

Simulated pre-spawning catch and release of wild Atlantic salmon (*Salmo salar*) results in faster fungal spread and opposing effects on female and male proxies of fecundity

Magdalene Papatheodoulou, Libor Závorka, Barbara Koeck, Neil B. Metcalfe, and Shaun S. Killen

Abstract: Atlantic salmon (*Salmo salar*) are increasingly being released after capture by anglers. Yet, there are still unknown effects on the fish being subjected to the process of catch and release. Capture too close to spawning could have adverse effects on fish, and such data are important for setting appropriate closed seasons. This study examines how stressors related to catch and release experienced shortly before spawning affects adult mortality, vulnerability to *Saprolegnia* spp., and reproductive traits. Adult salmon were collected from the river Blackwater, Scotland, towards the end of their migration and were exposed to one of four protocols comprising exercise and air exposure of different durations. The experimental stressors increased the growth rate of the fungus *Saprolegnia* spp. over the body of the fish. Moreover, male salmon from the most disturbed group exhibited an increase in the maximum duration of their sperm motility. Lastly, females that experienced exercise and (or) air exposure spawned at the usual time but with fewer eggs. These suggest that there may be benefits from preventing angling close to the time of spawning.

Résumé : Si les saumons atlantiques (*Salmo salar*) sont de plus en plus souvent remis à l'eau après leur capture par des pêcheurs à la ligne, des effets sur les poissons du processus de pêche avec remise à l'eau demeurent inconnus. La capture trop près du moment du frai pourrait avoir des effets délétères sur les poissons, et de telles données sont importantes pour l'établissement de périodes de fermeture. L'étude se penche sur l'incidence de facteurs de stress associés à la pêche avec remise à l'eau à l'approche du frai sur la mortalité, la vulnérabilité aux *Saprolegnia* spp. et des caractères reproductifs des adultes. Des saumons adultes ont été prélevés de la rivière Blackwater (Écosse) vers la fin de leur migration et exposés à l'un ou l'autre de quatre protocoles comprenant de l'exercice et des expositions à l'air de différentes durées. Les facteurs de stress expérimentaux ont entraîné une augmentation du taux de croissance de champignons *Saprolegnia* spp. sur le corps des poissons. La durée maximum de motilité des spermatozoïdes des saumons mâles du groupe assujéti à la plus grande perturbation a en outre augmenté. Enfin, les femelles assujéties à de l'exercice et/ou une exposition à l'air ont frayé au moment habituel, mais ont produit moins d'œufs. Ces constatations donnent à penser que l'interdiction de la pêche à l'approche du frai pourrait présenter des avantages. [Traduit par la Rédaction]

Introduction

Recreational fisheries have been implicated in the heavy exploitation of fish within marine and freshwater ecosystems (Cooke and Schramm 2007; Arlinghaus et al. 2013). To preserve stocks, maintain ecosystem balance, and ensure long-term resilience of recreational fishing, fisheries managers in many areas have implemented the concept of “catch-and-release” (C&R) angling, in which captured fish are returned to the water rather than retained and killed (Cooke and Schramm 2007; Wedemeyer and Wydoski 2008; Smukall et al. 2019). With the global growth of both mandatory and voluntary C&R practices, it has been estimated that, depending on location and species, at least 60% of all rod-caught fish are being returned after capture to the water (Cooke and Cowx 2004; Ferter et al. 2013; Cowx et al. 2017; Simms et al. 2017; Van Leeuwen et al. 2021), amounting to billions of fish being released on a yearly basis (Casselman 2005; Arlinghaus et al. 2007, 2013). The success of this management practice is dependent on both the fraction of the

population that is caught and the capacity of the fish to recover from angling, with minimal impact on their survival and reproductive success (Dempson et al. 2002; Richard et al. 2013, 2014; Lennox et al. 2016). In Atlantic salmon (*Salmo salar*), the exploitation rate is relatively low, typically figures in the order of 10% (ICES Advice 2020). However, regardless of the fishing gear and technique, C&R may act as a significant acute stressor, with possible adverse effects over different timescales and biological levels (from cellular to ecosystem), and so its impact on conservation is unclear (Arlinghaus et al. 2013; Raby et al. 2015).

Research has indicated that mortality of fish immediately following release is usually low (Bartholomew and Bohnsack 2005; Cook et al. 2015; Twardek et al. 2018; Smukall et al. 2019). However, there are several physiological and behavioural disturbances that a fish may experience during capture that may have sublethal effects (Donaldson et al. 2014; Cook et al. 2015; Raby et al. 2015; Lennox 2018; Twardek et al. 2018; Smukall et al. 2019).

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M. Papatheodoulou, B. Koeck, N.B. Metcalfe, and S.S. Killen. Institute of Biodiversity, Animal Health and Comparative Medicine, College of Medical, Veterinary and Life Sciences, Graham Kerr Building, University of Glasgow, Glasgow G12 8QQ, UK.

L. Závorka. Institute of Biodiversity, Animal Health and Comparative Medicine, College of Medical, Veterinary and Life Sciences, Graham Kerr Building, University of Glasgow, Glasgow G12 8QQ, UK; WasserCluster Lunz–Inter-university Centre for Aquatic Ecosystem Research, A-3293, Lunz am See, Austria.

Corresponding author: Magdalene Papatheodoulou (email: mpapatheodoulou@hotmail.com).

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In addition, C&R can lead to immunosuppression and leave fish more vulnerable to pathogens like the ubiquitous, opportunistic fungi *Saprolegnia* spp. (Wedemeyer and Wydoski 2008; Olsen et al. 2010; Arlinghaus et al. 2013; Havn et al. 2015; Smukall et al. 2019). Fish can become immunocompromised either directly through physical damage of the skin through scale loss, abrasions, loss of the protective mucus layer or hook injury during handling, or indirectly through metabolic, osmoregulatory and hormonal disturbances due to stress (Wedemeyer and Wydoski 2008; Olsen et al. 2010; Smukall et al. 2019). Moreover, the effects of environmental conditions experienced by parents, whether around the time of breeding or earlier in life, can be transmitted directly or indirectly to future generations (Burton and Metcalfe 2014). These are known as parental (or sometimes more narrowly as maternal) effects, and they can be either adaptive or maladaptive for offspring (Burgess and Marshall 2014; Burton and Metcalfe 2014; Jonsson and Jonsson 2014; Haussmann and Heidinger 2015; Blount et al. 2016). Parental effects have been observed in a wide range of organisms, both from the terrestrial and aquatic environment. In fish, adults that experience stress prior to reproduction have been shown to exhibit changes in hormonal profiles, delayed spawning, decreased gamete quality and quantity, and suppressed ovulation (Sopinka et al. 2016; Smukall et al. 2019). In species with external fertilisation and polyandrous mating systems, such as salmonids, male mating success is governed by the balance of three key sperm factors; quantity, longevity, and velocity (Gage et al. 2004; Crean et al. 2012; Beirao et al. 2019). In sockeye salmon (*Oncorhynchus nerka*), for example, 80% of eggs are fertilised in the first 5 s of sperm–egg mixing (Hoysak and Liley 2001). Therefore, if stressors experienced by the male prior to spawning affect the activity levels of sperm this could have a major impact upon fertilisation success. However, the attributes of the sperm do not only influence the reproductive success of the parents, but the fitness of the offspring as well (Immler et al. 2014). There remains uncertainty regarding the effects of C&R angling on the reproductive fitness of fish, particularly when capture occurs during the gamete developmental stage (Richard et al. 2013; Arlinghaus et al. 2013; Smukall et al. 2019).

