Does catch and release affect the mating system and individual reproductive success of wild Atlantic salmon (*Salmo salar* L.)?

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Abstract

In this study, we documented the breeding system of a wild population of Atlantic salmon (*Salmo salar* L.) by genetically sampling every returning adult and assessed the determinants of individual fitness. We then quantified the impacts of catch and release (C&R) on mating and reproductive success. Both sexes showed high variance in individual reproductive success, and the estimated standardized variance was higher for males (2.86) than for females (0.73). We found a weak positive relationship between body size and fitness and observed that fitness was positively correlated with the number of mates, especially in males. Mature male parr sired 44% of the analysed offspring. The impact of C&R on the number of offspring was size dependent, as the reproductive success of larger fish was more impaired than smaller ones. Also, there was an interactive negative effect of water temperature and air exposure time on reproductive success of C&R salmon. This study improves our understanding of the complex reproductive biology of the Atlantic salmon and is the first to investigate the impact of C&R on reproductive success. Our study expands the management toolbox of appropriate C&R practices that promote conservation of salmon populations and limit negative impacts on mating and reproductive success.

Keywords: alternative reproductive tactics, catch and release, fitness, reproductive success, *Salmo salar*, salmon

Introduction

Studies of breeding systems enable us to understand the processes underlying the different reproductive strategies adopted by both sexes of a species. In particular, variance in reproductive success is thought to be higher among males than among females, which may result from the strong correlation in males between the number of mates and fertility (Bateman 1948; but see Gowaty *et al.* 2012). Intrasexual selection drives the evolution of alternative reproductive tactics (ARTs) (Oliveira *et al.* 2008), which are particularly frequent in fish (Taborsky 2008). Species of the salmonid family are well known for their great diversity of breeding systems and the morphological differences associated with males adopting different ARTs (Fleming 1998). In Atlantic salmon (*Salmo salar* L.), males may either mature as parr, which are young, nonmigratory individuals, or after one (known as grilse) or two winters at sea (large salmon), whereas females normally mature after two winters at sea (Klemetsen *et al.* 2003). Early parentage genetic analysis on the species breeding system revealed an unexpected high level of polygamy for both sexes (Garant *et al.* 2001; Taggart *et al.* 2001) and, in apparent disagreement with sexual selection theory (Andersson 1994), an equally high variance in reproductive success for both sexes (Fleming *et al.* 1997; Garant *et al.* 2001). Other studies have found differences in reproductive success (RS) realized by males adopting

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different reproductive strategies. For instance, Garant *et al.* (2003) showed that large, multi-sea-winter salmon had higher RS than grilse. Previous studies also confirmed that mature parr, though at least one order of magnitude smaller than their anadromous counterparts, can fertilize up to 60% of the eggs/fry in a given population (Taggart *et al.* 2001; Saura *et al.* 2008; Weir *et al.* 2010). So far, there has been no study that documented the mating system and reproductive success at the scale of a whole Atlantic salmon population in a natural North American river. An in-depth understanding of the factors that may influence mating systems and reproductive success in nature may in turn improve the efficiency of management and conservation programs (Araki *et al.* 2008).

Despite concerns about the species' conservation status (ICES 2012), Atlantic salmon remains a highly prized game fish and many populations still sustain important recreational fisheries. To maintain the socioeconomic benefits resulting from angling while reducing its impact on wild population restoration, catch and release (C&R) angling has been introduced in many Atlantic salmon rivers. Globally, the total number of released salmon is increasing yearly and was over 206 000 in 2011 (ICES 2012) and represented 59% of the total catch in Canada in 2011. In Canada, C&R has been mandatory for large salmon (≥ 63 cm fork length) since 1984, with the exception of the province of Québec, where large salmon retention is allowed only on rivers that sustain healthy populations (Dionne *et al.* 2012). Atlantic salmon is not an exception when it comes to the importance of C&R in stock management. In the context of the global depletion of wild fish abundance and the evidence that sport fishing can impair stock persistence, the proportion of released fish across all sport fisheries has increased over the last decades and global release rate estimates are now about 60% (Arlinghaus *et al.* 2007).

