NRC Research Press

ARTICLE

Biologging in combination with biotelemetry reveals behavior of Atlantic salmon following exposure to capture and handling stressors

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Abstract: We investigated the response of Atlantic salmon (*Salmo salar*) to capture and handling stressors by analyzing fine-scale locomotor activity using accelerometer data loggers and broader-scale movements by tracking migration with radiotelemetry. Half the sample population was exposed to experimental exercise and air exposure and released with a control group to simulate fisheries handling. All but two of the surviving fish (both in the treatment group) returned to the counting fence to resume the 2016 spawning migration (survival = 86%–91%). There were no differences in postrelease locomotor activity, measured by an index of total body action (jerk), between control and treatment salmon ($p = 0.81$). Comparison of mean time to return to the counting fence against a null model revealed that treatment salmon were significantly delayed in returning to the counting fence ($p < 0.01$), whereas control fish were not ($p = 0.24$). Both the abiotic environment and human interactions influenced locomotor activity of the migratory fish and synchrony of the migration with untreated conspecifics.

Résumé : Nous avons étudié la réaction des saumons atlantiques (*Salmo salar*) à des stresseurs associés à la capture et à la manipulation par l'analyse de l'activité locomotrice fine en utilisant des enregistreurs de données d'accéléromètre et des déplacements à plus grande échelle en suivant la migration par radiotélémétrie. La moitié de la population étudiée a été exposée à l'exercice expérimental et à l'air et relâchée avec un groupe témoin afin de simuler la manipulation associée à la pêche. Tous les poissons ayant survécu sauf deux (tous deux dans le groupe traité) sont retournés à la barrière de dénombrement pour reprendre la migration de frai de 2016 (taux de survie = 86 %–91 %). Il n'y avait pas de différence sur le plan de l'activité locomotrice après le lâcher, mesurée par un indice de l'action corporelle totale (saccade), entre les saumons témoins et les saumons traités (p = 0,81). La comparaison du temps moyen avant le retour à un modèle nul révèle que le retour des saumons traités à la barrière de dénombrement était significativement retardé (p < 0,01), alors que celui des poissons témoins de l'était pas (p = 0,24). Le milieu abiotique et les interactions avec les humains ont tous deux influencé l'activité locomotrice des poissons migrateurs et la synchronisation de la migration avec celle de conspécifiques non traités. [Traduit par la Rédaction]

Introduction

Migration is a large-scale (relative to the size of a given animal) synchronized movement of animals across a landscape between habitats, which allows them to optimize lifetime reproductive potential by exploiting multiple habitats (Dingle and Drake 2007). Timing and synchronicity of migration are critical to success, because animals must reach the correct location at the correct time with enough energy (Alves et al. 2013; Freshwater et al. 2019). To migrate, animals may undergo extensive physiological remodelling of the organs or physical traits and then confront further disturbances that disrupt navigation, delay progress and arrival time, or deplete energy (Lennox et al. 2016*a*). Migrants may be vulnerable or tolerant to stressors, and there is variation in this response among and within species and populations (Wilcove and Wikelski 2008; Robinson et al. 2009; Lennox et al. 2016*a*).

Natural (e.g., warm water temperature, low flow) and anthropogenic (e.g., dams, fisheries) stressors exist in the migratory arena, and it is crucial to understand how these factors operate and interact with wild animals (Cooke et al. 2006; Wilcove and Wikelski 2008; Lennox et al. 2016*a*). Elevated stress can distract energy from critical systems and can enhance the probability of contracting disease or suffering premature mortality (Altizer et al. 2011; Hinch et al. 2012). For example, warm temperature can delay migration (Baisez et al. 2011), enhance capture stress (Dempson et al. 2002; Gale et al. 2013; Lennox et al. 2017), influence obstacle passage (Booth et al. 1997; Gowans et al. 1999), and contribute to premature mortality by collapsing aerobic scope (Farrell et al. 2008; Eliason et al. 2011). Monitoring animals using electronic tags has assisted with revealing mechanistic ecological relationships in the wild, including important details about migration biology (Kays et al. 2015; Hussey et al. 2015). Studies of migratory salmonids have linked anthropogenic stressors to the progress towards spawning habitat relative to the release location (Lennox et al. 2017), fallback distance away from the release location (Mäkinen et al. 2000; Havn et al. 2015), total migration distance (Lennox et al. 2015), or spawning position (Lennox et al. 2016*b*).

Received 4 December 2018. Accepted 3 March 2019.