Catch-and-release schemes clearly have less of an impact on the population than the alternative of captured fish being killed. However, given our limited knowledge of the effects of C&R on gamete development and reproduction of Atlantic salmon, further studies are necessary to understand the immediate effects that this fisheries management policy will have on spawning (Olsen et al. 2010). The greatest effects of C&R are likely to occur if the capture occurs near the time of spawning, therefore data on pre-spawned salmon are important in considerations of appropriate closed seasons during which angling may be prohibited. We hypothesised that adult salmon experiencing the most cumulative disturbance from C&R angling prior to spawning, would be most susceptible to fungal infection and would experience the greatest impacts on reproduction. We therefore examined whether simulated C&R (adult pre-spawning stress) influences their mortality rate and vulnerability to pathogens (*Saprolegnia* spp.), as well as quantified its effects on the reproductive traits of both sexes (time of spawning, clutch and egg size, and sperm quality and quantity).

Materials and methods

Salmon collection

Mature anadromous Atlantic salmon were collected from November to December 2018 during their upstream spawning migration, using the permanent fish trap set up by the Cromarty Firth Fishery Board on the river Blackwater, Scotland. They were transferred using large individual water-filled bags from the fish

trap to circular holding tanks (diameter 4 m; depth 1.5 m; water flow 60 L·min⁻¹; maximum stocking density = 60 fish per tank, but exact number varied based on the timings of fish capture and the onset of treatments), where they were held in single-sex groups and given 24–48 h to recover from the stress of the fish trap and collection of the baseline data (see below). There was a total of four holding tanks (two per sex; one for experimental and one for non-experimental fish — see below for definitions of fish categories). The water in the holding tank was supplied directly from the river Blackwater, and the temperature (6 ± 1.5 °C) was recorded on an hourly basis using a temperature data logger (HOBO Pendant Temperature/Light 64 K Data Logger, Onset Computer Co., USA). All procedures carried out in this study were approved under UK Home Office Project License PB948DAAO. A flow chart summarising the number of experimental fish used in each procedure can be seen in the online Supplementary material, Fig. S1¹.

Catch-and-release simulations

Fish were subjected to treatments that simulated the experiences potentially encountered by fish during C&R angling, following the approach used by previous studies (Struthers et al. 2018; Smukall et al. 2019). The simulation protocols on the fish, however, were conducted outside the normal salmon fishing season in Scotland, which normally closes by late October, to see whether a later end to the fishing season (or the late capture by rod and line of brood stock fish for hatchery purposes) would have adverse effects. Male fish were selected haphazardly from the pool of captured anadromous migrants, as were females with the proviso that they had not yet released their eggs into the body cavity (e.g., were “hard”) and so were not immediately ready to spawn. Selected fish were lightly anaesthetised on the day of capture with the trap using clove oil (diluted to the recommended concentration in an unaerated water bath) until they had lost equilibrium and did not respond to stimulation, a process that took approximately 2 min. They were then measured for fork length (to the nearest 0.5 cm), weight (to the nearest 0.001 kg; using a DEFENDER 5000 XTREME W electronic balance, OHAUS, Switzerland) and photographed on both sides (using a Sony Cyber-shot DSC-WX100 camera, USA) for later calculation of the percentage of the body covered by the fungus *Saprolegnia* spp. (see below; also see Supplementary Table S1¹). To minimize handling and processing time, the photographs documenting fungal infection were taken while the salmon were still on the fish measuring board. Water was slowly poured over the fish body and gills to minimize dehydration and mucus removal during the process of data collection. Individuals were then randomly (number generator random; version 2.0) allocated to one of four pre-determined treatment groups based on stressor protocols, before being tagged with an individually colour-coded Floy tag (indicating treatment; TENEQ, UK) and passive integrated transponder (PIT) tag (individual ID) and allowed to recover for 24–48 h. While all fish (including controls) will have inevitably experienced some stress due to handling or tagging, this was minimised as much as possible and was standardised across all treatment groups, so that any subsequent differences among groups would be the result of the C&R protocols and not due to handling (which could perhaps be considered as standardised prior mild C&R episode). Any fish that died after the C&R simulations, but still within the overall trapping period ($n = 5$ males and 1 female), was replaced to maintaining the sample size of 15 fish per treatment per sex ($n = 120$ in total; see Supplementary Fig. S1¹ for details).

An equal number of males and females were assigned to each of four treatments (Table 1): (1) a control treatment in which fish were not exercised or air-exposed; (2) a treatment in which fish

¹Supplementary data are available with the article at <https://doi.org/10.1139/cjfas-2021-0089>.

Table 1. Summary of the four treatment groups used in the experiment and the cumulative levels of acute disturbance they represent, indicated by the number of asterisks.

| Treatment | Exercise | Air exposure | Cumulative disturbance |
|----------------------------------|----------|--------------|------------------------|
| Control | No | No | — |
| Exercise | 210 s | No | * |
| Exercise + Air Exposure | 210 s | 60 s | ** |
| Exercise + Extended Air Exposure | 210 s | 120 s | *** |

were exercised for 210 s without rest by manually chasing in an arena (diameter 4 m; tank height 1.5 m; water depth 0.18 m), by lightly tapping the fish on its sides or on its tail using a hand and gloves, intended to simulate the exercise that occurs during angling; (3) a treatment that consisted of this exercise, plus air exposure for 60 s (by being held in a knotless net), simulating the experience of being caught and then held up for hook removal or to be measured and photographed; or (4) a treatment that consisted of exercise plus air exposure for 120 s. The air exposure treatments were based on actual times that anglers have been observed to hold salmonid fish in air during real C&R angling episodes (maximum time = 160 s; Lamansky and Meyer 2016). Following treatment, fish were placed in one of two new holding tanks (one tank per sex) containing fish that had been through the protocols (Struthers et al. 2018; Smukall et al. 2019). Control fish went through the process of being transferred to the post-treatment holding tanks but using water-filled plastic bags to minimise the disturbance that they experienced. The water in both the arena and holding tanks was supplied directly from the river blackwater (temperature = 6 ± 1.5 °C).