The effectiveness of C&R relies on the assumption that released fish survive and reproductively contribute to the exploited populations (Arlinghaus *et al.* 2007). Post-release survival is highly variable and related to air exposure and water temperature (Bartholomew & Bohnsack 2005; Cooke & Suski 2005; Arlinghaus *et al.* 2007; Gingerich *et al.* 2007). Experiments at low water temperature reported high (up to 100%)-survival rates, suggesting that in favourable conditions, C&R fish do survive (Booth *et al.* 1995; Wilkie *et al.* 1997; Anderson *et al.* 1998; Whoriskey *et al.* 2000; Dempson *et al.* 2002; Thorstad *et al.* 2003).

To date, sublethal C&R studies focused on physiological and behavioural aspects, but never on reproductive success in natural settings (Thorstad *et al.* 2008). Thus, previous sublethal studies leave one of the crucial management questions unanswered: does C&R impair fitness? Although Atlantic salmon is one of the most studied species in terms of the impact of C&R (Cooke & Suski 2005), there is no direct evidence that surviving, released salmon successfully reproduce. Anadromous mature Atlantic salmon migrate to rivers for the sole purpose of reproduction. Although the species is iteroparous, generally <10% of the anadromous population represents successful repeat spawners (Fleming 1998). It is therefore essential to quantify the impact of C&R on salmon reproductive success throughout the spawning period following release (in Canada, the fishing season is restricted to the prespawning period). In a lab-based study, Booth *et al.* (1995) found that the eggs from C&R and noncaught salmon showed no difference in terms of survival. In nature, the introduction of mandatory C&R resulted in a 2.3-fold increase in the number of spawning redds on the Sautso River in Norway (Thorstad *et al.* 2003) and in higher parr and fry densities on the Ponoi River in Russia (Whoriskey *et al.* 2000). These observations, however, cannot confirm the participation of C&R salmon in reproduction, as many factors were not controlled.

Here, we document the genetic mating system at the scale of an entire population of North American Atlantic salmon and determine the factors affecting individual reproductive success. We also quantify the variance in reproductive success for both sexes and relate this to their reproductive strategies. Second, we quantify the impact of C&R on reproductive success. Based on the previous C&R studies, we expect C&R to have a positive impact on the global population reproductive output compared with systems that are exploited but C&R is not mandatory. However, we expect that C&R will impact caught and released individuals via diminished chances to reproduce and fewer offspring. Finally, we also tested the impact of air exposure and water temperature on C&R salmon fitness and expected to observe stronger negative impacts with higher water temperature and longer air exposure.

Materials and methods

Study site

The study was conducted on the Escoumins River, in Québec, Canada (Fig. 1). Mean annual flow 9 km upstream from the outlet is 14.8 m³/s. During summer months, water temperature frequently exceeds 20 °C and can reach 26 °C. In 1901, a dam was built 1 km upstream of the river mouth, just upstream of tidal influence. In 1969, a fish ladder was built to allow the passage of Atlantic salmon. In that same year, a second fish ladder was built at the Grand Sault waterfall, a
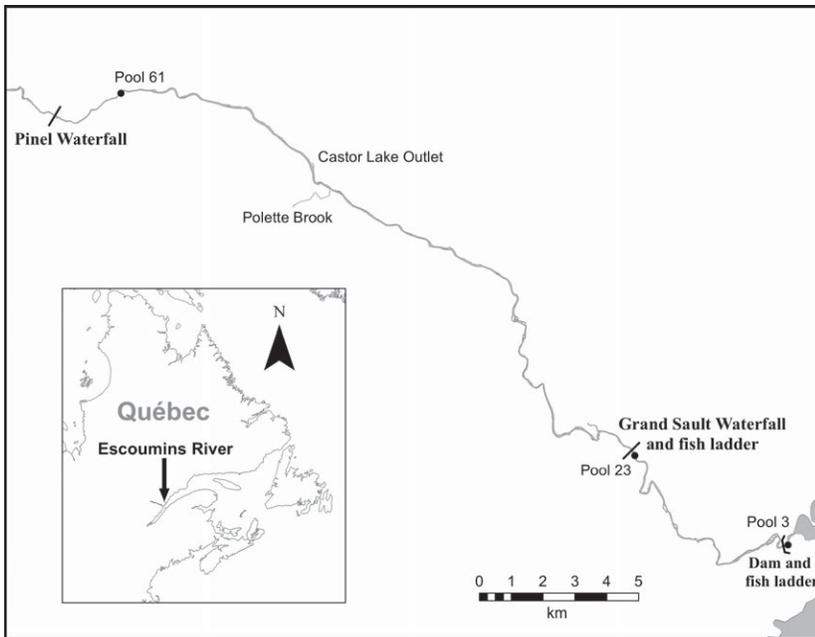
Fig. 1 The Escoumins River, and its tributaries, on the north shore of the St-Lawrence River in Québec showing the positions of the obstacles to salmon migration, as well as the three pools (•) where salmon were caught and released in 2009.