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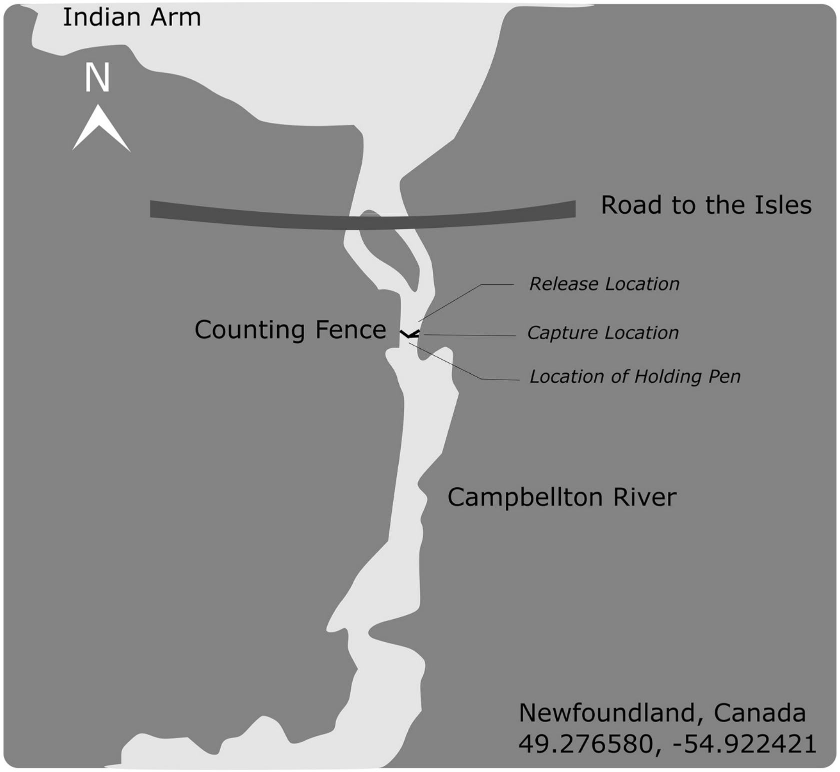
Can. J. Fish. Aquat. Sci. **76**: 2176–2183 (2019) dx.doi.org/10.1139/cjfas-2018-0477

Fig. 1. Map of the experimental area used to investigate migrations of Atlantic salmon (*Salmo salar*) in the Campbellton River, Newfoundland. Salmon were captured in the counting fence trap on 8 and 9 July, treated, tagged, and released below the trap on 9 and 10 July, and monitored within the arena by radiotelemetry for 1 week and at counting fence trap until 6 September 2016. Searching with the radio receiver was conducted within the entire area below the counting fence within the river and along the right side of the peninsula out to the estuary (see Fig. 2 for detections).



Costs of exposure to stressors may be observed or inferred when an individual's capacity to reach spawning territory at the appropriate time is inhibited or when excessive energetic costs are imposed (e.g., Cooke et al. 2006; Richard et al. 2013). At finer scales, such investigations are lacking, however, and experimental approaches to determine the extent to which migrants are impacted by disturbance would benefit from more fine-scale observations of individuals exposed to stressors, which may be acute but transient.

Combining biotelemetry with biologging tags equipped to measure the individual's environment, physiology, or fine-scale behaviour reveals context for the broader-scale movements observed with biotelemetry (Cooke et al. 2016). Tri-axial accelerometer biologgers record the position of an animal in three-dimensional space at a very fine scale to remotely observe flying, walking, and swimming (Brown et al. 2013). Accelerometers recording at <1 Hz can be used to measure the individual activity, which can be applied to relate fine-scale behaviour to individual or environmental metrics (e.g., Wang et al. 2015; Shamoun-Baranes et al. 2016; Gutowsky et al. 2017). These tools have been used to provide insight into the postrelease condition and fate of fish released from fisheries (Brownscombe et al. 2013; Whitney et al. 2016; Lennox et al. 2018*a*). In combination, biotelemetry and biologging offer the potential to quantify physiology and behaviour of animals at multiple scales and can assist with interpreting the status and changes over time of free-ranging animals exposed to stressors (Donaldson et al. 2008).

Our study applied both biotelemetry and biologging tools to investigate Atlantic salmon (*Salmo salar*) migration in the context of experimental capture and handling stressors to fish freely migrating soon after entering fresh water. Atlantic salmon is an anadromous migrant that normally makes rapid progress upriver towards the spawning destination and will hold for weeks or months before reproduction (Økland et al. 2001; Klemetsen et al. 2003; Richard et al. 2014). Migrants are exposed to stressors such as drought or warm water temperatures (Alabaster 1990; Baisez et al. 2011) or by human interventions such as pollution (Thorstad et al. 2005), obstructions (Gowans et al. 1999; Croze 2008), or fisheries (Mäkinen et al. 2000; Thorstad et al. 2003). A river with an impermeable fish counting fence provided a site to observe experimental animals and monitor migration. We predicted transient reductions to locomotor activity and delayed upriver progress of salmon exposed to simulated catch-and-release fisheries interactions during their migration.