Fish were left undisturbed in the post-protocol holding tanks for a minimum of five days (Table 2). They were then stripped of gametes once the females became ripe (i.e., had released their eggs into the abdominal body cavity such that their belly was soft), as determined by staff from the hatchery who were blind to experimental treatment groups.

Artificial fertilisation and gamete collection

Each experimental fish was mated with a single non-experimental fish taken from the holding tanks; the time at which male experimental fish were mated was determined by when female non-experimental fish were ripe. A total of 112 crossings were conducted (experimental females = 60, and experimental males = 52). Fish were initially anaesthetised in clove oil. Their identity was noted from the PIT tag and they were then photographed on both sides as before for later calculation of the increase in percent body cover of the *Saprolegnia* spp. fungus since the time of exposure to their experimental treatment. To prevent contamination and activation of the gametes, the ventral surface of the salmon was dried of any excess water. The body mass of all experimental fish was then measured pre-stripping to the nearest 0.001 kg.

Egg collection was achieved by gently massaging the abdomen in a unidirectional manner, from below the pectoral fins to just above the urogenital opening, until all eggs had been released into a bowl. About 1 mL of milt (semen) was then collected from a single male, using a similar approach, and placed directly onto ice for assessment of sperm quality and quantity. All remaining milt from the male was stripped and released on top of the eggs, and both the eggs and milt were gently mixed together. Water was then added to activate the sperm, and the eggs left for ~60 min before being rinsed. This allowed the eggs to swell up and the shell to harden. Once adult fish had been stripped of their gametes they were re-weighed (somatic mass) and released back into the lake (loch) close to the site of capture.

The eggs were then transferred to the SSE (Southern and Scottish Energy) hatchery in Contin, Scotland, where they were drained of water and ovarian fluid. Subsequently, the weight of a counted subsample of eggs (to the nearest 0.01 g; Scout Pro electronic balance, OHAUS, Switzerland) and of the total clutch (to the nearest 1 g) were measured to estimate the total number of eggs produced by each crossing (see below). The eggs were then allowed to incubate at the hatchery, with each family being reared in a separate tray.

The person responsible for stripping adults of eggs and sperm was blind to the treatment group of the experimental fish. Each of the fish were used only once during the crossings, with two exceptions: on one occasion two non-experimental males were used to fertilise an experimental female since the first male proved to have insufficient milt to be guaranteed to fertilise all the eggs. Secondly, a shortage of ripe non-experimental females led to the clutch of one non-experimental female being split in half and fertilised by two experimental males.

Mortality and vulnerability to disease

Adult pre-spawn mortality (between capture and spawning) was recorded throughout the experiment. The fungus *Saprolegnia* spp. was quantified by calculating the percent body cover with fungus (including fins) from the photographs taken at capture and at mating, using the software ImageJ (version 1.51r). The analysis was blind to treatment and conducted in a random sequence. The fungal spread was then determined by calculating the increase in the percent body cover between these two time points.

Effects on male gametes

The volume of milt produced by experimental males was determined using the change in the body mass of the fish pre- and post-stripping. This was then converted to a volume by assuming that 1 g of milt was equal to 1 mL. Sperm concentration in diluted milt was quantified using a Neubauer haemocytometer (milt solution dilution factor 1:75; MUHWA, China), counting the number of spermatozoa per grid square in the field of view using ImageJ (version 1.51r). Then, the approximate concentration was calculated using the following formula:

$$\begin{aligned} \text{Sperm concentration (cells} \cdot \text{L}^{-1}) \\ = \text{avg. number of sperm cells per square} \\ \times \text{dilution factor} \times 10^4 \end{aligned}$$

The quantity of sperm produced by a male could then be estimated using the formula below:

$$\begin{aligned} \text{Sperm quantity (cells)} = \text{sperm concentration (cells} \cdot \text{L}^{-1}) \\ \times \text{milt volume (L)} \end{aligned}$$

Sperm quality was assessed in terms of its period of activity. Within 60 min of being collected, the chilled milt samples were warmed to ambient air temperature and the sperm were activated by adding 20 μ L of milt to 1.5 mL (20:1500) of fresh water. The movements of the activated sperm were then filmed under a light microscope (40 \times , HM-Lux Pol. Monocular microscope, Leitz, UK) using a digital camera (14MP HDMI HD 1080 P Digital Microscope Magnifier Industrial Camera). Sperm quality was quantified in terms of maximum duration of sperm motility, which was defined as the total time (s) taken from the initial activation until all sperm in the microscope's field of view had stopped moving (Alavi and Cosson 2005; Fauvel et al. 2010). Maximum duration of sperm motility for the experimental males was determined by measuring the maximum duration of motility in two separately activated samples, and then calculating their mean value. Several males ($n = 17$) only had one recorded measurement of sperm activity.

Table 2. Description of the mean time delay (days) between the date that the fish were exposed to the treatments and the day they were artificially stripped of their gametes.

| Treatment | Mean time delay until mating (days) | | | | | |
|----------------------------------|-------------------------------------|--------|---------------|---------|--------|--------------|
| | Males | | | Females | | |
| Control | 12.5 | N = 17 | Range = 7–18 | 10.3 | N = 16 | Range = 6–13 |
| Exercise | 11.5 | N = 18 | Range = 7–18 | 9.1 | N = 15 | Range = 6–12 |
| Exercise + Air Exposure | 13.6 | N = 14 | Range = 10–18 | 9.5 | N = 15 | Range = 5–12 |
| Exercise + Extended Air Exposure | 12.9 | N = 15 | Range = 7–17 | 10.2 | N = 15 | Range = 6–15 |

Note: Presented are also the number of fish per treatment group (N) and the range in this delay for each of the treatment groups.