natural obstacle to migration 9 km upstream of the dam, thus giving salmon access to two tributaries and 36 km of river ending at Pinel waterfall, an impassable obstacle to migration. Also, hatchery-reared fry (3250 in 2009), resulting from adults captured in the Escoumins River, are released in the river section located upstream of the Pinel waterfall. The river is now home to a small anadromous Atlantic salmon population (annual mean of 312 ± 100 returning salmon for the 2004–2009 period). In this population, the three different male alternative reproductive tactics are present.

Salmon fishing (fly fishing only) on the river is open from June 1st until September 15th. All fishermen must register at the 'ZEC (Zone d'Exploitation Contrôlée or Area of Controlled Exploitation) de la rivière des Escoumins', which manages the use of the river. Provincial regulation allows fishermen to keep up to two grilse (defined as salmon <63 cm in fork length) a day, but they must release all large salmon (≥ 63 cm).

Sample collection

Adult sampling. In 2009, all salmon entering the River were measured and sampled (punch of 5 mm diameter from the adipose fin) at the fish ladder situated 1 km from the river mouth. During measurement and sample collection, fish were kept in the water and free to swim, so it was only possible to measure length to the nearest 5 cm.

Caught and released fish sampling. Fishermen collaboration was solicited throughout the 2009 fishing season to collect tissue samples (punch of 5 mm diameter from the adipose fin) and information from catch and release events. When registering, all fishermen received punch pliers and indications on how to collect tissue samples on the fish they would eventually release, as well as a few fishermen kits. Each kit contained a 1.5 mL Eppendorf filled with 95% ethanol to preserve the adipose punch and a questionnaire to record information about the catch and release event. The fishermen were asked to record, for each C&R, the date, the time of the day, the pool, the duration of the event (from hooking to landing), the kind of hook used (single or double, barb or barbless), the hooking location on the fish, the presence of bleeding, air exposure duration, condition at release (a subjective evaluation whether the fish was in excellent, good or bad shape) and any other observations about fish condition (injuries, etc). Temperature data loggers were placed in all frequently fished pools. Combining the information obtained from the fishermen and data loggers provided exact prevailing water temperature for each event. Fishermen participation was not mandatory, but strongly recommended, and the scientific team was consistently present on the riverbank promoting the project and assisting fishermen in the sample collection.

Fry sampling. From August 2nd to 24th 2010, electrofishing was performed on a total of 94 preselected rearing sites to capture 2577 fry produced by the fish that reproduced during the fall of 2009. Sites were preselected as a function of the quality of the habitat and to be representative of the river and its tributaries. Each site

was ~100 m long and 2 m wide. Fry sampled was preserved in 95% ethanol for later genotyping.

