NRC Research Press

ARTICLE

Telemetry reveals how catch and release affects prespawning migration in Atlantic salmon (*Salmo salar*)

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Abstract: With the decline of many exploited fish populations, catch and release has become an increasingly used management practice to allow sport fishing while reducing its impact on wild populations. However, survival and reproductive success can vary according to the catch and release technique and environmental conditions, suggesting a potential impact of this practice on prespawning behaviour. Here we evaluate how some critical aspects of salmon freshwater migration are influenced by catch and release and by environmental factors. For this purpose, 40 multi-sea-winter Atlantic salmon (*Salmo salar*) (20 catch and release and 20 control) were followed by telemetry from June 2011 to March 2012. Temperature was found to influence movements and the daily probability that a fish would cross a fish ladder, while water discharge influenced daily distance travelled during the prespawning migration. Catch and release was found to influence the daily probability of fish to cross a barrier as well as the total distance traveled in the river. Overall, this study suggests that salmon caught and released by fishermen survive and reproduce, but that prespawning exploration behaviours could be altered compared with those of uncaught salmon.

Résumé : Avec le déclin de plusieurs populations de poissons exploitées, la remise à l'eau est devenue une approche de gestion populaire afin d'assurer la pêche sportive tout en minimisant ses impacts. Néanmoins, comme la survie et le succès reproducteur peuvent varier selon les conditions environnementales et la méthode employée, la remise à l'eau pourrait avoir un impact non-négligeable sur le comportement pré-reproducteur. Cette étude évalue comment certains aspects critiques de la migration en eau douce du saumon atlantique (*Salmo salar*) sont influencés par la remise à l'eau et les conditions environnementales. Quarante saumons rédibermarins (20 remis à l'eau, 20 contrôles) ont été suivis par télémétrie de juin 2011 à mars 2012. Les résultats indiquent que la température influence la probabilité de mouvement et de franchissement d'obstacle, alors que le débit influence la distance journalière parcourue. Par ailleurs, la remise à l'eau influence la probabilité journalière pour un individu de franchir un obstacle et la distance totale parcourue par celui-ci. Cette étude suggère que même si les saumons remis à l'eau survivent et se reproduisent, le comportement pré-reproducteur peut en être altéré.

Introduction

As is the case with many other fishes worldwide, Atlantic salmon (*Salmo salar*) has been declining rapidly since the middle of the 20th century and is now near historic lows in most of its distribution area (Hutchings 2000; ICES 2013). In Canada, some Atlantic salmon populations are listed as endangered while most are threatened or under special concern (COSEWIC 2010). Despite the species status, Atlantic salmon remains a highly prized game fish, and many populations still sustain important recreational fisheries. For example, anglers spend at least $128 million each year in Canada for this activity (ASF 2012). To maintain the socio-economic benefits resulting from angling while reducing its impact on wild population conservation and restoration, catch and release (C&R) angling has been introduced in many countries. While the percentage of the total rod catch released differs greatly from one country to another, the total number of released salmon has increased each year and exceeded 173 000 in 2012 (ICES 2013). In Canada, C&R mainly targets large salmon (≥63 cm fork length) and represents at least 50% of the catch (Dionne et al. 2012).

The efficiency of C&R for ensuring the sustainability of exploited salmon populations relies on the premise that postrelease mortality rates are low and that surviving individuals successfully resume their migration and then reproduce (Cooke and Schramm 2007). The postrelease survival of salmonids can be high (up to 100%) when done in favourable conditions, but it can decrease rapidly when water temperatures exceeds 18 °C (Wilkie et al. 1996; Thorstad et al. 2003; Boyd et al. 2010) or when fish are exposed to air for 30 s or more (Ferguson and Tufts 1992). Recently, Richard et al. (2013) reported the first results concerning the reproductive success of C&R salmon. They showed that C&R fish reproduce and contribute to the next generation as much as an uncaught congener and in accordance to their proportion in the river. However, reproductive success was significantly influenced by the entry date of the fish into the river, the temperature during C&R, and whether the fish was exposed to air (Richard et al. 2013). Reproductive success can then vary according to the C&R technique and environmental conditions, suggesting a potential impact of this practice on prespawning behaviour. Considering that freshwater behaviour and migration timing represent important features in Atlantic salmon fitness (Hansen and Jonsson 1991) and considering the increase in popularity of C&R as a management practice worldwide, it is of prime importance to complement information gained from the genetic analyses on reproductive success and to

Received 7 February 2014. Accepted 27 June 2014.

Paper handled by Associate Editor Bror Jonsson.

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evaluate the impact of C&R on salmon migratory behaviour to fully understand its impact on population sustainability.

Recent advances in biotelemetry have enabled researchers to study the riverine prespawning behaviour of salmon, including C&R individuals (Pollock and Pine 2007; Donaldson et al. 2008). Økland et al. (2001) suggested that normal river migration in salmon can be divided into three distinct phases: (1) an active upstream migratory phase, (2) a searching phase with upstream and downstream movements, and (3) a holding phase prior to spawning. Most telemetry studies have reported unexpected behaviour in C&R individuals, typically downstream movements and (or) delayed migration (Mäkinen et al. 2000; Whoriskey et al. 2000; Thorstad et al. 2003, 2007; Halttunen et al. 2010), although these studies generally lacked a control group. As a result, C&R salmon behaviour was often considered abnormal based on this theoretical knowledge on salmon migration. In addition, C&R effects could be confounded with tagging effects in some studies. One study that included a control group found no significant differences in migratory behaviour between C&R and control salmon (Jensen et al. 2010). However, the methodology employed by Jensen et al. (2010) (they tagged large numbers of salmon in the marine habitat prior to river entrance, and 10 fish happened to be C&R once in the river) only allowed them to track a limited number of C&R salmon, thereby limiting the interpretation of their results. Finally, most of the C&R telemetry studies published to date have been done in large subarctic rivers (the Alta River in Norway: Thorstad et al. 2003; Thorstad et al. 2007; Halttunen et al. 2010; Jensen et al. 2010; the Ohcejohka River in Finland: Mäkinen et al. 2000; the Ponoi River in Russia: Whoriskey et al. 2000), which could offer optimal environmental temperatures for C&R (below 16 °C; Thorstad et al. 2003), thus potentially minimizing its detectable impact. It is uncertain how applicable these observations are to more southern Canadian and European rivers.

