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# Effect of catch-and-release and temperature at release on reproductive success of Atlantic salmon (*Salmo salar* L.) in the Rimouski River, Québec, Canada

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## Abstract

Catch-and-release fishing is a common conservation practice in recreational fisheries for Atlantic Salmon, although the effects on the reproductive success of caught-and-released fish are poorly understood. Herein, we compared the relative reproductive success of caught-and-released to non-caught salmon and tested the effect of temperature at release on reproductive success in the Rimouski River, Québec, Canada. At least 83% of caught-and-released salmon that moved upstream of a dam successfully reproduced, including fish that have been released in water above 20°C. However, the reproductive success of caught-and-released female salmon was only 73% of the reproductive success of non-caught salmon. Moreover, the increasing temperature did not affect the reproductive success of released fish that entered a trap, but fish caught at warmer temperatures were less likely to enter the trap. Our findings should be useful for evaluating the risks and benefits of catch-and-release, and for optimising conservation practices used for the preservation of Atlantic salmon populations.

KEYWORDS
Atlantic salmon, catch-and-release, management, recreational fisheries, reproductive success, temperature

## 1 | INTRODUCTION

The Atlantic salmon (*Salmo salar*) is an emblematic species that supported subsistence fisheries for thousands of years, as well as commercial and recreational fisheries for decades (Aass et al., 2011; MacCrimmon & Gots, 1979). Yet, many populations have declined drastically in abundance throughout the species' range, which led to closures and restrictions of fisheries (Chaput, 2012; Lehnert et al., 2019). Nevertheless, the species remains a highly prized game fish that is targeted by recreational anglers across North Atlantic during its upstream spawning migration (ICES, 2019). In Eastern Canada alone, recreational fisheries targeting Atlantic salmon generate over $100 million annually, which makes it a high priority for both fishery management and conservation efforts (Atlantic Salmon Federation, 2011). Towards this goal, catch-and-release fishing has increasingly been used to minimise negative impacts on exploited populations (Brownscombe et al., 2017; ICES, 2019; Ministères des Forêts, de la Faune et des Parcs (MFFP), 2016). For instance, in Canada, the number of caught-and-released salmon increased by 109% from 1991 to 2019 (ICES, 2019).

The success of catch-and-release as a management tool relies on released fish surviving to reproduce (Arlinghaus et al., 2007; Brownscombe et al., 2017). However, catch-and-release angling can reduce survival by increasing stress, altering migration and reducing growth (Arlinghaus et al., 2007), and modifying the species' role in biological communities (Cooke & Sneddon, 2007). Indeed, catch-and-release is generally considered an exhaustive exercise that contributes to the accumulation of lactate and metabolic protons in the white muscle through anaerobic glycolysis (i.e. glycolytic ATP production; Pörtner, 2002). While lactate requires time and energy to clear from muscle tissues (Wood, 1991), the accumulation of metabolic protons reduces intramuscular pH, which can lead to intracellular acidosis (Wood et al., 1983). These by-products ultimately increase the risk of mortality of released fish, although mortality rates vary greatly among species (ranging from 0% to 95% across a variety of marine and freshwater organisms; Bartholomew & Bohnsack, 2005).

While several factors increase the risk of post-release mortality, water temperature at capture is generally a good predictor of risk (Gale et al., 2013; Lennox et al., 2017). Being ectotherms, fishes' internal temperature is directly controlled by the environment. Hence, variation in water temperature modulates metabolic processes and cardiac output, so fish function normally within a limited window of temperature (Fry, 1971). When temperature increases beyond this window, the basic metabolic rate increases beyond what oxygen intake can deliver such that anaerobiosis eventually replaces aerobic respiration (Pörtner & Knust, 2007).

Combined with high temperature, exhaustive exercise from catch-and-release can impair the ability of released fish to replenish intramuscular glycogen and thereby increase the risk of intramuscular acidosis due to high levels of lactate content (Wood et al., 1983). In the case of Atlantic salmon, decades of research have demonstrated that elevated water temperatures pose a risk for the survival of released fish, although this risk is also influenced by air exposure time, gear and bait types and angler experience (Cooke & Suski, 2005; Lennox et al., 2017). Recent modelling showed that post-release mortality was low (<5%) at water temperatures ranging from 0 to 12°C, but increases with temperature up to 35% at water temperatures ranging from 20 to 25°C (Van Leeuwen, Dempson, Burke, et al., 2020; Van Leeuwen, Dempson, Cote, et al., 2020).