Methods

Study site

We collected Atlantic salmon from the Campbellton River, Newfoundland, Canada. The Campbellton River is ~40 km long and drains ~296 km² into Indian Arm, Notre Dame Bay, near the community of Campbellton, Newfoundland and Labrador. The Campbellton River is one of the most popular fishing rivers among Atlantic salmon anglers in Newfoundland (Downton et al. 2001). The wild stock returning to the Campbellton River has been enumerated annually by a Fisheries and Oceans Canada (DFO) counting fence about 345 m from the river mouth (49.276681°N, 54.922011°W; Fig. 1; Downton et al. 2001; Veinott et al. 2018). The fence prevents fish from passing upriver until salmon ascending the river are manually counted in the facility's trap and then passed upriver. Respective counts of adult salmon from 2014 to 2016 were 4055, 4016, and 2748 individuals of predominantly one sea winter (Veinott et al. 2018).

Experimental treatments

Salmon were collected from the trap at the counting fence the day before experimentation (8 or 9 July 2016) and held overnight in an in-river flow-through holding pen. Overnight holding likely stimulated a stress response from the fish (Portz et al. 2006); however, this was consistent for both treatment and control fish. On 9 and 10 July, salmon were dip-netted from the holding pen and transported in a water-filled container approximately 20 m to a circular experimental arena filled with ambient water at the start of each trial. Fish were assigned to one of two groups, either a treatment group that simulated a generalized fisheries stressor that simulated the swimming to exhaustion and air exposure that could be associated with capture in a net or angling ($N = 21$; mean ± standard deviation (SD) fish length 54.2 ± 2.6 cm fork length, FL) or a control group ($N = 18$; 54.1 ± 2.6 cm FL). The fisheries stressor involved a chase to exhaustion (74 ± 29 s) followed by an air exposure of 10 s (Cooke et al. 2013). Animals were then tagged with an accelerometer and a radio tag following the stressor and released. Control fish were transferred to the experimental arena but were not exposed to exhaustive exercise prior to inserting the gastric radio tag and attaching the accelerometer (see below). Exhaustion of treatment-group animals was characterized as cessation of burst swimming in response to chasing. Exhaustion times were shorter than the exhaustion times normally recorded for salmon in this size range being captured by anglers (Lennox et al. 2017). Salmon in the control group were only tagged and were not chased or air-exposed. All fish were released into the river approximately 3 m below the fish trap into a holding pool.

During the study period, the trap operated from 8 June to 6 September continuously during the day and was monitored for the presence of experimental fish by closed circuit video camera (0700–1800). Members of the science team could then ensure they were present during fence operations to retrieve tags. Water temperature during the experiment averaged 18.9 ± 1.3 °C.

Tagging and tracking

All salmon in both the control and treatment groups were externally tagged with an accelerometer data logger (55 mm × 17 mm, 28 g in air, 50 Hz, 10-bit resolution, ±8 g_0; Maritime bioLoggers, Halifax, Nova Scotia) waterproofed with a plastic rubber coating (Performix Brand Plasti-Dip, Blaine, Minnesota, USA, additional 0.10 g). Accelerometers were affixed with steel wire by passing two hypodermic needles through the dorsal musculature behind the dorsal fin. To confirm the fates of released fish, radio-transmitting tags (Sigma 8, Newmarket, Ontario, Canada) were inserted into the stomach with the antenna protruding out the mouth, which were used to track the position of fish in the river following release and to recover accelerometer tags from any mortalities in the river. No anaesthetic was used. All animal handling was approved by the Carleton University Animal Care Committee.

The fish's return migration to the counting fence was manually tracked using a handheld radio receiver (SRX 600, Lotek Wireless, Newmarket, Ontario) and a six-element Yagi antenna (AF Antronics, Urbana, Illinois). Daily surveys for the tagged salmon were conducted beginning at the counting fence and descending by foot along the riverbank to the highway bridge along both sides of an island (Fig. 1). Surveys continued beyond the estuary to the peninsula in an attempt to find salmon that were not found in the river. The small width and relatively shallow depth of the river indicated that it was highly improbable that a salmon in the river would go undetected. Visual surveys by snorkel were also conducted in the river and estuary to identify and recover dead fish and tags that dislodged prematurely.