The objective of this study was to evaluate how some of the critical aspects of the freshwater migration in salmon, namely barrier crossing, propensity to move, and distanced travelled, were influenced by C&R and environmental factors. We hypothesized that C&R salmon would be slower at crossing barriers (such as a fish ladder or waterfall) and at migrating towards spawning grounds and would be generally less active in the river, thus ultimately selecting downstream spawning sites when compared with the control group. We used an alternative method to assess the potential impact of C&R on the migratory behaviour of multi-sea-winter Atlantic salmon in a river in southern Quebec, Canada, by following them from the beginning of summer through the spawning period in fall and locating them again the following spring. This allowed us to use an increased number of tracked C&R fish compared with previous studies and include a control group to evaluate the impact of C&R alone.

Materials and methods

Study site

The study was conducted in the Escoumins River, located on the north shore of the St. Lawrence River in Quebec, Canada (Fig. 1). The river is 84 km long and has a mean annual discharge of 14.8 $m^3 \cdot s^{-1}$, representing an average-sized river for the province of Quebec (Cauchon 2014). Anadromous fish have access to 35 km of the river, as far as the impassable Pinel waterfall, which prevents any further upstream migration. Salmon typically enter the river between early June and late September, and they first have to cross the municipal dam fish ladder situated just upstream of tidal influence. Nine kilometres further upstream, a second fish ladder allows fish to cross the Grand Sault waterfall (hereinafter, all distances will be expressed as the distance from the municipal dam). The most important spawning grounds are situated upstream of those obstacles, between kilometres 15 and 30, although a small proportion of the population is known to spawn in the river section downstream of the Grand Sault waterfall. For the whole river, the spawning period is from mid-October to the beginning of November, when water temperature is between 6 and 10 °C (F. Barnard, Ministère des Forêts, de la Faune et des Parcs, personal communication, 2011).

Salmon fly fishing on the river is open from 1 June until 15 September, and this is the only way of capturing salmon on this river. Fishermen have to register with the local organization that manages the fishery. The river is divided into four fishing sectors comprising 66 pools that are easily accessible by road. The most productive pool is pool 3, which is located at the foot of the municipal dam; more than 50% of annual C&R events occur in this pool. Provincial regulations allow fishermen to keep up to two one-sea-winter salmon a day (salmon < 63 cm fork length), but they must release all large salmon (multi-sea-winter, ≥63 cm). As a result, C&R in this river — as is the case all over Quebec — primarily targets multi-sea-winter salmon, which are mainly females for this species.

Tissue sample collection

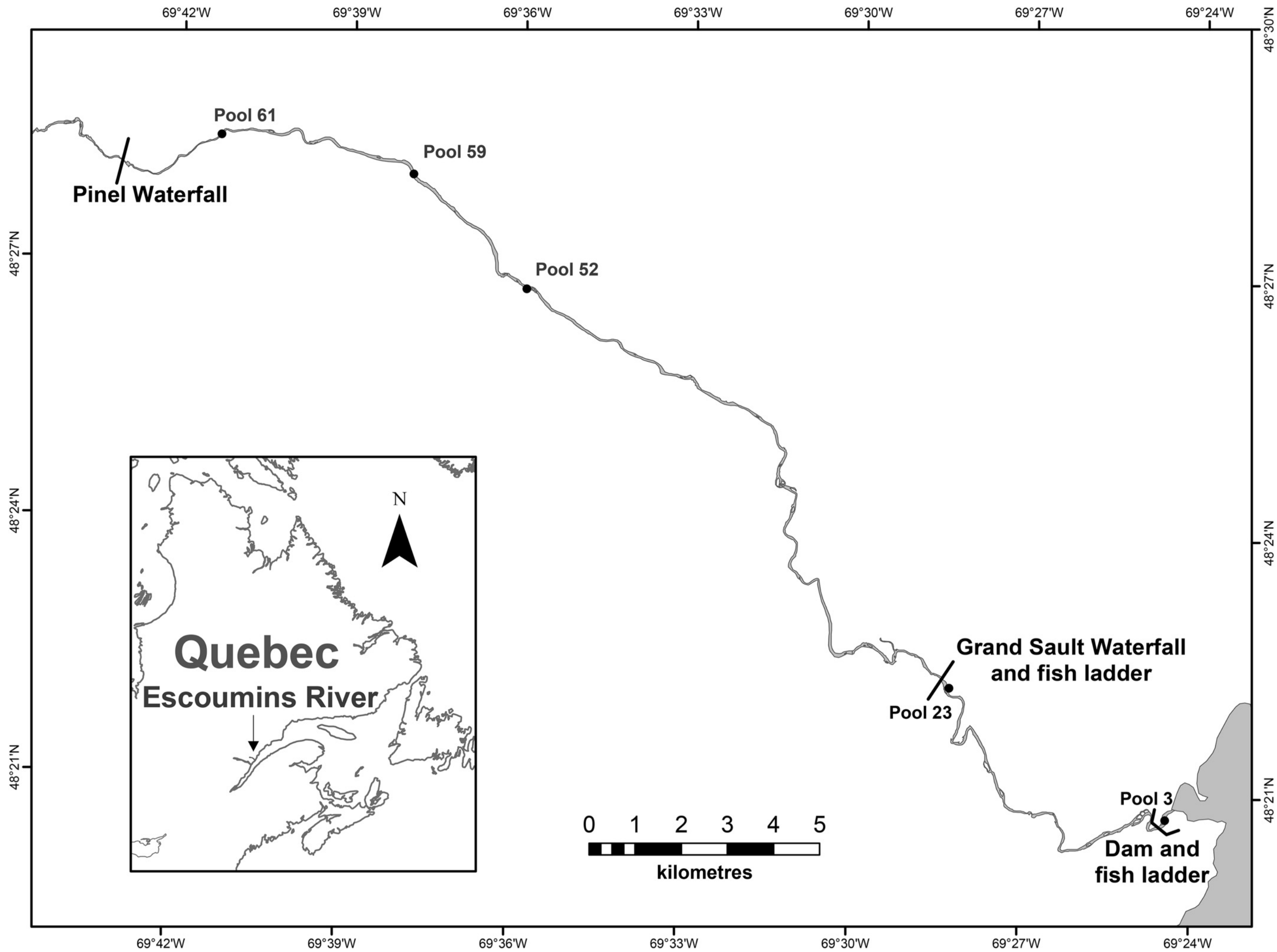
Fishermen collaboration was solicited throughout the 2011 fishing season to collect tissue samples (5 mm diameter punch samples of the adipose fin) and information from each catch and release event (e.g., landing time, air exposure time, bleeding). The punch pliers provided to the fishermen allowed them to sample their catch prior to release and left an easily recognizable mark on the adipose fin. This mark allowed us to visually separate fish that had undergone C&R (in pool 3) from uncaught fish (control group) when we captured them for telemetry tagging at the fish ladder.