Given the physiological impact of elevated river temperature on released fish, evaluating its consequences on reproductive success is key to determining the long-term sustainability of catch-and-release fishing (Gale et al., 2013). Caught-and-released salmon can reproduce at a similar reproductive fitness as non-caught salmon, albeit in a river that rarely exceeded 20°C during the fishing season (Richard et al., 2013). However, released fish tended to have reduced reproductive success when the water temperature at capture ranged from 12°C to 18°C (Richard et al., 2013). Hence, while temperatures above 20°C are known to increase sublethal impairment and post-release mortality through anaerobiosis (Wilkie et al., 1996, 1997), the effects of reduced reproductive fitness of caught-and-released salmon have become increasingly important to understand as climate change exerts additional pressure on fisheries (Lennox et al., 2017; Van Leeuwen, Dempson, Burke, et al., 2020).

Herein, we evaluated the relative reproductive success and the effect of temperature at release on the reproductive success of caught-and-released to non-caught Atlantic salmon. We used molecular parentage analysis to link putative parents with their young-of-the-year progeny. Our study system was a wild anadromous population spawning in the Rimouski River, Québec, Canada. The Rimouski River salmon population is increasingly exploited by recreational anglers who use catch-and-release, such that 100 salmon are now caught-and-released annually (Ministères des Forêts, de la Faune et des Parcs (MFFP), 2020). The Rimouski River is also one of the warmest salmon rivers in Québec which frequently exceeds 20°C during the fishing season (MFFP, rivtemp.ca/mffp_qc/). Thus, this system allowed us to assess the ability of caught-and-released salmon to reproduce when released at elevated water temperature, which is expected to increase post-release physiological impacts and mortality (Van Leeuwen, Dempson, Burke, et al., 2020).

## 2 | MATERIALS AND METHODS

### 2.1 | Study area and anadromous adults sampling

The Rimouski River is located on the south shore of the St. Lawrence Estuary, Québec, Canada (48°44′N; 68°53′W; Figure 1a). A dam acting as a complete barrier to upstream migration is located 4 km upstream from the river mouth where was previously located an impassable natural waterfall. Before human intervention allowed salmon to colonise the river upstream of the dam in 1997, all salmon spawned downstream of the dam. During their upstream migration, most adult fish are now trapped in a cage and transported 1 km above the dam to be released upstream. The proportion of anadromous adults remaining downstream of the dam is not known. Spawning occurs downstream of the dam, but salmon that remained in this minor section of the river were excluded from our study because they were not counted or sampled. Fork length was measured, and fin samples (adipose or caudal) were taken from all anadromous adults crossing the dam in 2018 when fish were released across the dam. The genetic sex of every returning adult was determined using King and Stevens (2019) PCR-amplification-based method.

### 2.2 | Atlantic salmon recreational fishery in the Rimouski River and sampling of caught-and-released salmon

Recreational Atlantic salmon angling on Rimouski River is restricted to summer months beginning on June 15th and closing on September 30th. Anglers must register at the Rimouski ZEC (Area of Controlled Exploitation), which monitors recreational fishing activities on the river. Provincial regulations allow anglers to keep up to two grilses (salmon <63 cm in fork length) or to catch and release three salmon, whichever is reached first. All large salmon (>63 cm) must be released. During the 2018 fishing season, angler participation was requested to collect tissue samples from caught-and-released salmon (punch of 5 mm diameter of adipose fin or caudal fin if adipose was