Effects on female gametes

To estimate the mean volume of fertilised eggs per female, the clutch of each female was photographed (Sony Cyber-shot DSC-WX100 camera, USA) within their individual family trays alongside a size reference. This photograph was taken on the day of fertilisation but after the eggs had finished swelling after exposure to water. The diameter of 20 randomly selected eggs was subsequently measured blind to experimental treatment from the photographs in ImageJ (version 1.51r); this was used to calculate the average volume (mm^3) of an individual egg from each family using the formula of a sphere:

$$\text{Volume of egg (mm}^3\text{)} = \frac{4}{3}\pi r^3$$

where r is the egg radius. Clutch size was calculated based on the measurements of total clutch weight and weight of a counted subsample of eggs ($n = 19 \pm 8$ eggs) using the formula below:

$$\text{Total clutch size} = \frac{\text{weight of total clutch (kg)} \times \text{number of eggs in subsample}}{\text{weight of subsample of eggs (kg)}}$$

Statistical analyses

Adult mortality (from the time the treatments were applied up until the time of spawning) was examined in R (Version R386 3.4.4) using a Cox Proportional Hazards model. The analysis included all fish ($n = 125$) that had gone through the stress protocols, including the 110 fish that survived to mating (see Fig. S1¹ in the Supplementary information for explanation of sample sizes). Along with the treatment, percent fungal infection of the fish at the time of trapping was also added to the model as an explanatory variable. General linear models (GLMs) were used to examine whether the experimental treatments had a significant effect on the fish vulnerability to disease (defined as the increase in the percentage of body of salmon covered in fungus *Saprolegnia* spp.). The model also included the sex of the experimental salmon, days elapsed between the day the stressor was applied and stripping, the fork length of the fish at the time of trapping and the percent fungal infection of the fish at the time of trapping as explanatory variables. GLMs were also used to investigate whether the stressor protocols influenced reproductive traits of males (sperm quantity and maximum duration of sperm motility) and females (days elapsed until females were ready to spawn, egg volume and clutch size). The model for sperm quantity included the percentage increase of the fungus *Saprolegnia* spp. as an additional explanatory variable, while the model for maximum duration of sperm motility used days elapsed and date of trapping. Moreover, the model for days elapsed until females were ready to spawn include date of trapping, clutch size and percent fungal infection of the fish at the time of trapping as an explanatory variable. Finally, the model for egg volume used clutch size and fork length of the female at the time of trapping as explanatory variables, while female clutch size used fork length and egg

volume. All GLMs used treatment as the main explanatory variable. To normalise the residuals of the data, some of the dependent variables underwent either logarithmic (spread of fungus and maximum duration of sperm motility) or squared transformation (clutch size). The variables sex, date of trapping (day of the year), fish fork length and somatic mass, initial percent body cover with fungus, spread of fungus, order at which fish underwent experimental stressor, date fish experienced the stressor, clutch size, and days elapsed from the time of the stressor to spawning (days elapsed), were tested within the models as explanatory variables, and used as indicated in the GLMs. The interactions between treatment and each of sex, days elapsed from stress protocol to spawning, and spread of fungus were also initially included. The models with the lowest AIC scores were selected, and assumptions of linearity, normality of residuals, and homogeneity of variance were verified by inspection of model residual-fits plots. Significance was then determined using p values ($\alpha = 0.05$), and if a treatment effect was found, differences among treatment groups were explored using a Tukey multiple comparison of means. A Levene's test for homogeneity of variance was run for each model. Lastly, the correspondence between the two recorded measurements for the maximum duration of sperm motility was investigated using a Pearson's correlation test. The strong positive correlation between these two measurements (see below), allowed for the single recorded measurements of sperm motility to be included in the rest of the statistical analysis.

Results

Mortality and vulnerability to disease

While mortality was not affected by the C&R simulations, individuals that had a higher percentage of the body covered by the fungus *Saprolegnia* spp. on the date of trapping had a higher probability of mortality (Supplementary Table S2¹).

The increase in coverage of *Saprolegnia* spp. fungus on the body of the fish after the experimental treatments was greater in fish that had a higher percent body cover of fungus at the time of trapping, and those that were caught in the trap early in the experiment. Moreover, males tended to have a higher percent fungal spread in comparison to females and showed less of an effect of treatment. Fungal spread in females was greater in individuals from the "Exercise" and "Exercise + Extended Air" groups (Table 3; Fig. 1).

Effects on male reproduction

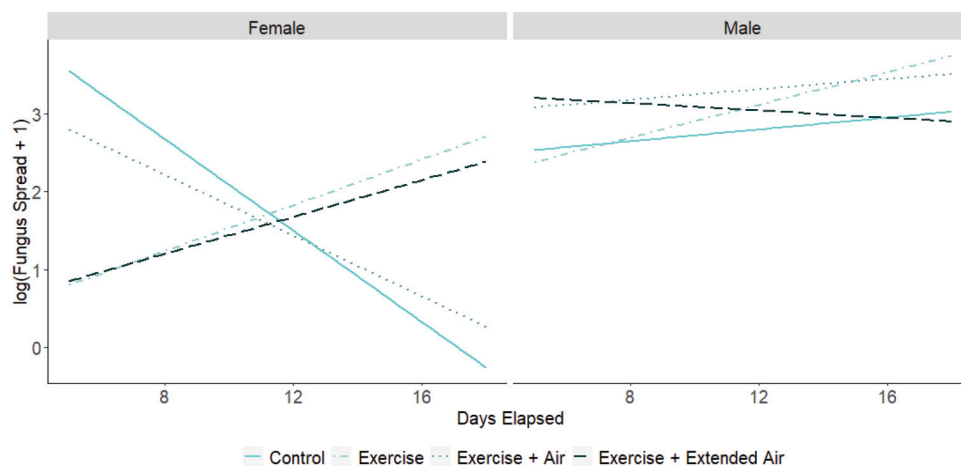
There was a strong positive correlation ($r_{30} = 0.832$, p value < 0.001) between the two independent measurements of the maximum sperm survivability (Supplementary Fig. S2¹), indicating that the assay was robust. Males from the Exercise + Extended Air group produced sperm that survived for a longer period once activated than did sperm from control males (Table 4; Fig. 2A). Furthermore, males from the Exercise + Extended Air group showed a positive relationship between the days elapsed from experiencing the stressor protocol until spawning and maximum duration of sperm motility, but the pattern was the opposite in

Table 3. Summary of general linear models (GLMs) investigating the factors influencing the increase in the percentage of the body covered by the fungus *Saprolegnia* spp. from the day of capture until the day of spawning.