Capture and tagging

Between 18 June and 20 July 2011, 40 multi-sea-winter salmon were captured and tagged in the last section of the municipal dam fish ladder (20 C&R and 20 uncaught fish for the control group). We attempted to tag the same number of C&R (punched) and control (nonpunched) fish each day, and control fish were selected to match the lengths of C&R fish. Fish were measured (total length ± 5 cm) prior to capture using a ruler fixed to the bottom of the fish ladder. Stress related to capture may be non-negligible (Mäkinen et al. 2000), so precautions were taken to minimize every possible source of stress. Salmon were first trapped in a shaded section of the fish ladder (155 cm long, 82 cm wide, and 100 cm deep), where the floor could be slowly lifted while leaving at least 60 cm of water for the salmon to swim. A specially designed stretcher was slowly slipped under the fish that allowed gentle transfer onto an adjacent larger stretcher filled with an anaesthetic solution of clove oil (34 $mg \cdot L^{-1}$). Salmon were kept in water and in complete darkness at all times, thus they stayed calm throughout the capture process, which took less than 5 min.

Once anaesthetized, each fish was visually inspected (any fish showing serious wounds was not used) and tagged with a radio transmitter (model MCFT2-3A, LOTEK, Canada; 16 mm diameter, 46 mm length, 6.7 g water mass, 3 year minimum life). The transmitter was coated with glycerin and gently inserted into the fish's stomach using a plastic tube. Regurgitation of the transmitter is a potential drawback associated with intragastric tagging (Bridger and Booth 2003). Thus, two rings (5 mm wide) of surgical tubing were strapped around the transmitters to increase their roughness and hence limit regurgitation (Keefer et al. 2004*a*). Each tag transmitted a unique digitally coded signal and was equipped with a motion sensor that allowed the identification of regurgitated tags or dead fish. To facilitate the detection of each transmitter in areas of salmon aggregation, four different frequencies (151.380, 151.420, 151.460, and 151.640 MHz) were used, and tags transmitting on the same frequency had different burst rates (5, 5.5, or 6 s). Finally, a tissue sample was collected from the adipose fin to genetically confirm the identity (either C&R or control) of

Fig.1. Location of the Escoumins River on the north shore of the St. Lawrence River in Quebec, Canada. The positions of obstacles to salmon migration as well as the main holding pools (●) in the river are indicated.



each tagged salmon by comparing their genotypes at 12 microsatellites with those from samples collected by fishermen using the identity check function available in the software cervus (Kalinowski et al. 2007; for further details on the genetic analyses, see Richard et al. 2013). By combining the information from cervus, fishermen, and temperature data loggers, the condition at release of each C&R salmon equipped with a transmitter was known. After tagging, fish were transferred to a 400 L recovery tank with oxygenated circulating river water. They were then released by opening a trap situated on the side of the tank, which, once open, forced the water and the fish to slide back into the fish ladder, less than a metre upstream from the capture site.

Salmon tracking and environmental monitoring

A fixed data logger receiver (LOTEK model srx400a) connected to a four-element Yagi antenna and installed on the municipal dam allowed us to detect any fish leaving the area while a mobile receiver (LOTEK model srx400a) was used to track the salmon in the river. This receiver was connected to a three-element Yagi antenna installed in the back of a pickup truck. From the road that runs beside the river, it was possible to detect the presence of a salmon within a radius of approximately 250 m. When a fish was detected, the receiver was used with a handheld three-element Yagi antenna to precisely identify the location, and a GPS was used to record the fish's exact position. The whole river was scanned every 2 days between 18 June and 30 August 2011, except for the river section between the two fish ladders that was scanned every day, until all salmon had either crossed the Grand Sault fish ladder or settled near a spawning ground. Starting in September, the river was scanned at least once a week until the end of the spawning season in early November. At the end of the winter (8–9 March), we used a snowmobile and snowshoes to access the river and localize the overwintering habitat selected by each salmon.

Water temperature was recorded hourly by four temperature data loggers (TidbiT v2 Temp logger from Onset Computer Corporation) situated in pool 3, at the exit of the municipal dam fish ladder, at the entrance of the Grand Sault fish ladder, and on a known spawning ground situated between pools 53 and 54 (24.6 km upstream of the municipal dam). Water discharge data, recorded every 15 min, was taken from the Centre d'Expertise Hydrique du Québec gauge station No. 070204 (http://www.cehq.gouv.qc.ca/depot/historique_donnees_instantanees/070204_Q_2011.txt), which is situated in pool 24, 80 m upstream of the Grand Sault waterfall (9 km upstream of the municipal dam).

Statistical analyses

To facilitate analyses, all recorded latitude–longitude positions were first transformed into distance (in metres) from the municipal dam. The general migratory patterns (most upstream location, spawning site, total distance travelled, and wintering site) of the C&R group and the control group were compared with Kolmogorov–Smirnov (K–S) tests. An individual's spawning site

Table 1. Water temperature and water discharge models selected by AIC_c and tested for fish ladder crossing, propensity to move, and distance travelled when moving.

	Fish ladder crossing		Propensity to move		Travelled distance	
Model	AIC_c	ΔAIC_c	AIC_c	ΔAIC_c	AIC_c	ΔAIC_c
Water temperature						
ΔWT	200.31	6.55	420.55	29.54	5603.48	14.02
Null	199.16	5.40	432.25	41.24	5603.82	14.35
WT^2	194.13	0.37	**391.01**	**0.00**	5591.53	2.07
WT_{max}	195.58	1.82	399.11	8.10	5596.75	7.29
WT_{mean}	**193.76**	**0.00**	394.29	3.28	**5589.47**	**0.00**
WT_{min}	198.04	4.28	405.64	14.63	5591.75	2.29
Discharge						
Δ*Q*	200.75	2.75	431.61	7.45	5605.12	18.42
Null	199.16	1.16	432.25	8.09	5603.82	17.12
Q^2	199.96	1.96	426.06	1.90	5593.14	6.44
Q_{max}	198.54	0.54	432.04	7.88	5594.41	7.71
Q_{mean}	**197.99**	**0.00**	428.81	4.65	5591.10	4.40
Q_{min}	198.31	0.31	**424.16**	**0.00**	**5586.70**	**0.00**
Tested hypotheses						
Null	199.16	6.80	432.25	39.74	5603.82	20.87
C&R × WT	**192.36**	**0.00**	394.40	1.89	5593.13	10.19
C&R + WT	194.41	2.05	**392.59**	**0.08**	5591.26	8.32
C&R + *Q* + WT	195.68	3.32	394.26	1.74	**5582.94**	**0.00**

Note: The selected models are in bold. Only the selected models are shown for the tested hypotheses; all 32 models can be viewed in Table S1[1]. An interaction between variables is represented by a times symbol (×).

was defined as the mean distance separating the salmon from the municipal dam during the spawning period, which was determined to be between 14 and 28 October in 2011 (based on water temperature and field observations). The total distance travelled represents the minimum distance covered by a salmon from its entrance into the river and its position on 28 October. This was obtained by summing the absolute values of the distances travelled between each detection. The wintering site corresponded to the fish's position on 8 or 9 March 2012.