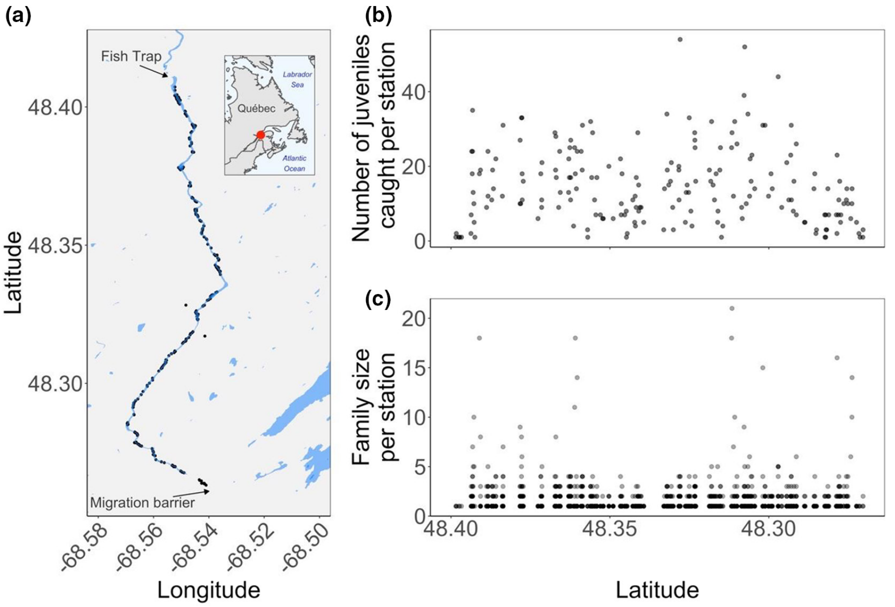


**FIGURE 1** (a) Rimouski River, Québec, Canada. Atlantic salmon return to Rimouski River from the ocean throughout the summer and migrate upriver to spawning grounds via the fish trap. Note that the river flows from south to north, draining into the St-Lawrence River. For this study, 31 of 33 caught-and-released salmon were caught north of the fish trap, and 18 of 33 salmon crossed the fish trap. All the 252 electrofishing stations are indicated on the river and the number of juveniles caught per station and the family size per station are displayed in (b and c) respectively.

previously clipped) and to gather information on the event. To facilitate sampling, anglers received punch pliers coupled with a kit that contained a 1.5-ml Eppendorf filled with 95% ethanol to preserve the adipose punch and a waterproofed sheet to record information on the catch-and-release event. After each event, anglers recorded the date, time of day, pool number, presence of bleeding, and approximate air exposure duration. Temperature data loggers were placed in all frequently visited river pools. Given the information collected by the anglers, we could record the water temperature during the release. Angler participation was not mandatory, the scientific team was present every fishing day in the main pools to promote the project and assist anglers during sample collection. Most catch-and-release events were below the fish trap in the Rimouski River. We expected that some fish would not cross the dam, so we evaluated whether released salmon that did not enter the fish trap were released at a warmer temperature and if they were exposed to air longer than fish that entered the trap.

## 2.3 | Electrofishing

From July 15 to August 15, 2019, young-of-the-year (or fry, age 0+) Atlantic Salmon born in the river were sampled using electrofishing over a stretch starting from the dam and ending 21 km upstream at an impassable waterfall. The very small tributaries of this river stretch do not provide known spawning grounds (i.e. significant habitat for juveniles) because of their limited accessibility. Fry samples were conserved in 15-ml Falcon tubes filled with 95% ethanol. Within every 1 km reach, 12 electrofishing sites (mean area 100 $m^2$; Figure 1a) with a suitable fry habitat suitability index were sampled (provided by the Québec Minister of Forests, Wildlife and Parks (MFFP)). Each site was electro-fished once to maximise the number of sites sampled each day.

## 2.4 | Molecular analyses

DNA was extracted from adult adipose fin tissue and fry caudal fin tissue using a salt extraction method (Aljanabi & Martinez, 1997). Fifty-two microsatellite loci were then amplified by PCR in two multiplexes (panels 1a and 2a) developed by Bradbury et al. (2018). Locus amplification followed the protocol of Zhan et al. (2017). Libraries were sequenced at 10–12 pM concentration at the genomic platform of the Institut de Biologie Intégrative et des Systèmes (IBIS), Université Laval, Québec (http://www.ibis.ulaval.ca/). Sequencing was performed using Illumina MiSeq (Illumina) and the MiSeq Reagent Kit V3 with 150 cycles in one direction and dual indexing. Indexed individuals were demultiplexed with the MiSeq Sequence Analysis software. Allelic sizes were then scored using MEGASAT (Zhan et al., 2017) setting minimum depth (per sample per locus) at 20 reads (i.e. alleles with fewer than 20 reads were not called). Examination of histogram outputs (depth vs. allele size) from MEGASAT confirmed allele scores, and scores were adjusted when necessary. Loci with more than 10% missing data for both parents and offspring were removed from the dataset to ensure the precision of parentage analysis.

## 2.5 | Parentage assignment and analysis of the relative reproductive success

Parentage was allocated using Cervus v 3.0 (Kalinowski et al., 2007; Marshall et al., 1998). Cervus3 uses simulated parents and offspring to determine cut-off points of log-likelihood (LOD) scores for true parents, which are then used to identify parent–offspring pairs in empirical data. The number of offspring assigned to a spawner was used as a measure of reproductive fitness. Then, the ratio of reproductive fitness was computed as the ratio of caught-and-released/

non-caught fish, as a measure of relative reproductive success (Equation 14 of Araki & Blouin, 2005):

$$RRS_{[unbiased]} = \frac{\widehat{W_x} - \left(\frac{N_{offspring} - N_{assigned}}{N_{parent}}\right)\left(\frac{\hat{b}}{1-\hat{b}}\right)}{\widehat{W_y} - \left(\frac{N_{offspring} - N_{assigned}}{N_{parent}}\right)\left(\frac{\hat{b}}{1-\hat{b}}\right)}$$