| | df | Estimate | SE | t value | p value |
|--|----|----------|----------------------|---------|---------|
| Intercept | — | 5916 | 1078 | 5.491 | <0.001 |
| Exercise | 1 | -5.584 | 1.417 | -3.941 | <0.001 |
| Exercise + Air | 1 | -2.526 | 1.408 | -1.795 | 0.08 |
| Exercise + Extended Air | 1 | -5.351 | 1.306 | -4.097 | <0.001 |
| Days Elapsed | 1 | -0.201 | 0.107 | -1.878 | 0.06 |
| Sex — Males | 1 | -2.767 | 1.273 | -2.173 | 0.03 |
| Fork Length | 1 | -0.002 | 0.009e ⁻¹ | -1.892 | 0.06 |
| Date of Trapping | 1 | -0.136 | 0.025 | -5.486 | <0.001 |
| Fungus Pre-treatment | 1 | 0.685 | 0.123 | 5.588 | <0.001 |
| Exercise × Days Elapsed | 1 | 0.519 | 0.141 | 3.668 | <0.001 |
| Exercise + Air × Days Elapsed | 1 | 0.239 | 0.139 | 1.713 | 0.09 |
| Exercise + Extended Air × Days Elapsed | 1 | 0.474 | 0.126 | 3.770 | <0.001 |
| Exercise × Sex — Males | 1 | 5.605 | 1.688 | 3.320 | 0.001 |
| Exercise + Air × Sex — Males | 1 | 2.653 | 1.879 | 1.412 | 0.16 |
| Exercise + Extended Air × Sex — Males | 1 | 6.728 | 1.614 | 4.169 | <0.001 |
| Days Elapsed × Sex — Males | 1 | 0.252 | 0.118 | 2.127 | 0.04 |
| Exercise × Days Elapsed × Sex — Males | 1 | -0.491 | 0.160 | -3.067 | 0.003 |
| Exercise + Air × Days Elapsed × Sex — Males | 1 | -0.218 | 0.167 | -1.304 | 0.20 |
| Exercise + Extended Air × Days Elapsed × Sex — Males | 1 | -0.546 | 0.146 | -3.742 | <0.001 |
| Residuals | 98 | | | | |

Note: Shown are the comparisons of each of the three stressor protocols to the control, together with the effect of fish fork length, sex, date of trapping, days elapsed from capture until spawning and percent body cover of the fungus *Saprolegnia* spp. on the date of trapping.

Fig. 1. Effects of the three-way interaction between the catch-and-release (C&R) simulation protocols, days elapsed, and sex of the salmon, on the increase in the percentage (%) of the body covered by the fungus *Saprolegnia* spp. from the date of capture until the date of spawning. The coloured lines indicate the four treatment groups (see Table 3 for statistical analysis). [Colour online.]



the other three treatment groups (Table 4; Fig. 2B). Thus, the viability of sperm from the males exposed to the highest levels of disturbance increased with the duration of the male's recovery period, whereas males exposed to lesser disturbance displayed a decline in sperm viability over time after the C&R simulation. Additionally, later-trapped males had a lower duration of sperm motility compared to those caught early on, while sperm quantity was unaffected by either exercise or air exposure (Table 5; Fig. 3).

Effects on female reproduction and spawning

For females, there was no difference across the treatments in the time elapsed (number of days) between the date of the C&R simulation and the date they were considered ripe for mating (Supplementary Table S2¹). The date of trapping had a positive effect on the time elapsed ($t = 3.45$, $p = 0.001$), with later-trapped fish being ripe later, while the level of fungus on the fish at the

time of trapping had a negative effect, such that fish with more fungus became ripe sooner ($t = 2.45$, $p = 0.02$; Table 6a and Supplementary Table S3¹).

Larger females produced larger eggs, but there was no effect of treatment on egg size (Fig. 4A). After controlling for the effect of female size, females with relatively larger clutches for their size produced smaller eggs. Females that experienced the C&R simulations produced smaller clutch sizes relative to their body size (Tables 6 and 7; Fig. 4B). The Levene's test also indicated a decreased variability in the number of eggs (clutch size) produced by stressed females ($p = 0.04$).

Discussion

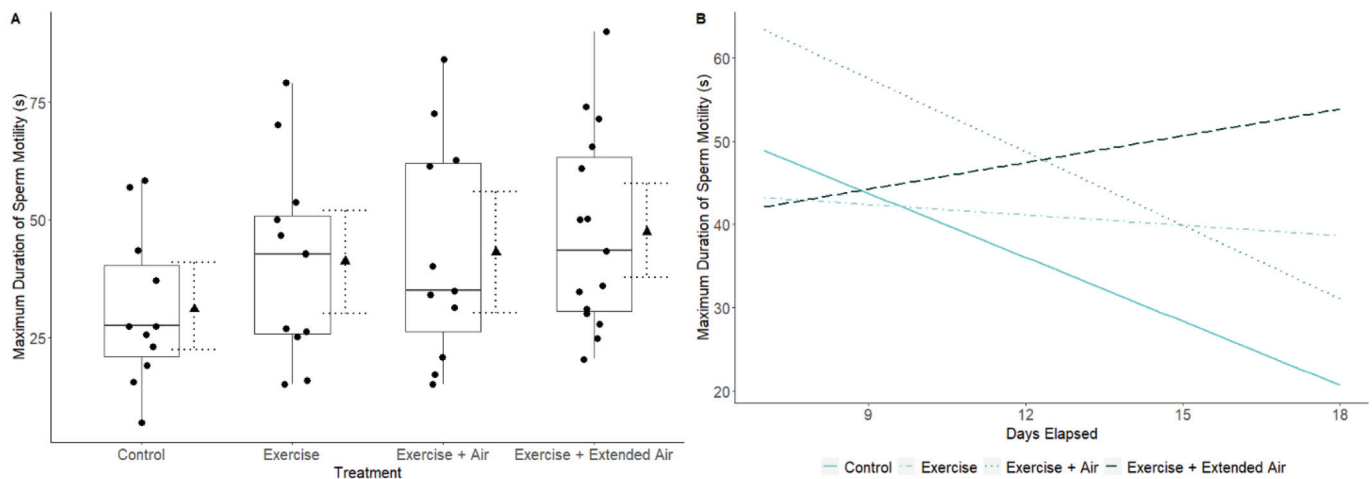
The results demonstrate that the set of stressors used as a representative disturbance of a typical C&R practice, for salmon angling, do not necessarily lead to immediate lethal effects, at least under

Table 4. Summary of general linear models (GLMs) for the factors influencing on the maximum duration (s) of sperm motility.