To measure the impact of C&R on three main aspects of freshwater salmon migratory behaviour — namely barrier crossing, propensity to move, and travelled distance — we modelled each with a generalized linear mixed model (GLMM) including salmon ID as a random effect to allow for temporal correlation in the data recorded for a single individual. Explanatory fixed effects included in the models were environmental variables (date, water temperature (WT), and discharge (*Q*)), an individual physical characteristic (total length (LT)), and a C&R variable (0 = control, 1 = C&R). Since salmon behaviour has been shown to be associated with different water temperature and discharge measurements (Salinger and Anderson 2006), the best predictor associated with water temperature and discharge to be included in the models was first assessed with a set of six univariate models for each of the two environmental variables. The tested predictors were the mean value between two detections (WT_{mean}, Q_{mean}), the maximum (WT_{max}, Q_{max}) and minimum (WT_{min}, Q_{min}) values between two detections, the quadratic effect of the centered mean value (WT^2, Q^2), and the short-term change in the value (difference between mean values of two consecutive detections: ΔWT, Δ*Q*) (Table 1). The best predictors were selected using the Akaike information criterion corrected for small sample sizes (AIC_c; Burnham and Anderson 2002). This model selection approach measures the relative quality of each tested model based on its goodness of fit and complexity. We then built a set of 32 models (including a null model) made from a combination of the aforementioned variables and of their biologically significant interactions (Table 1; also see Supplementary materials, Table S1[1]). We limited the number of variables in a model to a maximum of six (including interaction terms and intercept). Since the experimental plan was designed to measure the effect of C&R, the C&R variable was included in all models. Models were then ranked by AIC_c (Burnham and Anderson 2002); selected models had the lowest AIC_c value. When equivalent models were found ($\Delta AIC_c \leq 2$), we selected the more parsimonious model (i.e., the model with fewer parameters).

Barrier crossing

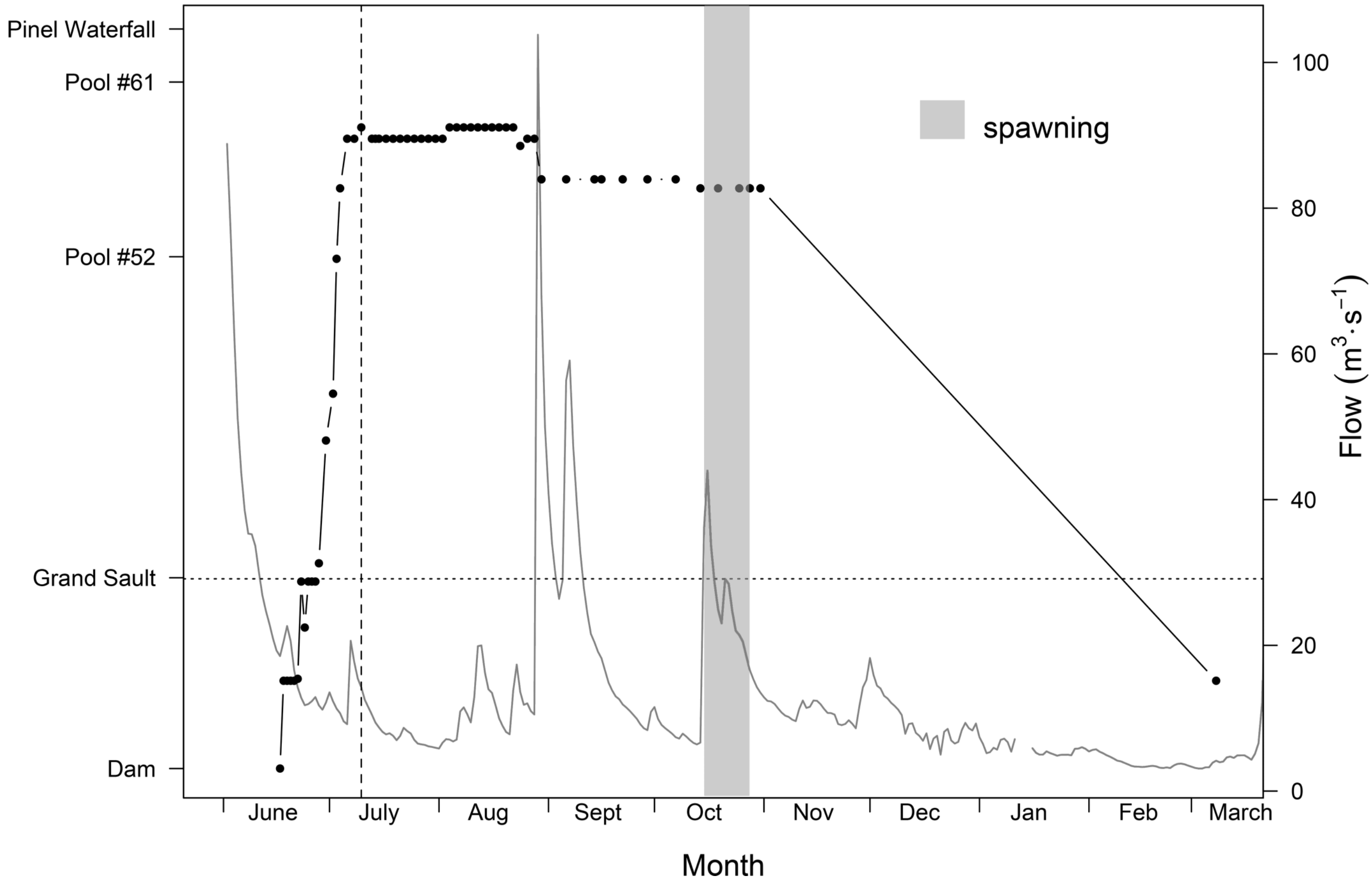
Logistic GLMMs were used to model the daily probability of a salmon to cross the Grand Sault fish ladder. For each salmon, we retained only data from days when it had reached the Grand Sault waterfall without crossing it (coded as 0) and from days when the salmon had crossed the obstacle (coded as 1). All salmon crossed the obstacle except salmon C32, which never crossed the fish ladder — it spawned near pool 18, so it was excluded from this analysis. Finally, we calculated the area under the receiver operating characteristic curve (AUC; Fawcett 2006) to evaluate the predictive performance of the best model using the rocr package in R (Sing et al. 2005).