where $\widehat{W_x}$ and $\widehat{W_y}$ are the mean fitness of individuals in each group, $N_{offspring}$ is the total number of offspring sampled, $N_{assigned}$ is the number of offspring assigned to a parent, $N_{parent}$ is the total number of parents and $\hat{b}$ is the rate that an offspring, which is not assigned to its true parent, is assigned to an untrue parent. Analyses were performed first on both sexes and then separately for each sex because males and females may respond differently to catch-and-release. To test for statistical significance, non-parametric two-tailed permutations were used to test the hypothesis that caught-and-released fish were less fit than non-caught fish (i.e. relative reproductive success <1.0). The numbers of offspring assigned to each parent were permutated 1,000,000 times without replacement and the probability of obtaining a value equal or larger than the observed fitness difference was evaluated (see Araki & Blouin, 2005 for details). Following Araki and Blouin (2005), the maximum-likelihood method developed by Kalinowski and Taper (2005) was used to calculate confidence intervals for relative reproductive success.

### 2.6 | Effect of temperature and air exposure time on the reproductive success of C&R salmon

Temperature and air exposure were tested as stresses involved in catch-and-release on the number of fries produced by caught-and-released salmon (Richard et al., 2013). A global negative binomial model was fitted with the pscl package in R using predictor variables for temperature, air exposure and body length (Jackman, 2020). A negative binomial model was used because it better describes over-dispersed count data than a Poisson model. To assess the fit of the global model, quantile–quantile residual distributions and rootograms were used to graphically compare empirical frequencies to fitted frequencies using the package countreg in R (Zeileis & Kleiber, 2018). Three candidate models were nested within the global model, along with an intercept-only null model, to test biological hypotheses (Table 2). Models were ranked using AICc (a corrected measure of AIC for small samples) and Δ AICc (AICc of the model minus the AICc of the best model).

## 3 | RESULTS

From June 15 and October 30, 2018, 475 anadromous Atlantic salmon (273 males and 202 females) entered the fish trap and were transported above the dam. The anadromous population that entered the fish trap was composed of 57% ($n = 271$) multi-sea-winter salmon >63 cm and of 43% ($n = 204$) one-sea-winter salmon <63 cm (MFFP, 2016, 2020).

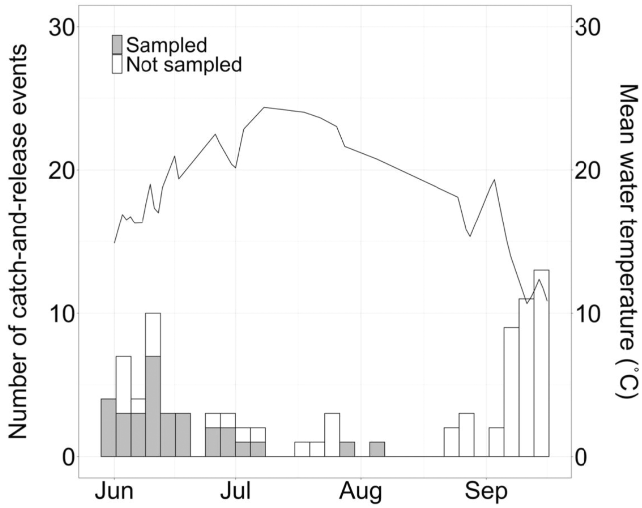


**FIGURE 2** Number of Atlantic salmon caught-and-released (bars) and daily mean water temperature (line) in the Rimouski River, Québec, Canada, during the 2018 angling season.

Of the 89 salmon that were caught-and-released by anglers, 33 were sampled (Figure 2). Most catch-and-release events were below the dam (31/33), 3 km upstream from the mouth of the river and 1 km downstream from the dam. Of the 31 caught-and-released salmon below the dam, 18 entered the fish trap (Table 1; Figure 1). Thus, reproductive success was estimated for 13 multi-sea-winter females (mean ± SD length = 78.1 ± 5.6 cm), 3 multi-sea-winter males (length = 76.1 ± 4.79 cm) and 1 one-sea-winter male (length = 55 cm; Figure 3). Most salmon that entered the fish trap were multi-sea-winter (17 MSW and 1 1SW), whereas salmon that did not enter the fish trap were evenly distributed between multi-sea- and one-sea-winter fish (7 MSW and 8 1SW).