Genetic analysis

DNA was extracted from adult adipose fin tissue and from fry caudal fin tissue using a salt-based method (Aljanabi & Martinez 1997). Microsatellite polymorphism was analysed at 12 loci, and polymerase chain reaction (PCR) amplifications were performed in two multiplexes (see Supporting information for protocols). The same PCR protocol was used for both multiplexes and performed on Biometra® T1 thermocycler or Biometra® Tgradient. Cycling conditions were as follows: 15 min at 95 °C, 34 cycles of 94 °C for 30 s, 58 °C for 3 min, 72 °C for 60 s and a final elongation step at 60 °C for 30 min. DNA amplified fragments were electrophoresed on a ABI™ 3130 (Applied Biosystems), and results were analysed with GeneMapper™ software. Software implanted automatic scoring option was used, but alleles were visually inspected twice to minimize scoring errors.

To control for human errors and sample contamination, negative and positive controls were placed in each 96-well plate used for PCR and electrophoresis. The presence of null alleles, large allele dropout and the scoring of stutter peaks were estimated using MICROCHECKER 2.2.3 (Van Oosterhout *et al.* 2004). F_{IS} at each locus and the significance of departure from HWE were computed using FSTAT (Goudet 1995). To estimate the genotyping error rate, all samples from 2009 (the 268 putative parents) were reamplified, reelectrophoresed and reanalysed with GeneMapper.

Parentage analysis

We first used the identity check function in CERVUS 3.0.3 (Kalinowski *et al.* 2007) to find matching genotypes, allowing the identification of fish that were caught and released more than once. Only the last C&R event of these fish was considered in the analysis of the effect of C&R on reproductive success. Identity analysis was also used to determine whether a C&R salmon crossed the fish ladder and, if so, to associate the information recorded in the fish ladder (total length and date of river entrance) to the C&R salmon.

As sexing of the putative parents at their passage in the dam fish ladder was not possible, sex determination was performed with the help of a preliminary parentage analysis and the known sex ratios for grilse and large salmon. The sex of an individual was inferred based on its size, the size of its mates and the probability of the parentage network (see details in Supporting Information).

To reduce the computation time required by COLONY (Jones & Wang 2010) to analyse our large dataset, CERVUS and PASOS (Duchesne *et al.* 2005) were first used to find highly probable mother–offspring and father–offspring pairs that were then identified in the input file of COLONY as known maternity and paternity. These pairs had zero mismatches across all loci and were selected by both CERVUS and PASOS as the most probable parent–offspring pairs. A total of 1247 known paternities and 2395 known maternities were identified in this way. The full likelihood approach implemented in COLONY was then used to allocate a mother to the 153 fry that were not in the known maternity file and to allocate a father to the 1301 fry that were not in the known paternity file. As we sampled absolutely all anadromous salmon that entered the river in 2009, and considering that female mature parr are extremely rare in Atlantic salmon, the probability that an actual mother was included in the candidates female file was set to 1. The probability that an actual father was included in the candidate male file was set to 0.6 as suggested by the results of preliminary assignments performed with PASOS and CERVUS.

Reproductive success analysis

Description of the mating system of Atlantic salmon. The best configuration (with the maximum likelihood) given by COLONY was used to determine the number of fry produced by each anadromous salmon and by mature parr. Although mature parr were not sampled, COLONY could infer their genotypes from the pedigree analysis. The results from COLONY also allowed the identification of the number and type of mate (anadromous or/and mature parr) for each salmon. The total number of fry inferred to mature parr was used to estimate the relative contribution of mature parr and anadromous male to the production of fry in the river.

COLONY actually gives a list of many plausible configurations with high likelihood values, including the best configuration with the maximum likelihood. For a large data set with many known relationships and a moderate number of markers like our one, however, the vast majority of relationships in different plausible configurations remain the same, and therefore, it does not matter much which configuration is used in the downstream analysis. Although not all relationships in the best configuration might be correctly inferred, there should be no bias resulting in over- or underestimating relatedness except when marker information is scarce, as checked by many simulations (Wang & Santure 2009).

Determinants of individual reproductive success. The results from the parentage analysis were then used to

quantify the relative influence of the variables of interest on the individual fitness of anadromous salmon. A C&R variable was also added to test whether C&R impairs salmon fitness. As the gender of unsuccessful fish remained unknown, we used a two-part modelling approach.