Propensity to move

To find out which variables influence the upstream migration of Atlantic salmon in natural river segments, we used a two-part modelling approach. First, we modelled the propensity of salmon to move (0 = same location as the last detection, 1 = different location) using logistic GLMMs. The number of the pool from which the salmon started its movement was added to these models as a second random effect to consider, since pools are not evenly distributed along the river and some are better holding pools than others. The data used in tested models included only detections from the active migratory phase of each individual and excluded the detections used to model the fish ladder crossing. An individual's active migratory phase was visually determined by

[1]Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2014-0072.

Fig.2. Example of the migratory behaviour through time of salmon C13 from the C&R group. The vertical gray bar indicates the spawning period, and the vertical dashed line indicates the end of the active migratory phase. Water flow during the study period is represented by the gray curve.



analyzing the salmon's migration pattern graphically (Fig. 2), and it typically corresponded to the time period between river entrance and the moment it reached its most upstream location. The methodology used to assess the fit of the selected best model was the same as for models of fish ladder crossing.

Travelled distance

We then modelled the distance travelled by salmon using GLMMs with a Gaussian distribution. The number of the pool from which the salmon started its movement was added to these models as a second random effect for the reason stated above. In addition, to take into account that salmon were detected every day or every 2 days depending on their position in the river, the dependent variable was the travelled distance divided by the number of days elapsed since the last detection. The fit of the most parsimonious model was assessed using Pearson's goodness-of-fit test and Nagelkerke's R^2. We then used a Markov chain Monte Carlo sample to assess the significance level of the best model's parameters.

Effects of the C&R conditions

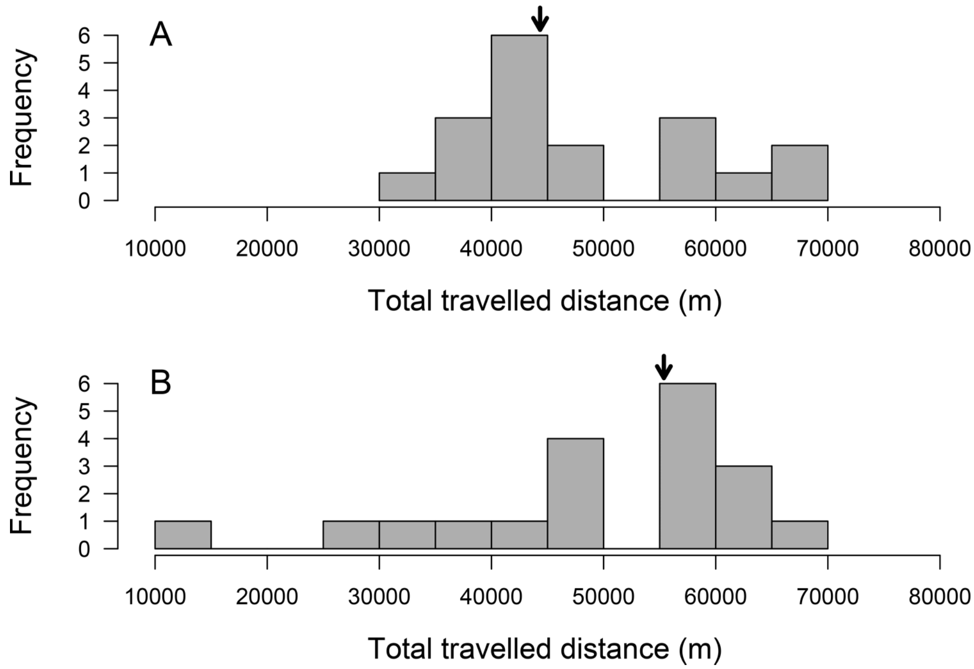
To test whether the stress involved in a C&R event and its associated conditions have an impact on the active migratory phase of the fish, models were refitted for C&R salmon only. The number of C&R salmon for which we had data limited the number of predictor variables that could be included in the models to four. The explanatory variables used were water temperature at release, air exposure time, date of C&R, time elapsed between C&R and the municipal dam crossing, bleeding (blood; 1: yes, 0: no), and the time elapsed between hooking and landing of the fish. For the three migratory aspects mentioned above, 12 models built by combining these variables and their biologically significant interactions were tested. The best model was selected according to the AIC_c criteria.

Results

The results of the genetic identity analysis confirmed that all 20 punched salmon equipped with a transmitter had previously undergone C&R in pool 3 (perfect match for the 12 microsatellites) between 9 June and 8 July 2011. For these 20 salmon, the mean time elapsed between their C&R and their passage in the fish ladder (20 m upstream) was 12 days (range = 3–27 days). Two C&R salmon, C13 and C37, underwent C&R twice in pool 3 before their tagging, and the time elapsed between events was 2 and 4 days, respectively. Only the last C&R event of these fish was considered in the analysis on the effect of C&R conditions on migration.

Owing to their size, all tracked salmon were identified as multi-sea-winter salmon, and the mean total length (range = 70–95 cm) did not differ between groups (C&R = 76 cm, control = 78 cm, Welch two-sample t test, P value = 0.33). One salmon, C49, regurgitated its transmitter when it entered the Grand Sault fish ladder, whereas the transmitter of C23 was faulty, rarely allowing its position to be determined. Both salmon were C&R individuals, and they were excluded from all analyses. An individual from the control group, C46, underwent C&R farther upriver in pool 61 on 13 September. This salmon was kept in the control group for all analyses prior to 13 September but was excluded thereafter.

Fig.3. Observed cumulative distribution of the total travelled distance for C&R (A) and control (B) salmon. Arrows indicate the median of each distribution, which are significantly different (K–S test: *P* value = 0.049).