Caught-and-released salmon that did not enter the fish trap was released at significantly warmer water temperature than salmon that entered the fish trap (Figure 4a; $t$: 3.832, $p = 0.0006$), although they were not kept out of water longer (Figure 4b; $t = -0.93$, $p$-value = 0.36). Two salmon that did not enter the fish trap and two salmon that entered the fish trap suffered hook wounds that caused mild superficial bleeding.

After filtering out loci with more than 10% missing data for both parents and offspring, 38 polymorphic microsatellite loci were retained for subsequent analyses. The number of alleles ranged from 3 to 13 per locus (average = 7) and heterozygosity ranged from 0.024 to 0.8396 (average = 0.55). For the 475 adults transported above the dam, complete genotypes were obtained for 468 individuals that were then used for parental allocation (Table 1). Of 2495 fry sampled over 252 electrofishing stations during July and August in 2019 (Figure 1a), 101 fries (SD: 72.2) were sampled per station, with an average family size per station of 12.1 fries (SD: 14.8) (Figure 1b,c). Every sampled fry was genotyped and assigned to putative parents that spawned above the

TABLE 1 Relative reproductive success (RRS) of naturally spawning $F_1$ Atlantic salmon parents in the Rimouski River, Québec, Canada, during the 2018 angling season: RRS is the reproductive success (RS) of caught-and-release (C&R) fish over the RS of non-caught fish

| Sex | RRS | $n\ F_1$ (C&R/N-C) | $n\ F_2$ (C&R/N-C) | RS C&R | Variance C&R | RS N-C | Variance N-C | *p*-value | 80%/95% power |
|---|---|---|---|---|---|---|---|---|---|
| Female and male | 0.736 | 17/254 | 161/2362 | 9.47 | 103 | 12.7 | 196 | <0.01 | 0.864/0.844 |
| Female | 0.732 | 13/174 | 124/2362 | 9.54 | 77.8 | 13.5 | 206 | <0.01 | 0.900/0.848 |
| Male | 0.797 | 4/75 | 37/869 | 9.25 | 236 | 11.6 | 173 | 0.0738 | 0.821/0.709 |

*Note*: nF1 is the sample size for naturally spawning caught-and-released (C&R) and non-caught (N-C) parents; nF2 is the number of offspring assigned to each group of parents; RS is reproductive success measured as the mean number of offspring assigned per parent; Variance is the average of squared differences from mean reproductive success; *p*-values are based on two-tailed permutation tests; and statistical power is the RRS value that would be significant with 80% and 95% probability.

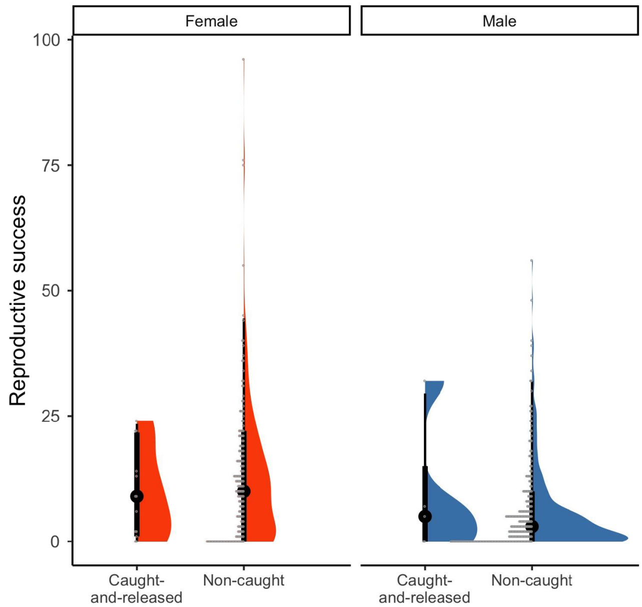


FIGURE 3 Reproductive success of caught-and-released and non-caught females (left) and males (right) Atlantic salmon in the Rimouski River, Québec, Canada, during the 2018 angling season. Half-violin plots represent the density of reproductive success (y-axis), while points represent individual salmon. Median reproductive success is represented by black dots, 25 and 75 percentiles are represented by thick lines and the maximum value is represented by thin lines.

dam during Autumn 2018. The paternity of 1617 offspring and the maternity of 2495 offspring were unambiguously assigned to anadromous adults. The unassigned paternity was caused by the presence of sneaker males.

Overall, the reproductive success of caught-and-released salmon was significantly lower (73.6%) than non-caught salmon (Table 1). Reproductive success of multi-sea-winter females (73.2%) and males (79.7%) was also lower than their non-caught counterparts but was only significant for females.