Data analysis

Position

To investigate differences in the distribution of animals from the two treatment groups following release, we used positions derived from radio transmissions to calculate 95% kernel utilization distributions using the "kernelUD" function in the R package adehabitatHR (Calenge 2006). To account for absence of animals that were not detected, we assumed a position in the ocean given that our radio coverage would have detected any fish in the estuary or river. Distributional area was calculated for the two groups using the "kernel.area" function, and the difference was established by dividing the area of each distributional polygon. Three individuals recovered the day after release were excluded from positional analyses.

Acceleration

Acceleration data were downloaded from accelerometer loggers recovered from treatment ($N = 6$) and control ($N = 7$) survivors as well as three individuals that died soon after release. Acceleration-derived activity was calculated using a moving variance window applied to the jerk time series ($m \cdot s^{-3}$), described below. First, high-frequency noise was removed (IIR Butterworth filter with a 10 Hz cut-off) from the acceleration series, then jerk (change in acceleration, $m \cdot s^{-3}$) was computed as the differential of the acceleration for each axis. The total jerk was taken as the norm of the tri-axial jerk (i.e., the square root of the sum of the squared value in each axis) at each time instant (see, e.g., Simon et al. 2012) and represents the specific contribution of animal movement to vectoral acceleration. We then calculated hourly estimates of activity as the root-mean-square of jerk based on a 60 min moving window for each fish. All acceleration processing was performed using MATLAB (The MathWorks Inc., USA).

To test if this measure of activity of salmon was significantly related to the treatment variable, as well as other potentially relevant variables, we considered the time since release (h), water temperature measured hourly at the counting fence, and diel effects of ambient light as predictor variables. Ambient light was considered as a binary variable, light or dark, by checking whether a sample fell within or beyond values of nautical dawn and dusk based on values extracted with the "getSunlightTimes" function in the suncalc package for R (Agafonkin and Thieurmel 2017). We also considered the interaction between treatment group and time to check whether there was a difference in the activity across time for treatment compared with control salmon (i.e., a recovery profile). We selected a generalized least squares model implemented with the "gls" function in the nlme R package (Pinheiro et al. 2017). Nested effects by individual and temporal autocorrelation were incorporated using a correlation structure and comparison of common correlation structures by AIC value (Zuur et al. 2009). The data structure suggested an exponential structure in the form corExp(form = ~time|ID), in which the time variable was the sample date time and ID was the individual fish. No model reduction was attempted, and all fixed effects were retained for the final model.

Resumption of migration

Dates of upriver ascent were recorded when fish were recovered in the counting fence trap. To test the hypothesis that the fisheries stressor delayed the upriver migration of salmon, we generated a probability distribution of the mean date of ascent to the fish trap for the surviving fish. To generate the distribution, we assigned a probability of ascent equal to the proportion of untagged salmon ascending to the fish trap on each day of the season (following the start of the experiment) as enumerated at the counting fence and then used the "sample" function in R to select an ascent date for each fish, weighted by the assigned daily probabilities, with 10 000 iterations. A p value testing the null hypothesis that mean timing of ascent was not different from the null model was then computed by calculating the proportion of simulated values smaller than the mean observed arrival dates for tagged and untagged salmon.

Table 1. Summary of 39 tagged Atlantic salmon (*Salmo salar*) in the Campbellton River, Newfoundland and Labrador.

Group	Date released	Length (mm)	Fate	Date fate determined
Control	9 July	535	Returned	14 July
		546	Returned	1 August
		509	Returned	26 July
		520	Returned	27 July
		542	Returned	1 August
		515	Dead	10 July
		512	Returned	27 July
		550	Returned	25 July
	10 July	545	Returned	30 August
		566	Returned	30 August
		507	Returned	8 August
		563	Returned	27 August
		538	Returned	12 July
		518	Returned	27 July
		525	Returned	23 August
		625	Returned	26 July
		580	Returned	9 August
		554	Returned	1 August
Treatment	9 July	570	Returned	7 August
		560	Returned	26 July
		588	Returned	29 July
		547	Returned	26 July
		518	Unknown	—
		574	Returned	27 August
		520	Returned	27 August
		536	Dead	10 July
		515	Returned	25 July
		540	Returned	17 August
	10 July	540	Returned	30 August
		560	Returned	27 August
		542	Unknown	—
		535	Returned	1 August
		504	Returned	1 August
		558	Returned	27 August
		522	Returned	23 August
		524	Dead	11 July
		505	Returned	11 August
		564	Returned	1 August
		545	Returned	17 August

Note: Salmon were double-tagged with external accelerometer tags and radio transmitters implanted in the stomach and released on 9 or 10 July 2016. The fate of salmon was dead (died soon after release), returned to the counting fence, or unknown (tracked moving after release but never recaptured at the counting fence).