General migratory pattern

The freshwater migration of all tracked salmon was divided into four distinctive phases; (1) active upstream migration, (2) holding, (3) migration towards and between spawning grounds, and (4) movement towards wintering sites (Fig. 2; Supplementary materials, Fig. S2[1]). After tagging, all fish moved upstream rapidly (mean: 2050 m·day^{-1} during the active upstream migration phase) in a stepwise manner towards the holding pools in the upper sections of the river. This progression was only disrupted, to a variable extent, by the crossing of the Grand Sault fish ladder, where some salmon made downstream movements or long migratory stops. Once in holding pools, salmon were generally motionless for the rest of the summer. However, some of the salmon's holding periods were interrupted by downstream movements toward new holding pools after the freshet caused by Hurricane Irene, which swept through Quebec in late August. Just prior to spawning, most fish moved close to spawning grounds. The direction of these movements depended on the relative locations of holding and spawning sites. Most salmon made upstream and downstream movements throughout the spawning period. It is likely that all salmon spent the winter in the river, since none was detected by the fixed receiver at the municipal dam, and all but one (C44) were precisely located at the end of winter. Two types of behaviour were observed for wintering site selection: some salmon selected wintering sites far downstream from their spawning grounds, whereas others wintered in pools located in the same area where they spawned.

No significant differences were observed between the control and the C&R groups in (*i*) the location of spawning sites (two-sample K–S test; D = 0.23, P value = 0.38), (*ii*) the most upstream location visited in the river (two-sample K–S test; D = 0.20, P value = 0.47), or (*iii*) the wintering site location (two-sample K–S test; D = 0.22, P value = 0.41). However, salmon from the control group tended to travel greater total distances during summer than salmon from the C&R group (55 375 and 44 335 m, respectively), as observed with the cumulative distribution function for the total travelled distance (two-sample K–S test; D = 0.40, P value = 0.049) (Fig. 3).

Barrier crossing

All tracked salmon, except C32 (a control fish, excluded from this analysis), crossed the Grand Sault fish ladder. The daily probability of crossing the Grand Sault fish ladder was positively influenced by mean water temperature for control fish, whereas the probability for C&R salmon was lower and independent of water temperature (Fig. 4). The most parsimonious model for fish ladder crossing had three fixed explanatory variables: mean water temperature (WT), C&R, and their interaction (Table 1; Supplementary materials, Table S1[1]). The WT and WT × C&R variables had significant effects on the dependent variable (P values of 0.003 and 0.047, respectively), whereas the effect of C&R alone was not significant (P value = 0.062). The AUC for this model was 0.68, indicating fair performance of the model. Two tracked salmon crossed the fish ladder more than once (C24 twice and C46 three times), and both were control salmon. All salmon that took 9 days or more (up to 20) to cross the obstacle were C&R salmon.

Propensity to move

During the active migratory phase, salmon were seldom detected in the same pool for 2 consecutive days (total of 114 detections without movement and 312 with movement). The selected model had two fixed explanatory variables: WT^2 and C&R (Table 1). Propensity to move was influenced by the mean water temperature's quadratic term (P value = 0.026), but not by C&R (P value = 0.49; Fig. 5). The model's predictive performance was good, with the AUC being 0.89.

Travelled distance

When active, salmon travelled a wide range of distances between detections (47 to 10 550 m); the number of metres travelled per day was positively influenced by the mean water temperature (P value = 0.023) and negatively influenced by the minimum water discharge between fish detections (P value = 0.015), but not influenced by C&R (P value = 0.66; Table 1; Fig. 6). Indeed, the best model had three parameters (WT_{mean}, Q_{min}, and C&R), fitted the data (Pearson's goodness-of-fit test χ^2 P value = 0.52), and explained 27% of the observed variance (Nagelkerke's modified

Fig.4. The most parsimonious model predictions (solid lines) and associated standard errors (dashed lines) of the probability of crossing the Grand Sault fish ladder for control (gray) and C&R (black) multi-sea-winter salmon in relation to water temperature.

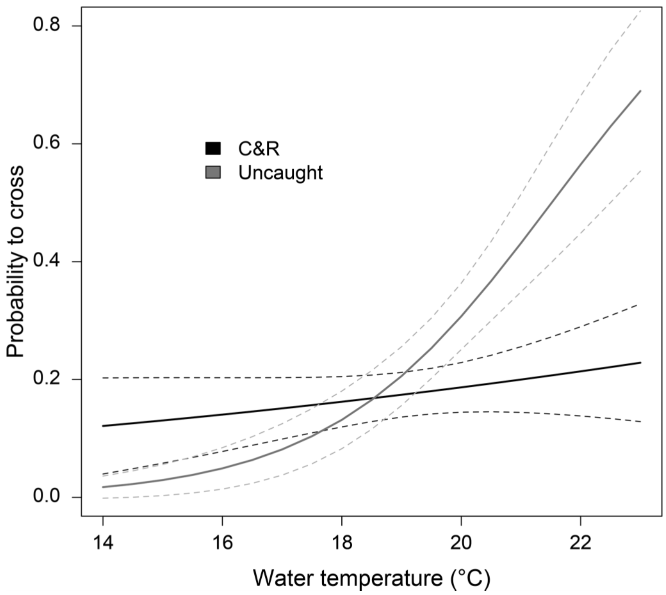
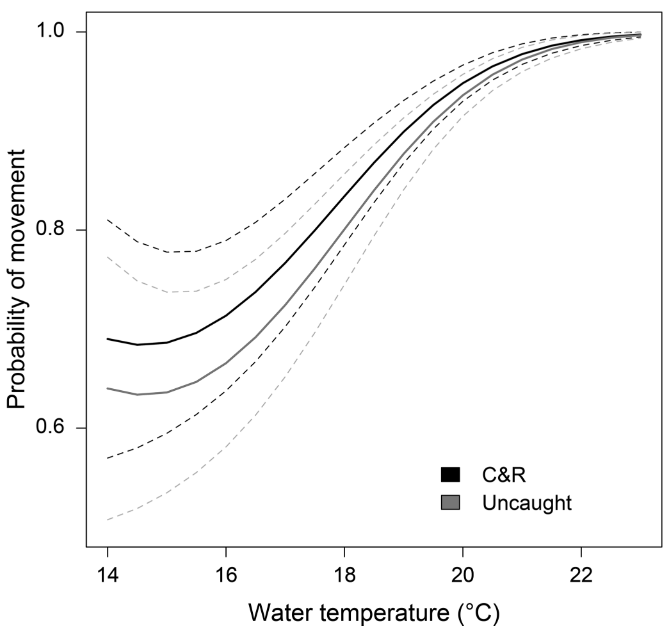


Fig.5. The most parsimonious model predictions (solid lines) and associated standard errors (dashed lines) for the daily probability of movement for control (gray) and C&R (black) multi-sea-winter salmon in relation to water temperature.