The model that best explained the reproductive success of caught-and-released salmon was the null model, whereas the global model was the least likely model among those considered (Table 2). Therefore, neither air exposure nor water temperature significantly affected the number of offspring produced. Surprisingly, the salmon that was caught-and-released at the warmest water temperature (23°C) was associated with the highest observed reproductive success among fish caught-and-released by anglers (Figure 5b).

## 4 | DISCUSSION

We found that catch-and-release events reduced the estimated reproductive success (number of assigned offspring) of salmon by 26% (CI:14%–37%). However, there was no evidence that elevated water temperature influences the reproductive output of caught-and-released fish. Nonetheless, fish caught at warmer temperatures were less likely to enter the trap which ultimately suggests that temperate at capture could potentially affect behaviour and possibly, spawning behaviour. Below, we highlight the conservation implications of these results which should contribute to guiding future directions for the management of Atlantic salmon populations

### 4.1 | Reduced reproductive success of caught-and-released salmon

Multiple mechanisms could cause reduced reproductive fitness of caught-and-released salmon. For instance, catch-and-release disrupts gametogenesis because of the reallocation of energy during reproductive maturation in sockeye salmon, *Oncorhynchus nerka* (Patterson et al., 2004), and alters courting and mating behaviour in smallmouth bass, *Micropterus dolomieu* (Cooke et al., 2002). However, the cause of reduced fitness is difficult to pinpoint in our study. Previous studies convincingly demonstrated that catch-and-release did not affect the gamete or fry quality of Atlantic salmon (Booth et al., 1995; Davidson et al., 1994). Nonetheless, a recent simulation of Atlantic salmon suggested that migration distances were shorter for caught-and-released salmon, likely from stress and exhaustion (Lennox et al., 2016; but see Thorstad et al., 2003). This suggests that breeding success could be influenced by stress that is strongly linked to physiological conditions on spawning grounds (Hendry & Beall, 2004). Ultimately, hindered migration after release that reflects reduced activity during spawning season could result in fewer reproductive encounters or nests built by released salmon which would reduce fitness.

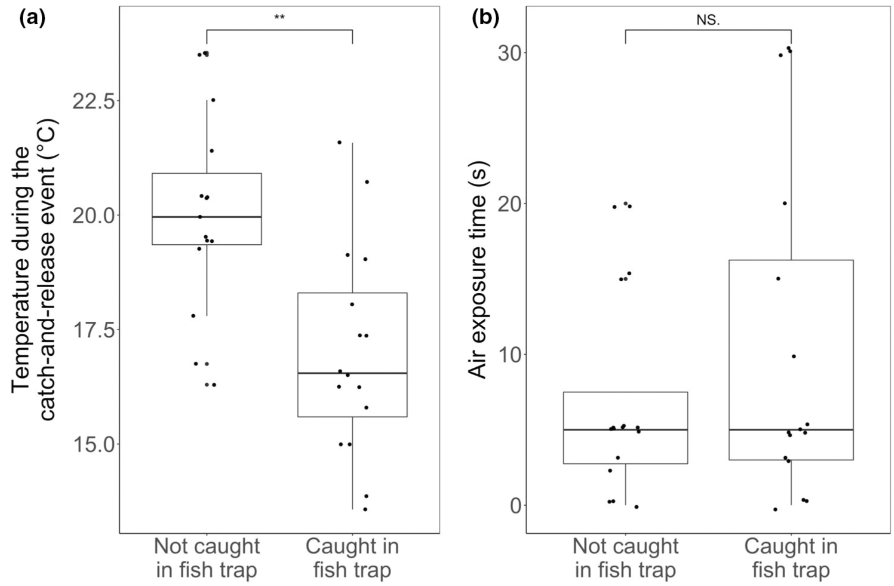


**FIGURE 4** Temperature during catch-and-release events (a) and air exposure time (b) for caught-and-released Atlantic salmon that were released downstream of the fish trap and were either caught or not caught in the fish trap in the Rimouski River, Québec, Canada, during the 2018 angling season. Caught-and-released salmon that did not enter the fish trap were released at significantly warmer water temperature than those that entered the fish trap (Figure 2a; $t$: 3.832, $p = 0.0006$), but were not kept out of water for a longer amount of time (Figure 2b; $t = -0.93$, $p$-value $= 0.36$).