| | df | Estimate | SE | t value | p value |
|--|----|----------------------|----------------------|---------|---------|
| Intercept | — | 2755 | 996.8 | 2.764 | 0.01 |
| Exercise | 1 | -0.059 | 0.627 | -0.094 | 0.93 |
| Exercise + Air | 1 | -0.400 | 0.789 | -0.506 | 0.62 |
| Exercise + Extended Air | 1 | -1.258 | 0.596 | -2.109 | 0.04 |
| Days Elapsed | 1 | -0.103 | 0.036 | -2.865 | 0.01 |
| Date of Trapping | 1 | -0.063 | 0.023 | -2.760 | 0.01 |
| Sperm Concentration (cells·L ⁻¹) | 1 | 0.009e ⁻⁶ | 0.002e ⁻⁵ | 0.416 | 0.67 |
| Exercise × Days Elapsed | 1 | 0.019 | 0.047 | 0.404 | 0.69 |
| Exercise + Air × Days Elapsed | 1 | 0.040 | 0.055 | 0.729 | 0.47 |
| Exercise + Extended Air × Days Elapsed | 1 | 0.122 | 0.045 | 2.719 | 0.01 |
| Residuals | 38 | | | | |

Note: The model also accounts for the date the fish were collected from the trap, the days elapsed from capture until spawning and experimental male sperm concentration (cells·L⁻¹).

Fig. 2. (A) Effects of the stressor protocols on the maximum duration of sperm motility (s). Each circular data point represents an experimental fish. The boxplot indicates the median, the interquartile range, and maximum and minimum values for each of the treatments. The dotted line represents the 95% confidence interval, and the triangle represents the mean. (B) Effects of the stressor protocols on the relationship between maximum duration of sperm motility (s) and days elapsed since the protocols took place. The coloured lines indicate the four treatment groups; see Table 4 for statistical analysis. [Colour online.]

**Table 5.** Summary of general linear models (GLMs) for the effects of the stressor protocols on the quantity of sperm (cells) produced by male salmon.

| | df | Estimate | SE | t value | p value |
|-------------------------|----|----------|--------|---------|---------|
| Intercept | — | 177 277 | 68 587 | 2.585 | 0.01 |
| Exercise | 1 | 37 758 | 79 016 | 0.478 | 0.64 |
| Exercise + Air | 1 | 160 601 | 86 600 | 1.855 | 0.07 |
| Exercise + Extended Air | 1 | 79 537 | 75 100 | 1.059 | 0.30 |
| Percent fungal spread | 1 | 3 023 | 2 617 | 1.155 | 0.25 |
| Residuals | 42 | | | | |

Note: Included in the model is the percent increase of the fungus *Saprolegnia* spp. on the body of the fish from the date of trapping to stripping.

the conditions examined. Notably, however, there were a range of important sublethal effects that could potentially impact the fecundity of salmon that experience C&R near to spawning time. There was evidence that the stressors influenced the reproductive capacity of female and male salmon, so leading to the potential for intergenerational effects of C&R angling. Furthermore, fish that experienced exercise or exercise + extended air (120 s) during simulated C&R subsequently experienced the fastest growth of the fungus *Saprolegnia* spp.

The pre-spawning mortality of the Atlantic salmon in the benign holding tank environment was independent of treatment group. Several other studies that investigated the effects of C&R angling or an equivalent stressor on adult Atlantic salmon have found a high post-treatment survival rate of more than 90% (e.g., Thorstad et al. 2007; Havn et al. 2015; and Lennox et al. 2016; Van Leeuwen et al. 2021). This has been shown in other salmonids, including Pacific salmon (pink *Oncorhynchus gorbuscha*) and chum (*Oncorhynchus keta*) and steelhead (*Oncorhynchus mykiss*) (Booth et al. 1995; Raby et al. 2013; Donaldson et al. 2014; Whitney et al. 2019). One possible explanation for salmonids being especially able to endure and tolerate angling might be that they are physiologically equipped to deal with shifting environmental conditions (e.g., moving from salt to fresh water) and undergo extreme exertion during upstream migration. This includes biochemical adaptation, such as increased anaerobic metabolism and protein catabolism, during their progressively harsher journey to the spawning grounds, which might equip them with the necessary adaptations to handle acute stressors such as C&R angling (Raby et al. 2013; Elmer 2020; Whitney et al. 2019). The salmon in our treatment groups were able to recover under relatively stable conditions, as they could recuperate without needing to continue their upstream migration. Additionally, the water temperature

Fig. 3. Effects of the stressor protocols on sperm quantity (cells). Each circular data point represents the sperm from an experimental male fish. The boxplot indicates the median, the interquartile range, and maximum and minimum values for each of the treatments. The dotted line represents the 95% confidence interval, and the triangle represents the mean (see Table 5 for statistical analysis).

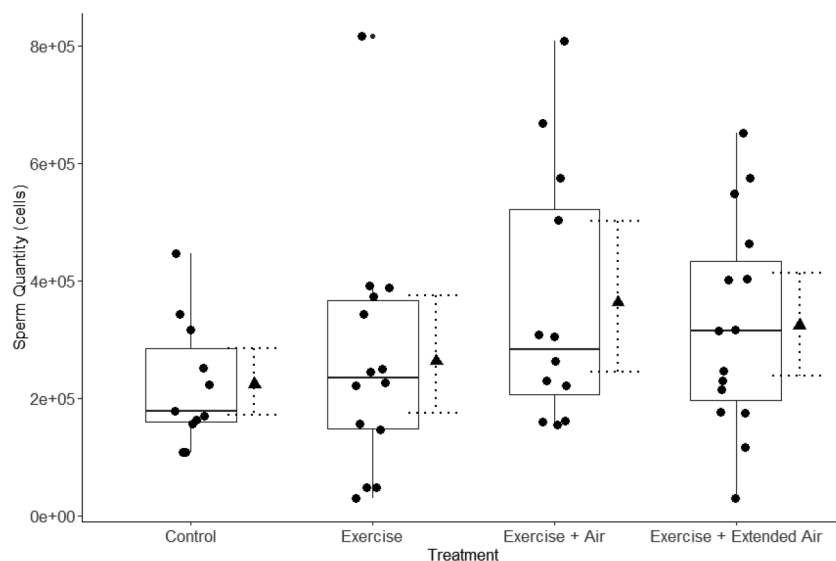


Table 6. Summary of general linear models (GLMs) for the effects of the stressors on the females' reproductive traits.