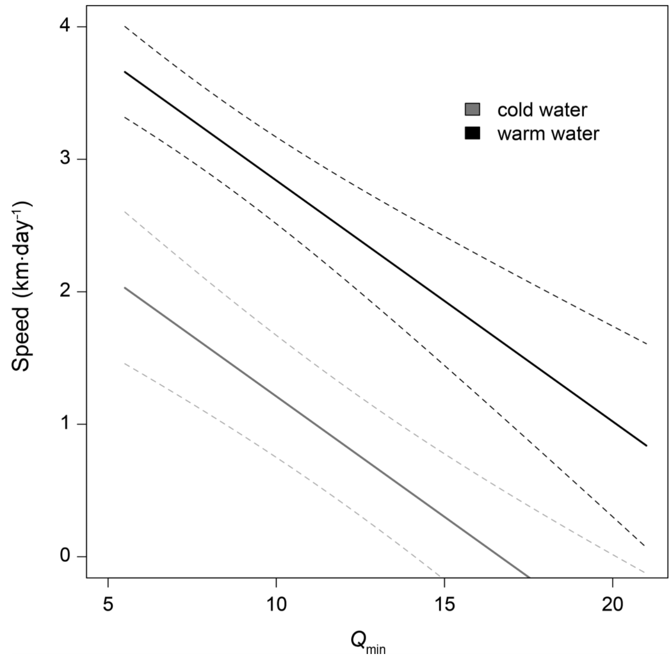


statistic = 0.27). During the active migratory phase, 92% of the recorded movements were directed upstream.

Effects of the C&R conditions

Six of the tracked C&R salmon were kept in the water through the C&R process while others were exposed to air for 5 to 30 s. The time required by fishermen to land their catch ranged between 4 and 22.5 min, and bleeding was reported for four C&R salmon. Water temperature recorded during C&R events varied between 11.6 and 16.4 °C (mean = 14.5 °C).

Fig.6. Effect of water temperature and discharge (Q_{min}) on the distance travelled by multi-sea-winter salmon per day as illustrated by predictions from the most parsimonious model (solid lines) and their associated standard errors (dashed lines). To show the influence of water temperature, the predictions are plotted for the maximum (black: warm = 22.4 °C) and minimum (gray: cold = 13.7 °C) temperature recorded during the active migratory phase.



Our analyses detected no significant effect of C&R on salmon probability of crossing the Grand Sault fish ladder or on the propensity to move. Indeed, in both cases the most parsimonious model was the null model. However, water temperature at release positively influenced the travelled distance per day by C&R salmon (P value = 0.009); the model with the lowest AIC_c had only water temperature at release as the fixed variable.

Discussion

This study sheds new light on the prespawning migratory behaviour of Atlantic salmon in a river system located in the southern part of the species' distribution area. Temperature was found to be determinant in influencing movement and the probability of a fish to cross obstacles, while water discharge influenced the daily travelled distance. All salmon from both C&R and control groups survived, and no difference in their spawning and wintering locations were detected. Nevertheless, C&R was found to decrease the probability of a fish to cross a barrier during an appropriate temperature window and, to some extent, to decrease the total distance travelled in the river. This suggests that while salmon that were caught and released by rod fishermen survive, prespawning exploration behaviour could be altered compared with uncaught salmon.

General migratory pattern

Returning Atlantic salmon were observed to have three successive phases of freshwater migration before spawning: (1) active upstream migration, (2) holding, and (3) migration towards and between spawning grounds. This migratory pattern, although observed in some Pacific salmonids (Berman and Quinn 1991; Strange 2012), differs from that observed for Atlantic salmon in the large Tana River in northern Norway, where the three main phases were found to be (1) migratory, (2) search, and (3) holding (Økland et al. 2001). This latter pattern had been generally accepted as the normal riverine migratory behaviour for Atlantic salmon and was used as a reference in previous C&R studies lacking control groups (e.g., Jensen et al. 2010). In the Tana River (mean annual discharge = 160 $m^3 \cdot s^{-1}$), the search and selection of spawning grounds thus occurred before the holding period, approximately 50 days before spawning (Økland et al. 2001), whereas we observed that the searching phase preceded spawning in the smaller Escoumins River system (mean annual discharge = 14.8 $m^3 \cdot s^{-1}$). This was also observed in Catamaran Brook, a tributary in the Miramichi River system in New Brunswick, Canada (Mitchell and Cunjak 2007), as well as in other small systems (Hawkins and Smith 1986; Laughton 1991; Bardonnet and Baglinière 2000). In large rivers, good holding pools may be abundant, enabling salmon to stay in the area of their selected spawning site while waiting to reproduce. However, quality holding pools may be sparser in smaller streams, potentially forcing salmon to first select an appropriate pool in which to spend the summer and then to reach the spawning grounds further upstream or downstream later in the season, during the fall freshets.

Influence of temperature and water discharge on migratory behaviour

Water temperature was found to positively affect a control salmon's daily probability to ascend a fish ladder, with probabilities increasing from 16 °C, reaching 20% at 19 °C, and being as high as 70% at 23 °C (Fig. 4). While this pattern was also reported elsewhere (Jensen et al. 1986; Gowans et al. 1999), no relationship between water temperature and fish ladder crossing was observed in other systems (Trépanier et al. 1996). Being poikilotherms, the maximum swimming speed (Salinger and Anderson 2006), scope for aerobic activity (Brett 1964; Booth et al. 1997), and recovery capacity (Wilkie et al. 1997) in salmonids all increase with water temperature to an optimal point (around 20–22 °C for Atlantic salmon; Elson 1969 in Todd et al. 2010) and then drop as oxygen concentration decreases (Salinger and Anderson 2006). In another study, where Atlantic salmon ascending a fish ladder were equipped with electromyogram transmitters, Booth et al. (1997) observed that the ascent of a fish ladder resulted in a lower oxygen debt at 18 °C than at 12 °C because of the relationship between critical swimming speed and temperature. Water temperature imposes important physiological constraints and thus influences activity, so fish adjust their movements accordingly (Wootton 1998). In our study, water temperature fluctuated hourly and ranged from 13.7 to 25.9 °C at the fish ladder, giving daily opportunities for fish to cross the obstacle at close to the optimal temperature while avoiding the more critical temperature ranges (0–7 and 22–33 °C; Jonsson and Jonsson 2009). Constant extreme low and high temperatures were not observed in this study, which can explain the observed monotonic increase in fish movement probability with temperature, in contrast with the unimodal relationship expected when salmonids are exposed to a wider range of temperatures (Salinger and Anderson 2006). At temperatures below 8 °C, Atlantic salmon did not ascend the Forsjordforsen waterfall in Norway (Jensen et al. 1986). According to our results and those from the literature (Todd et al. 2010), we could thus expect a low probability of fish to cross an obstacle below 10 °C and above 25 °C, but these temperature limits would need to be evaluated in future studies conducted in the wild, especially in the context of global warming.