**TABLE 2** Negative binomial model selection results for the reproductive success of caught-and-released Atlantic salmon in relation to temperature and air exposure in the Rimouski River, Québec, Canada, during the 2018 angling season

| Model no. | Intercept | Temperature | Air exposure | Length | K | LogLik | AICc | ΔAICc | $\omega_i$ |
|---|---|---|---|---|---|---|---|---|---|
| 1 | 2.23 | | | | 2 | −49.50 | 121.53 | 0.00 | 0.69 |
| 2 | 2.05 | | 0.015 | 0.0001 | 3 | −48.65 | 123.60 | 2.07 | 0.25 |
| 3 | 0.88 | 0.07 | | −0.05 | 3 | −49.09 | 127.43 | 5.90 | 0.04 |
| 4 | −3.74 | 0.16 | 0.05 | 0.03 | 4 | −48.30 | 128.46 | 6.93 | 0.02 |

*Note*: The number of parameters (K), log-likelihood value (LogLik), small sample bias-adjusted AIC (AICc), the difference in AICc from the model plausible model and (ΔAICc) Akaike weights (ωi) are provided for each model.

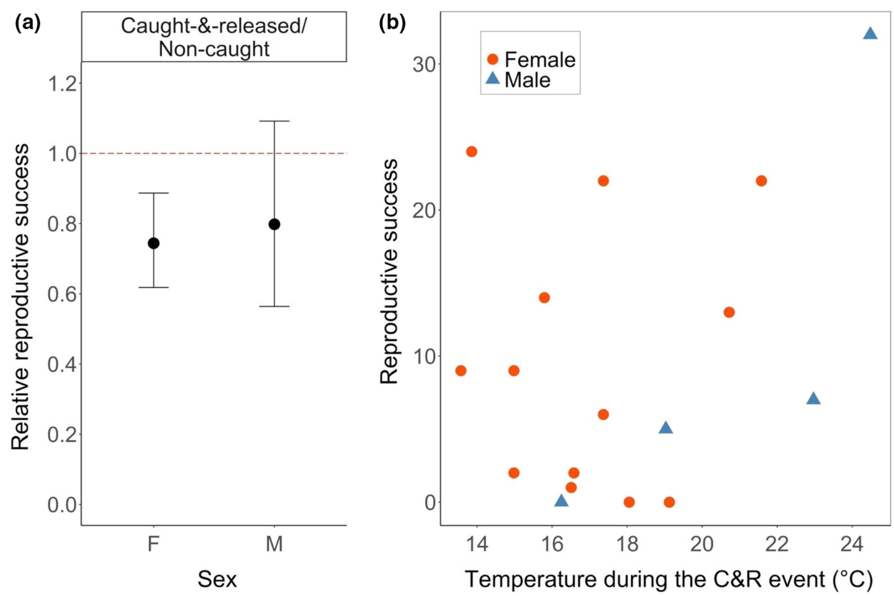


**FIGURE 5** Relative reproductive success (±95 confidence limits) for caught-and-released versus non-caught female and male Atlantic salmon (a) and reproductive success (estimated number of fries produced) of 18 caught-and-released female Atlantic salmon in relation to temperature (b) in the Rimouski River, Québec, Canada, during the 2018 angling season. Equal fitness of caught-and-released and non-caught salmon is indicated by a dashed red line in Panel a.

Understanding how catch-and-release affects the reproductive fitness of salmon is key for managing fisheries, so future research should focus on understanding physiological pathways affected by catch-and-release. For instance, experimental conditions used by Fleming and Gross (1993) to compare the breeding success of hatchery and wild coho salmon would be appropriate to determine if breeding success is directly affected by catch-and-release. Constructed experimental arenas in stream channels could be used to determine if: (1) caught-and-released and non-caught fish placed in direct competition for breeding opportunities differ in competitive ability and breeding success; (2) the relative competitive ability of caught-and-released and non-caught salmon differs between males and females; and (3) competitive ability of caught-and-released individuals decreases more rapidly than non-caught individuals with increasing population density.

Although we demonstrated that released salmon were reduced in reproductive fitness, it is worth mentioning that most caught-and-released salmon that entered the fish trap survived and reproduced. Here, 83% (15/18) of caught-and-released salmon that moved upstream of the dam reproduced. Our results corroborate studies that showed catch-and-release angling can be a valuable management measure by increasing the number of spawning redds in Norway (2.3-fold increase; Thorstad et al., 2003) and parr and fry density in Russia (Whoriskey et al., 2000).