| | df | Estimate | SE | t value | p value |
|-------------------------|----|-----------------------|----------------------|---------|---------|
| (a) Egg volume | | | | | |
| Intercept | — | 4.644 | 0.099 | 46.773 | <0.001 |
| Exercise | 1 | -0.004 | 0.030 | -0.125 | 0.90 |
| Exercise + Air | 1 | -0.012 | 0.029 | -0.404 | 0.69 |
| Exercise + Extended Air | 1 | -0.017 | 0.029 | -0.600 | 0.55 |
| Length | 1 | 0.001 | 0.002e ⁻¹ | 4.822 | <0.001 |
| Clutch Size | 1 | -0.002e ⁻² | 0.001e ⁻² | -1.829 | 0.07 |
| Residuals | 54 | | | | |
| (b) Clutch size | | | | | |
| Intercept | — | -70 750 171 | 9 784 808 | -7.231 | <0.001 |
| Exercise | 1 | -7 061 270 | 3 412 198 | -2.069 | 0.04 |
| Exercise + Air | 1 | -10 106 921 | 3 383 560 | -2.987 | 0.004 |
| Exercise + Extended Air | 1 | -7 691 627 | 3 369 692 | -2.283 | 0.03 |
| Length | 1 | 185 098 | 18 573 | 9.966 | <0.001 |
| Egg Volume | 1 | -219 639 | 89 191 | -2.463 | 0.02 |
| Residuals | 55 | | | | |

Note: (a) Egg volume (mm³); the model also corrects for the effects of the females' size (length) and the total clutch size produced by the female. (b) Clutch size (total number of eggs in the clutch); the model also corrects for the effects of the females' size (length) and egg volume.

(6 ± 1.5 °C) that the fish experienced during the C&R simulations and in the holding tanks was within the thermal optimum for Atlantic salmon spawning (Pankhurst and King 2010). In contrast, there is some evidence of a higher post-release mortality in salmonids (including Atlantic salmon) that experience the same stressors during the summer, or at higher temperatures (>16 °C) (Dempson et al. 2002; Thorstad et al. 2007; Olsen et al. 2010; Arlinghaus et al. 2013; Gale et al. 2013; Twardek et al. 2018; Van Leeuwen et al. 2021). Temperature plays a key regulatory role in all physiological processes within ectotherms, including fish, therefore the physiological stress caused by C&R may be intensified by water temperatures beyond the thermal optimum for a species (Olsen et al. 2010; Havn et al. 2015). Mortality at higher

water temperature may be triggered by increased metabolic demand, increased physiological disturbance (e.g., fuel depletion, ion loss) due to exercise and air exposure, and a reduced aerobic scope for recovery (Arlinghaus et al. 2013; Gale et al. 2013). Salmon may also lose more scales when caught in summer than closer to the time of spawning, when the scales become more firmly attached.

The C&R stressor protocols affected the rate of increase of the fungus *Saprolegnia* spp. on the body of the fish. Fish from the control group suffered virtually no increase in fungus, whereas females exposed to exercise or exercise + extended air showed significant increases in fungal infection over time. Similarly, Pacific salmon caught in gillnets show an increased infection of secondary pathogens, such as *Saprolegnia*, which exploit the damage to epithelial tissue caused by the combined effects of handling stress and physical damage caused by the fishing gear (Teffer 2018). Moreover, even though fish in the current study experienced no direct effects on mortality due to simulated C&R, mortality may have been higher if the fish were living in the wild rather than in the benign holding tanks. Elmer (2020) suggested that the burden of infection (presence and load) may influence the ability of Pacific salmon to survive other stressors encountered during the spawning migrations. In fact, previous research on salmonids (including Atlantic salmon) infected with *Saprolegnia* spp. has revealed higher secretion levels of prostaglandin E2 (PGE2), a hormone that has been linked to the deactivation of several immune-related genes (Bordeleau et al. 2018). Furthermore, previous research has shown that *Saprolegnia* spp. affects different body regions on male and female salmonids (Fleming 1996; Ciepliński et al. 2018). Females show signs of infection mostly in the dorsal half of the caudal peduncle and tail, due to epithelial damage caused from the effort of building redds, while males are affected predominantly on the flanks, because of spawning behaviour, territoriality, and competition for females (Fleming 1996; Hardie et al. 2007; Ciepliński et al. 2018). Moreover, infection rate tends to be higher during breeding due to the reduced body condition and immunocompromised nature of salmonids during the spawning migration (Hardie et al. 2007; Baker et al. 2013; Matthews 2019). *Saprolegnia* can also contribute to fish mortality in several ways, including via haemodilution, respiratory and osmoregulatory distress, and organ failure (West 2006; Lone and Manohar 2018). *Saprolegnia*-infected

Fig. 4. Effects of the stressor protocols on female reproduction: (A) average egg volume (mm^3) and (B) clutch size. Each circular data point represents an experimental fish. The boxplot indicates the median, the interquartile range, and maximum and minimum values for each of the treatments. The dotted line represents the 95% confidence interval, and the triangle represents the mean (see Tables 6 and 7 for statistical analysis).

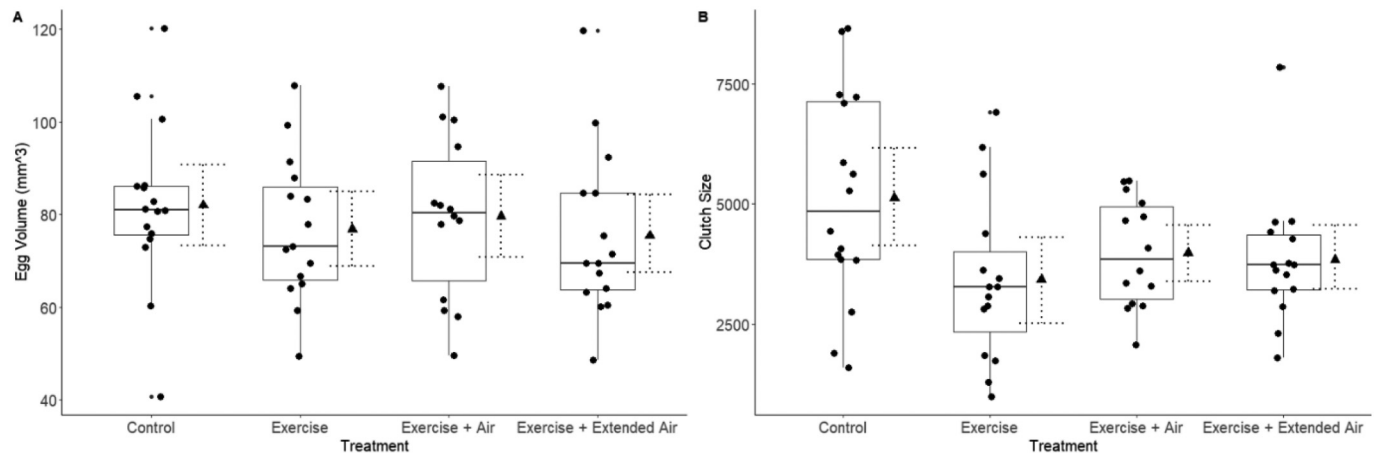


Table 7. Summary of Tukey multiple comparisons of means output (95% family-wise confidence level) for the effects of the stress protocols on female clutch size.