Increased temperature also positively influenced the daily probability of salmon movement in general, namely the propensity to initiate movements and the distance travelled daily. As was the case for ladder crossing, the propensity to initiate movement increased from approximately 65% at 16 °C and reached 100% probability at 23 °C. The propensity of Atlantic salmon to move and daily travelled distances have rarely been studied in the wild, since most studies focussed on factors affecting river entrance or fish ladder crossing (Jonsson and Jonsson 2011). However, Erkinaro et al. (1999) observed that changes in river discharge and air temperature in the Tana River were not different between days when the salmon were migrating and days when they were not. Although we found that temperature was the primary variable affecting fish movement in the river, water discharge was also an important factor influencing daily travelled distance. Indeed, daily travelled distance increased with decreasing water discharge, and minimum rather than mean water discharge was identified to be the best predictor. This could suggest that the salmon's daily swimming movements are concentrated within periods of the day when water discharge is at its minimum.

Water temperature and discharge have been identified as the two most important variables influencing upstream migration of adult salmonids in general (Jonsson and Jonsson 2011); however, the exact relationship was found to vary according to the system studied. In the Tana River, Erkinaro et al. (1999) found that an increase in discharge increased the migration speed of tracked Atlantic salmon, whereas Trépanier et al. (1996) observed that the ascent of landlocked Atlantic salmon was negatively influenced by an increase in water discharge in the Mistassini River, Quebec, Canada. Similarly contrasting results have been reported for other salmonids (Jonsson and Jonsson 2011). For instance, the travel rate of sockeye salmon (*Oncorhynchus nerka*) of the Columbia River increased over the years as water discharge decreased (Quinn et al. 1997), while Chinook salmon (*Oncorhynchus tshawytscha*) of the same river migrated more slowly when water discharge was high (Keefer et al. 2004*b*). Still other studies found no relationship between river discharge and salmon migration rate (Karppinen et al. 2004; Salinger and Anderson 2006), highlighting the complexity of the relationship between water discharge and migration rate. These variable results suggest that other factors, namely temperature, might be of importance and also influence travelled distance. However, since swimming costs increase with increasing water discharge levels (Enders et al. 2005), and considering that the number of good holding pools (and thus the opportunity to make rest pauses during migration) in a small river like the Escoumins River is directly related to water discharge, it could be advantageous for salmon to migrate longer distances in low water discharge conditions.

Effects of C&R on migratory behaviour

The distributions of C&R and control salmon were similar in the river. All salmon (C&R and control) reached spawning grounds, and no difference in the distribution of spawning and wintering site locations was observed between the groups. In other studies, most tracked C&R individuals were registered on known spawning areas during the reproductive period (Webb 1998; Thorstad et al. 2003, 2007; Jensen et al. 2010) and were thus considered as successful spawners; this hypothesis was supported by a recent study on the reproductive success of Atlantic salmon (Richard et al. 2013). Furthermore, the capacity of C&R salmon to reach the same spawning grounds as uncaught individuals was also observed in the Dee River in Scotland (Webb 1998) as well as the Alta River in Norway (Jensen et al. 2010). This observation is of primary importance, since individuals are known to return to specific areas within their natal river (Heggberget et al. 1988). This behaviour can result in the genetic differentiation of subpopulations within watersheds (Spidle et al. 2001; Vähä et al. 2007; Dionne et al. 2009) and allows the evolution of fine-scale local adaptations (e.g., Landry and Bernatchez 2001).

Compared with the behaviour of control salmon, C&R fish displayed lower probabilities of crossing obstacles, even at appropriate water temperatures, and consequently could have longer stops during freshwater migration (between 9 and 20 days at the foot of a fish ladder). Furthermore, C&R salmon travelled shorter distances overall during the summer and fall than the control fish; this behaviour has also been observed in the Upsalquitch River, Canada (Tufts et al. 2000). These results suggest that while C&R does not affect the salmon's capacity to reach spawning grounds in a small river, it can alter salmon migratory behaviour. This could be a consequence of the stress and physiological disequilibrium caused by C&R, as observed in previous laboratory studies (e.g., Tufts et al. 1991), although it was shown that salmon could recover their physiological stamina within 4 to 12 h after exhaustive exercises in warm water (above 18 °C) (Tufts et al. 1991; Brobbel et al. 1996; Wilkie et al. 1997). Another explanation could be that salmon are injured during C&R, and these injuries then alter their physical capacity and ultimately their migratory patterns. This could be a non-negligible factor, as has been found in other fisheries such as that for rainbow trout (*Oncorhynchus mykiss*) in Alaska, where up to 60% of the C&R fish were found to be injured (Meka 2004). However, fishermen in our study conducted C&R with great care and injuries were infrequent, which lends support the physiological disturbance hypothesis. Overall, based on these results and those of Richard et al. (2013), we propose that the observed influence of C&R on the migratory behaviour of Atlantic salmon likely has little or no impact on salmon fitness in terms of survival and reproductive success, although it could alter its prespawning exploration behaviours depending on the environmental conditions of the river system.

Acknowledgements

We acknowledge the collaboration of Escoumins River fishermen, without whom this project would have been impossible. We thank J. Bédard, E. Henry, J.-F. Tremblay, M. Racine, G. Gravel, M. Talbot, N. Harnois, D. Fournier, V. Cauchon, and W. Cayer-Blais for field assistance and Y. Demers, A. Dussault, and the staff at the Corporation de Gestion de la Rivière à saumon des Escoumins (CGRSE) for their warm welcome and help. This project was funded by the Ministère des Ressources naturelles et de la Faune du Québec (MRNF) and the CGRSE, and followed up an NSERC (Natural Sciences and Engineering Research Council of Canada) strategic project grant to L.B. Data are available on demand from the corresponding author.

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