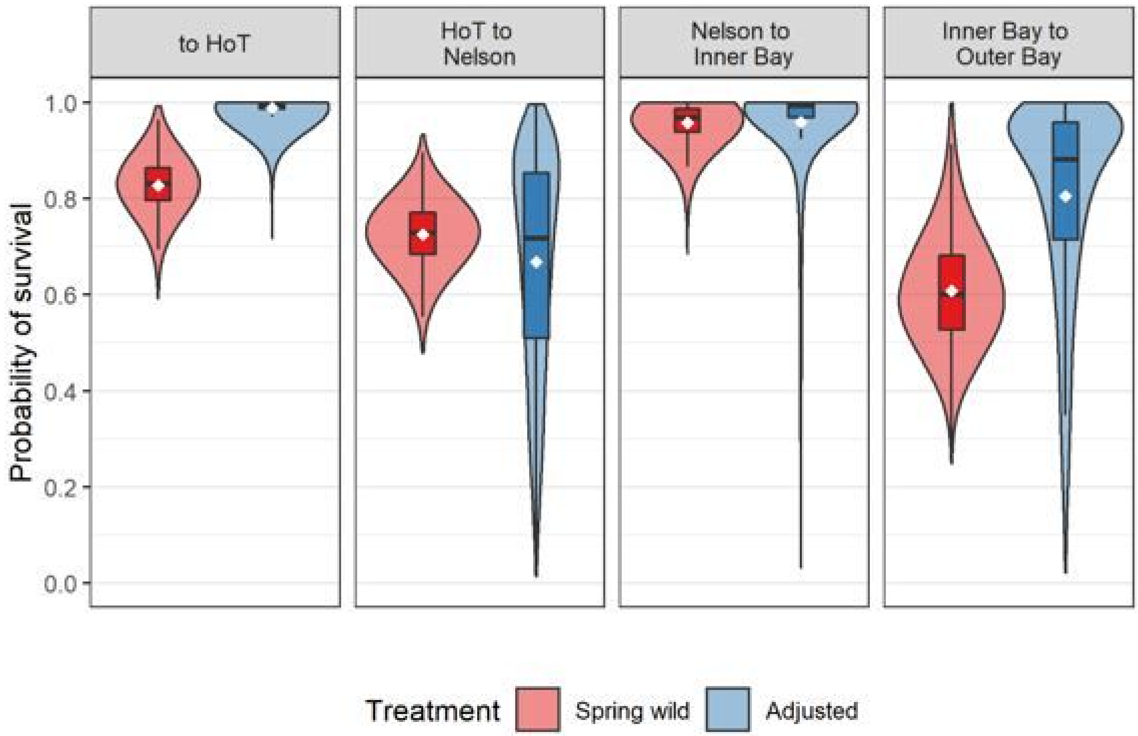


Figure 6

Posterior distributions of estimated probability of survival between gates for the spring wild treatment and the adjusted survival of spring wild treatment after correcting for hatchery and post recovery time effects. Violin plots are interpreted as in Figure 4.

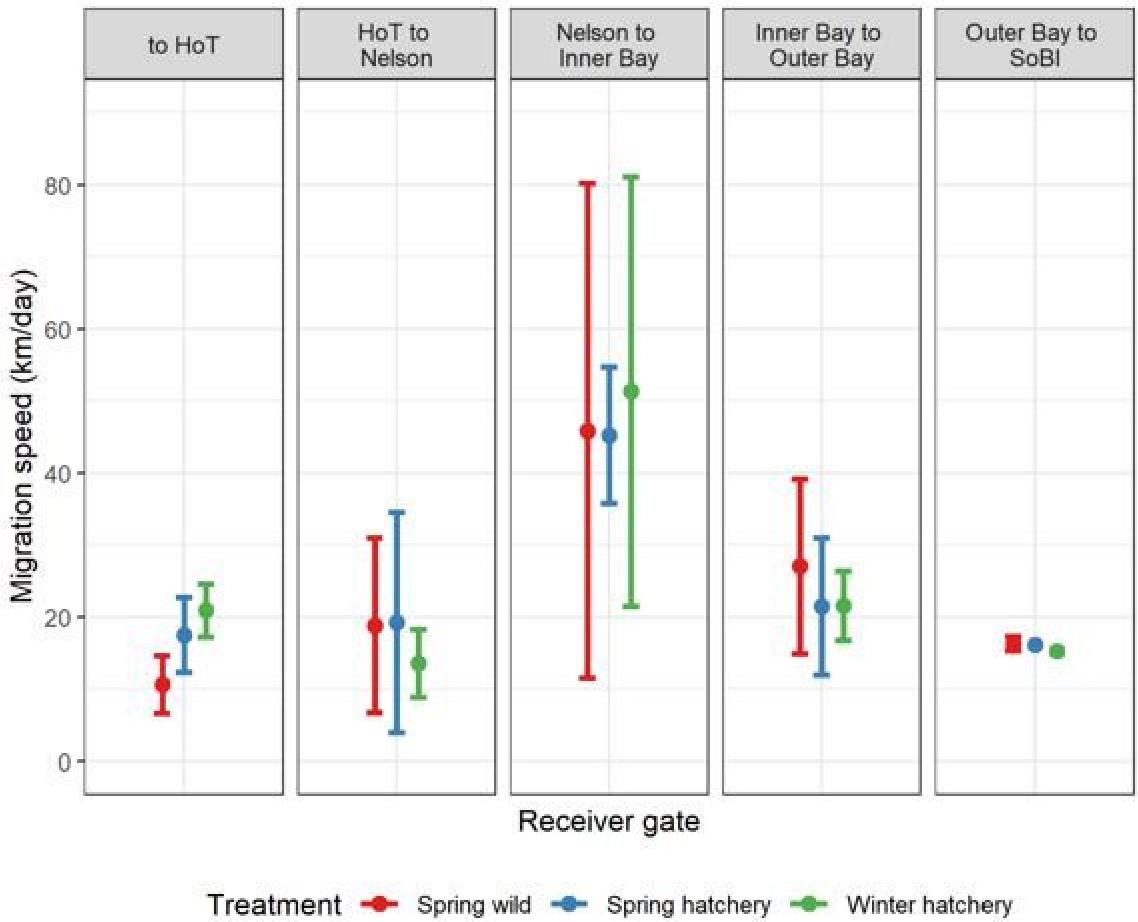


Figure 7

Mean and standard deviation of migration speed (km per day) of Atlantic Salmon smolts in three treatment groups between five receiver gates