| | Lower | Upper | <i>p</i> value |
|--|-------------|------------|----------------|
| Exercise – Control | –25 087 804 | –7 561 030 | <0.001 |
| Exercise + Air – Control | –22 762 449 | –4 915 525 | 0.001 |
| Exercise + Extended Air – Control | –23 131 890 | –5 605 117 | <0.001 |
| Exercise + Air – Exercise | –6 575 778 | 11 546 638 | 0.89 |
| Exercise + Extended Air – Exercise | –6 947 697 | 10 859 523 | 0.94 |
| Exercise + Air – Exercise + Extended Air | –9 590 725 | 853 691 | 1.00 |

individuals also exhibit lethargic behaviour, which increases their risk of predation (Lone and Manohar 2018). Thus, the migration success of fish such as salmonids could be governed by multiple interrelated variables, such as water temperature, fisheries interaction, infectious agents, and the overall fitness of an individual (Elmer 2020).

The quantity of sperm produced by ripe males was apparently unaffected by the treatments involving exercise and air exposure of any duration, although the method of quantifying sperm production from the change in male body mass was subject to noise if some males also released urine at the time of stripping, reducing our ability to detect treatment effects. However, salmon exposed to extended air exposure produced sperm with a longer period of motility once activated. This motility period tended to increase with number of elapsed days after the salmon were exposed to the stressor. This could be an outcome of stressed males redirecting more of their limited resources into reproduction, to provide their gametes with the ability to overcome the perceived environmental stressor they are facing and so have a higher chance of fertilizing the ova (Elgee et al. 2010; Duffield et al. 2017). Stressed and unstressed males should both maximise their reproductive success following migration, but since their experiences have been different, it is plausible that their resource allocation decisions might differ as well. Salmon that have experienced physiological stress can experience reduced immune function (Wedemeyer and Wydoski 2008; Olsen et al. 2010; Ardia et al. 2011; Arlinghaus et al. 2013; Havn et al. 2015), and altered movement patterns (Arlinghaus et al. 2013; Richard et al. 2014; Twardek et al. 2018). For example, Atlantic salmon that have gone through C&R exhibit difficulty crossing barriers, show erratic activity, postponed upstream migration, increased immediate

post-release downstream movement, and shorter overall travelled distances (Arlinghaus et al. 2013; Richard et al. 2014). Since these effects will tend to reduce access to mates and optimal spawning grounds, it is possible that they respond by enhancing the activity of their sperm to enhance the likelihood of fertilisation. This may reflect differing outcomes to the trade-off between sperm velocity and longevity (Leviton 2000; Lehnert et al. 2018; Taborsky et al. 2018). The eggs of external fertilizing fish, like Atlantic salmon, tend to be fertilised extremely quickly (Hoysak and Liley 2001; Islam and Akhter 2011; Beirao et al. 2019). Sockeye salmon for instance, have exhibited a high fertilisation success within the first 5–10 s after the eggs are released (Hoysak and Liley 2001). Allowing the gametes to be exposed for a longer period of contact prior to burial in the substrate may leave the eggs vulnerable to predation or to being washed away by the currents (Hoysak and Liley 2001).

Clutch sizes were reduced by both exercise and air exposure. Other studies have also found that female salmon produce smaller clutch sizes after exposure to the air or to higher levels of cortisol (McConnachie et al. 2012; Richard et al. 2013; Cook et al. 2015). For example, Richard et al. (2013) demonstrated that air exposure of just 10 s during the summer, when water temperatures were relatively high, could reduce clutch size of female Atlantic salmon by half, or more if the 10 s threshold was surpassed. In our study, however, the stressor was applied a short period prior to spawning, where the eggs had already developed, rather than earlier in the migration journey (e.g., during the preceding summer). This suggests that the effect was mediated not through changes to egg production (or resorption), but through females losing eggs prior to spawning. This could not have happened while experiencing the stressors, since none of the selected females had released eggs into the body cavity at the time of the stressor protocols. It is most likely that females lost the eggs some days later, while the fish were in the holding tanks. This, however, could not be corroborated since any released eggs falling to the bottom of the tanks would not have been visible due to low light levels and low water clarity, and would have been flushed out when the standpipes were temporarily removed to flush the tanks during cleaning, and to drop the water level when catching fish for stripping. While it is possible that some eggs remained in the body cavity after stripping (since this is not necessarily 100% effective at removing all eggs), the same person stripped all fish and was unaware of the females' treatment group, and so any failure to strip all eggs could not have introduced a

systematic difference in clutch size between treatments. Investigations of rainbow trout have illustrated that repeated acute stress during the early stages of vitellogenesis or during the nine months prior to spawning can influence oocyte development and result in smaller eggs (Campbell et al. 1992; Contreras-Sanchez et al. 1998). Parental treatment had no effect on egg volume in the present experiment, but that was probably due to the eggs already having developed by the time of the stressor treatments.

Our study indicates that even though C&R angling of Atlantic salmon during the spawning season may not affect the mortality of fish, angling-related stressors can have sublethal effects on fungal infection and proxies of reproduction, with possible indirect effects on fecundity or reproductive success. It should be noted that this study took place outside the normal salmon fishing season, which typically finishes by the end of October in Scotland, but it reinforces the need to cease angling well before the expected time of spawning. Previous work has shown that C&R angling of Atlantic salmon can affect the exploratory behaviour of angled fish, alter their migration patterns (reduced total distance travelled and stress-induced fallback), and impact their ability to cross barriers and obstacles (Tufts et al. 1997; Richard et al. 2014; Havn et al. 2015; Lennox et al. 2015, 2016). Changes in behaviour combined with influences in reproductive traits could result in reduced reproductive fitness of the adults (Thorstad et al. 2003; Lennox et al. 2016). C&R angling is clearly an improvement over the alternative policy of killing the salmon caught, however the time period and conditions under which the adult salmon are angled should be taken into consideration for regulations and management of C&R, as any extension of the fishing season could have adverse impacts on both the parents and offspring.

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