Data visualization

Figures were plotted using ggplot2 (Wickham 2016) with the packages ggridges (Wilke 2017) and gridExtra (Auguie 2017) in R (R Core Team 2017).

Results

Three salmon were confirmed to have died within 1 day of the experiment (Table 1). Accelerometer tags were recovered from those dead fish. Two of the three mortalities were in the treatment group and one was in the control group. This small sample size precluded formal analysis of factors influencing mortality. Two additional treatment group animals never returned to the counting fence; however, they were both tracked multiple times to different positions in the estuary within 1 week of release and hence survived treatment–tagging. These two fish may have gone back to sea and subsequent re-entered the river after the counting fence was removed (5 September 2016) or alternatively suffered delayed mortality. Overall, minimum survival was therefore 87%–92% (control 94%, treatment 81%–90%). A mortality rate of 4%–13% was attributed to the treatment effect. Owing to small sample size, however, it was not possible to determine whether this was a significant difference with mortality occurring in the control group.

Most radiotelemetry detections occurred in the pool directly below the counting fence where salmon were also visually observed holding alongside untagged fish. Fish were also detected below the outflow of two branches of the river on the estuary side of the highway bridge and in the estuary (Fig. 1). Salmon that were not detected were inferred to have entered saltwater where the tags transmissions were blocked from detection. Kernel density estimation of the distribution of control animals (0.79 km^2) equated to 78% of the distribution calculated for treatment (0.10 km^2) animals (Fig. 2).

Accelerometers were recovered from fish returning to the fence and those that came off prematurely onto the riverbed. Inspection of the accelerometer traces allowed us to determine when the tag was no longer attached to the fish and censor the data. Generalized least squares regression revealed a significant effect of water temperature on jerk-derived hourly activity index with a negative slope (Table 2), suggesting that salmon activity decreased as temperatures increased from 13.5 to 23.4 °C. Treatment salmon (1.52 ± 0.53 m·s^{-3} average hourly rate of movement) were observed to have similar activity across the study period as control salmon (1.48 ± 0.48 m·s^{-3}), and both treatment group and the time × treatment interaction had small but not significant test statistics (Table 2). Activity was similar during daylight (1.53 ± 0.52 m·s^{-3}) and dark (1.45 ± 0.50 m·s^{-3}; Table 2). Date time was also not a significant term, having a slope of zero (Table 2; Fig. 3).

Following the release of the tagged salmon and commencement of our monitoring for the study, 1504 salmon entered the trap at the counting fence after 10 July (first release group) and 1447 after 11 July (second release group). The average date of capture at the fence after both dates was 8 August (day 221), with a maximum of 57 salmon returning on 11 July (for the second release group, maximum = 52 on 14 July) and a minimum of 0 occurring on 9 days. The null distribution of days to return following tagging suggested a mean of 23 days for 34 salmon given the null hypothesis that timing of return was independent of treatment; however, tagged control salmon returned on average 26 days after release ($p = 0.24$), and tagged treatment salmon returned on average 32 days after release ($p < 0.01$; Fig. 4); therefore, the null hypothesis that resumption of migration was independent of treatment was rejected.

Discussion

Behaviour is a relevant metric to explore animal responses to stressors, but the scale of investigation must ideally be matched to the expected response (Schreck 1990; Schreck et al. 1997; Sopinka et al. 2016). Accelerometers provide information about animals that is fine in temporal and spatial scale and can be effectively applied to observe small changes in individuals after release, which other tracking technologies are only able to observe at coarse scales. For example, Brownscombe et al. (2013) released bonefish (*Albula vulpes*) with accelerometers and observed significant effects of a recovery treatment on the swimming behaviour within a few minutes of release. Broell et al. (2016) observed released shortnose sturgeon (*Acipenser brevirostrum*) resting, presumably to recover from catch-and-release, for 2–5 h. Observing tailbeats of blacktip sharks (*Carcharhinus limbatus*) with accelerometers also enabled Whitney et al. (2016) to calculate that 10.5 h is necessary to recover from angling. Our example used jerk, which has previously been applied for investigating animal behaviours (e.g., Simon et al. 2012; Ydesen et al. 2014) and provides a simple summary of tri-axial movement of instrumented animals.

We found that temperature was the only significant predictor of jerk-derived activity index in Atlantic salmon, which was otherwise independent of time, treatment group, and ambient light.