### 4.2 | Effect of elevated water temperature on caught-and-released salmon

Our study is the first to document the reproductive success of released salmon above their optimal ~20°C temperature for aerobic scope in Canada (DFO, 2012). Interestingly, our results suggested that increasing temperature did not affect the reproductive output of released fish. Warm river temperature reduces dissolved oxygen concentration in water while increasing the metabolic rate and oxygen demand of fish. Ultimately, when oxygen consumption becomes less than oxygen demand, fish physiology relies on anaerobic energy pathways (Casselman & Farrell, 2012; Pörtner, 2010; Pörtner et al., 2017; Steinhausen et al., 2008). When catch-and-release is paired with high water temperatures, their synergistic impacts can exhaust aerobic and anaerobic muscular fuels (Wilkie et al., 1996). Consequently, the survival of released salmon depends on water temperature, so mortality can be as low as 5% at cool temperatures (<12°C) but range between 7% and 33% at higher temperatures (18–20°C; Lenox et al., 2018; Van Leeuwen, Dempson, Burke, et al., 2020).

Mortality increases with water temperature and would be expected to increase sublethal effects on released fish as well. For instance, increasing temperature negatively impacted the reproductive success of salmon between 12 and 19°C (Richard et al., 2013). We did not find an effect of increasing water temperature on reproductive success, perhaps because colder water was available in the Rimouski River. During high-temperature events, Atlantic salmon often engage in behavioural thermoregulation by moving to available thermal refugia to alleviate physiological stress (Breau et al., 2011; Frechette et al., 2018; Lennox et al., 2018). All released salmon in our study were caught close to a thermal refugium that could have enabled escapement from high water temperature to enhance restorative processes (Frechette et al., 2018). Another possible explanation is that the Rimouski population could be locally adapted to high water temperature as with other salmonids (Anttila et al., 2014; Eliason et al., 2011). In addition, despite our study not finding an effect of temperature on reproductive fitness, salmon released at high water temperature were less likely to enter the fish trap, which suggests that temperature at capture affects behaviour, and possibly, spawning behaviour.

We did not detect a significant effect of water temperature on reproductive success, perhaps because ambient water temperatures were not exceptionally high or because our sample size was too small to detect an effect. Testing a larger number of salmon in extremely warm conditions would provide more power to detect effects over a greater temperature range. Moreover, we only had information on the reproductive success of 54% of caught-and-released salmon that were sampled by anglers. Some of the remaining 46% of salmon that stayed downstream may have died after catch-and-release because they were released at a warmer than average temperature (Van Leeuwen, Dempson, Burke, et al., 2020). Based on estimates of mortality from Van Leeuwen, Dempson, Cote, et al. (2020), ~8% of released salmon that did not enter the fish trap would likely have died after release. A significant proportion of Rimouski River salmon spawns below the dam, although no salmon carcasses were detected in this river section in 2018, which suggests that most caught-and-released salmon that remained below the dam survived and reproduced.

River temperatures above 18 to 20°C are now frequently associated with the implementation of river closures in Atlantic salmon recreational fisheries of Canada. Although post-release mortality of salmon increases with temperature, the catchability of Atlantic salmon decreases concomitantly (Van Leeuwen, Dempson, Cote, et al., 2020). This trend was also observed in Rimouski River, as the number of catch-and-release events was generally reduced when water temperature reached 20°C. Evidence of successful reproduction of salmon released at river temperatures above 20°C provides evidence that catch-and-release might benefit management and conservation in the face of global warming. However, considering that upstream migration and possibly spawning behaviour of caught-and-released salmon could be affected at a higher temperature, further study of these impacts is needed.

## 5 | CONCLUSION

Catch-and-release is now common in recreational fisheries management of Atlantic salmon. Accordingly, substantial efforts have been made to determine its sustainability and manage its risk (Lennox et al., 2017; Van Leeuwen, Dempson, Burke, et al., 2020). Atlantic salmon can now be considered a model system in catch-and-release science (Lennox et al., 2017; Van Leeuwen, Dempson, Burke, et al., 2020), although most research to date has focused on the risk of mortality after release. Here, we demonstrate for the first time that catch-and-release can also significantly impact the reproductive success of released females. These results provide important insight for managing recreational fisheries as female reproduction and egg deposition is a key metrics in salmon stock management and assessment (Hindar et al., 2011; MFFP, 2016; Prévost & Chaput, 2001), and stress the need to document the potential impacts of catch-and-release in a more holistic framework. Conservation of Atlantic salmon would benefit from the implementation of adaptive regulations that limits the total number of catch-and-released events per angler or that prohibits fishing in areas such as thermal refugia or during heat waves. Still, the success of catch-and-release as a management practice always relies on angler behaviour so effective management should prioritise raising awareness of the importance of effective catch-and-release techniques and fishing ethics (Arlinghaus et al., 2007).

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## CONFLICT OF INTEREST

The authors declare no conflict of interest for this article.

## DATA AVAILABILITY STATEMENT

The data and R scripts that support the findings of this study are openly available in dryad at https://doi.org/10.5061/dryad.73n5tb30q.

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