Fig. 2. Radio tracking positions of Atlantic salmon tagged and released (yellow diamond) in the Campbellton River, Newfoundland. Density contours indicate the relative distribution of Atlantic salmon based on radio positions for control and treatment group salmon, with higher density indicated by red rings. Note that most detections were recorded in the pool directly above the counting fence above the island. Most other detections were recorded at the confluence of the two branches of the river on either side of the island below the highway bridge. Map was generated with the "openmap" function in the R package OpenStreetMap (Fellows and Stotz 2016) with the Bing maps base layer (Microsoft 2018). [Colour online.]

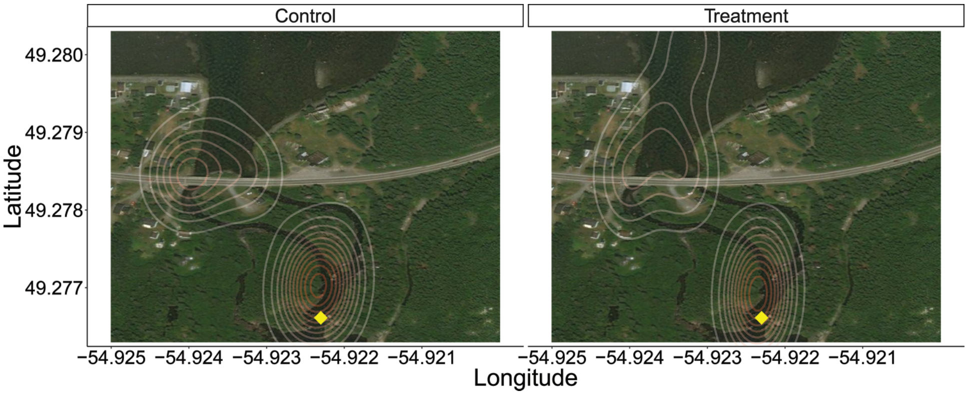


Table 2. Generalized least squares regression (gls function in nlme R package) modelling jerk, a metric summarizing the dynamic movement of the body across three axes.

Fixed effect	Coefficient ± SD	*t* value	*p* value
(Intercept)	193.26±201.79	0.96	0.34
Ambient light (light)	0.05±0.03	1.60	0.11
Group (treatment)	−454.90±307.79	−1.77	0.08
Time	0.00±0.00	−0.95	0.34
Temperature	**−0.05±0.02**	**−4.01**	**<0.01**
Group (treatment) × time	0.00±0.00	1.77	0.08

Note: The generalized least squares regression incorporated time nested within individual in an exponential correlation structure to account for temporal autocorrelation in the model residuals. Coefficients ± standard deviation are presented, and significant predictors are presented in bold for emphasis.

Frechette et al. (2018) showed that this species uses behavioural thermoregulation to buffer exposure to potentially stressful temperatures during the migration. Furthermore, Lennox et al. (2018*b*) established an exponential relationship between the rate of oxygen consumption and water temperature for Atlantic salmon at slow swimming speeds in the Norwegian river Lakselva; a reduction in activity at higher temperatures is therefore a logical behavioural response to reduce energy expenditure at high temperatures. Elsewhere, studies suggest that Atlantic salmon upriver migration is negatively related to temperature (Erkinaro et al. 1999; Karppinen et al. 2004). Climate change alterations that increase freshwater temperatures could be expected to prolong Atlantic salmon migration owing to delays associated with high temperature (Baisez et al. 2011).

Other factors considered in the model, specifically treatment, time postrelease, and diel period, were not significant. We predicted that activity may increase at night given that several studies have shown that migration activity is predominantly nocturnal (reviewed in Thorstad et al. 2008). Although patterns in the data were suggestive of diel effects, we found no effect of darkness on activity. Instead, activity was significantly related to water temperature, which peaks during the day but cools at night, yielding the patterns in the data we observed. There was weak evidence for a treatment effect and a treatment × time interaction. A significant interaction would have been interpreted as evidence that treatment affected the rate of change of activity or recovery from the treatment. Control animals were exposed to the same holding and tagging procedures as treatment fish, and although they did not differ in their postrelease activities, there was a difference in the timing of their migration. Holding is stressful for fish, but because fish were held in a moderate current, we have no reason to anticipate water quality issues, crowding stress, or exhaustion from swimming against fast flow (Portz et al. 2006). The relatively brief bout of exercise that treatment animals were exposed to may have not been extreme enough to calculate the time to recovery from the salmon acceleration data (see Cooke et al. 2013). This is a limitation of the method used because we chased the fish in experimental tanks until they were unwilling to continue. In fisheries, fish may not fight continuously and may make use of currents to cause resistance against the angler, and the flow may also facilitate re-oxygenation of tissues during the fight, allowing longer times to exhaustion. Manual chasing allows the fish to stop intermittently when acclimated to the chase. Even without evidence of impairment in fine-scale activity from the accelerometers, the coarse-scale investigation revealed that the treated salmon were delayed in resuming upriver migration through our experimental area based on timing of return to the fence.

Radio tracking revealed that the salmon that we released exhibited fallback. Although we released salmon directly below the counting fence, many salmon were tracked below the island at the river mouth, and several ostensibly re-entered the ocean because we could no longer detect them. Salmon early in the migration can probably transition relatively easily between salt- and fresh water, and Thorstad et al. (2005) observed salmon moving more than 14 km downriver to enter the sea during a pollution event in the river Numedalslågen. Temperatures experienced by the salmon that returned to marine waters would have been lower than in the river, which could prolong recovery. Wilkie et al. (1997) examined resynthesis of the primary anaerobic substrate glycogen, clearance of the anaerobic byproduct lactate, and correction of muscular pH in exercised Atlantic salmon and found it was slower at 12 than at 18 °C. Cooler temperatures experienced by salmon that returned to sea would mean an overestimation of the temperature experienced in our regression model that was based on river temperature.

Fallback from the release point as observed in this study is a commonly reported consequence of disturbances encountered by upriver migrants (Frank et al. 2009) and has been observed following various fisheries stressors for Atlantic salmon (Mäkinen et al. 2000; Havn et al. 2015). Mäkinen et al. (2000) suggested that more extreme stressors (gill netting compared with recreational angling) can increase the extent of Atlantic salmon fallback. Fallback may be either a mechanism driving delays or truncations in migration that have been observed for angled salmon (see Tufts et al. 2000; Lennox et al. 2015, 2016*b*) and perhaps a symptom of

Fig. 3. Summary plots describing activity of Atlantic salmon tagged and released in an experimental migration arena in the Campbellton River, Newfoundland, Canada. Jerk is a composite metric summarizing activity based on axes of tri-axial accelerometer loggers. The prespecified model tested whether ambient light (left panel), temperature (central panel), time, treatment group, and the interaction between treatment group and time (right panel) affected the activity of salmon in units of jerk. The final model incorporating an exponential correlation structure by time nested within individual ($N = 13$) suggested no effect of ambient light but a weak effect of treatment ($p = 0.08$), treatment × time interaction ($p = 0.08$), and a significant effect of temperature ($p = 0.001$) on salmon activity. Dashed horizontal lines indicate the mean value of jerk throughout the study (1.51).

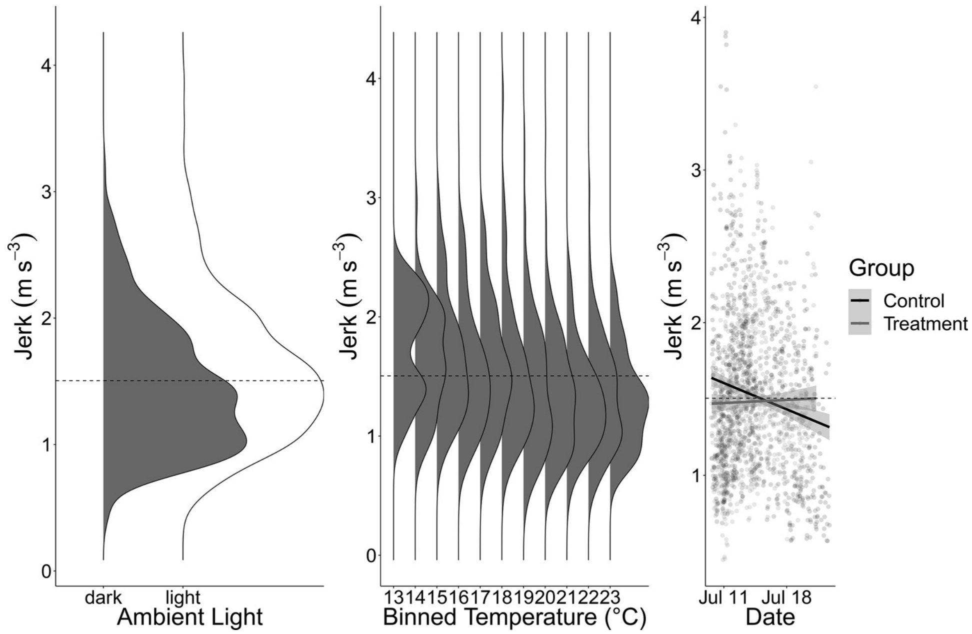
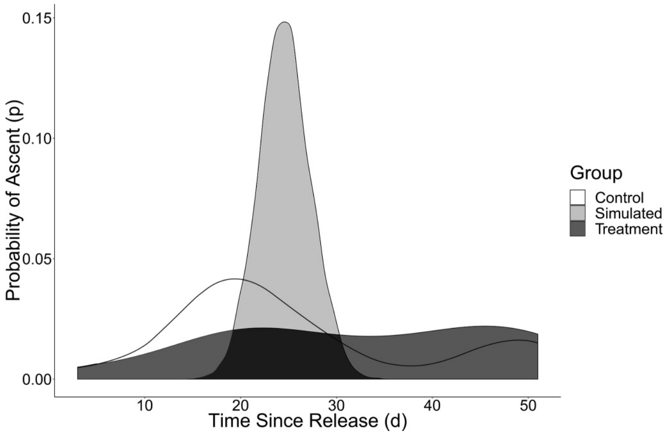


Fig. 4. Density plot displaying the most probable mean time to return after release (grey) for 34 Atlantic salmon tagged and released from experimentation in the Campbellton River, Newfoundland. The simulated distribution of most probable number of days to return was generated by assigning daily probabilities of tagged salmon to return on a given day equal to the proportion of untagged salmon trapped at the fish counting fence on that day. The area under the white curve indicates the observed distribution of days elapsed before returning for control salmon ($p = 0.24$), and the area under the black curve represents treatment ($p < 0.01$) salmon.



the underlying physiological disturbance leading to those observations.

Our modelling may have suffered from survivor bias, insofar as we were unable to recover all the accelerometer tags owing to unforeseen issues with tag retention. External tagging is an effective method for safely and rapidly instrumenting fish (Jepsen et al. 2015). However, a recent comparison of externally and internally tagged Atlantic salmon showed that external tags were associated with delayed and shorter migrations of Atlantic salmon in a river with waterfalls (Lennox et al. 2018*c*). Although tagged salmon have similar swimming performance to untagged controls (Thorstad et al. 2000), different flow fields in rivers and the design of the tag can affect the hydrodynamics in rivers, especially for fish ascending rapids. The actual tag burden assessed using the traditional ratio of tag mass to body mass was near the generally accepted 2% level (Jepsen et al. 2004); however, as discussed in Brown et al. (1999), tag shape and the physical size may be equally important, particularly when affixing tags externally (Jepsen et al. 2015). We opted for external attachment of accelerometers in this study to avoid prolonged holding and handling of fish and so as not to anaesthetize fish that would return to the river and potentially be captured and consumed by humans. However, we recommend that future studies consider internal implantation of accelerometers whenever possible, as we observed some evidence of potential tag shedding. Although nearly all the salmon returned to the fence, our inability to recover some tags may have meant that our subsample was biased in some way, for example by only being able to consider fish that remained close to the counting fence after release or the fish that were in the best condition and most resilient to capture and handling stressors.

Interpretation of the ultimate costs associated with our treatment and the fate of salmon following delayed migration is somewhat difficult. Total survival was high (87%–96%) and aligns with 93% postrelease survival predicted by Lennox et al. (2017) in a composite analysis of Atlantic salmon recreational fishing studies, including Havn et al. (2015) in which water temperatures were similarly high (86% survival at 18–21 °C). Both salmon that disappeared before the end of the study period were tracked on multiple days in multiple locations, including upriver movements after release; therefore, they would not have been considered mortalities based on the criteria typically used in catch-and-release studies where upriver movement after release was interpreted as evidence of survival (Thorstad et al. 2003; Havn et al. 2015; Lennox et al. 2015). Reproductive success of this age class of fish, one sea winter (i.e., grilse), in the Escoumins River, Quebec, Canada, was found to be highly dependent on run timing, with early arrival at spawning grounds contributing to higher realized reproductive output (Richard et al. 2013), meaning that delays in migration as observed in this study may affect fitness. It is uncertain whether early arrival affects salmon reproductive success (Tentelier et al. 2016), but if prior residence is important for Atlantic salmon to access high-quality substrate, then delays caused by fisheries could impose a substantial cost by offsetting the benefits of abandoning feeding opportunities at sea for early river entry.

Acknowledgements

Lennox, Chapman, Bøe, Whoriskey, Fleming, and Cooke were supported by Ocean Tracking Network Canada, which is funded by the Natural Sciences and Engineering Research Council of Canada (NSERC) and the Canada Foundation for Innovation. Lennox, Chapman, Twardek, and Cooke were further supported by NSERC. Cooke is supported by the Canada Research Chairs Program. We acknowledge the extensive assistance and in-kind support provided by DFO technical staff.

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