First, we modelled access to reproduction (that is, the production of at least one fry) by fitting logistic regressions. Because grilse and large salmon adopt different strategies on the spawning grounds (Fleming & Reynolds 2004) and because only one grilse was C&R in 2009, we conducted separate analyses. For grilse, the global logistic model contained three predictors (date of river entrance (DRE), length and the interaction between DRE and length), whereas large salmon global model predictors were DRE, length, C&R, the interaction between DRE and length and between C&R and length.

Second, for large salmon that produced at least one offspring, we modelled individual reproductive success (quantified as the number of fry produced) by fitting negative binomial regressions. The global negative binomial model had 10 predictor variables: DRE, length, C&R status, sex, number of mates and the following interactions: C&R status × length, sex × DRE, sex × length, sex × C&R status and sex × number of mates.

To statistically assess the effect of the different variables considered in the aforementioned global models, we used the information-theoretic-based approach of AIC multimodel inference (Burnham & Anderson 2002). The global model goodness of fit was assessed using Pearson's χ^2 test and by calculating the Nagelkerke's adjusted pseudo-R^2 for negative binomial regression and using the Hosmer and Lemeshow test for logistic regression. We then built a set of models made of all models nested within the global model (i.e. all combinations of including or excluding each variable) plus a null model (intercept only). Those models were ranked according to their AIC_c (a corrected measure of AIC for small samples), and ΔAIC_c (AIC_c of the model minus the AIC_c of the best model) was computed for each model. We then built a confidence set of model with all models with a $\Delta AIC_c \leq 6$ (according to Grueber et al. 2011). From the ΔAIC_c, we computed the Akaike weights (ω) of the models included in the confidence set. The Akaike weight of a model can be interpreted as the estimated probability that it is the best model given other considered models. We then ranked the predictor variables by calculating, for each predictor, the sum of the Akaike weights of the models that contained this particular predictor (importance weight). The larger the importance weight of a predictor variable is, the more important the variable is relative to the other variables. As we were also interested in identifying variables that

had a significant effect on the dependent variable, and because most of the analyses led to a set of many models with similar Akaike weights, we used the model-averaging approach to calculate an unbiased (i.e. not biased by the uncertainty related to selecting only one model) estimate and its confidence interval for each parameter present in the confidence set. These regression coefficients allow the measurement of the direction and magnitude of the effect size of each independent variable on the dependent variable. All analyses were performed with R (R Development Core Team 2011), logistic and negative binomial regressions were fitted with the glm function, and model-averaging approach was performed using the 'MuMIn' (Bartoń 2012) and the 'AICcmodavg' packages (Mazerolle 2011).

Effects of the C&R conditions. To test whether the stresses involved in a C&R event have an impact on the number of produced fry, we followed the above method, but by fitting only a negative binomial model. The small number of C&R salmon for which we had data limited the number of predictor variables that could be included in the model. We therefore chose variables with a known effect on C&R salmon physiology or mortality: water temperature (Thorstad et al. 2003), air exposure time (Ferguson & Tufts 1992) (as an ordinal variable: no exposure, 0–10 s exposure and >11 s exposure) and their interaction (Gingerich et al. 2007).

Results

Adult population

In 2009, between June 21st and September 11th, 268 anadromous Atlantic salmon entered the river, of which 72% ($n = 191$) were multi-sea-winter salmon and 28% ($n = 77$) were one-sea-winter salmon. Mean length (±standard deviation) was 78.4 ± 5.5 cm for large salmon and 54.1 ± 4.9 for grilse.

Caught and released salmon

Information and tissue were collected from 42 of the 46 C&R events that occurred on the river in 2009. Most C&R (38/42) happened just downstream of the dam, at the entrance of the river (i.e. pool #3) (Fig. 1). Other events were reported further upstream, in pool #23 ($n = 1$) and pool #61 ($n = 3$). Identity analyses, performed with CERVUS, revealed that two salmon (P149 and P194) were caught and released twice in the summer. Consequently, the 42 C&R events reported involved 40 different salmon. Individuals P149 and P194 were both captured and recaptured in pool #3, and the time elapsed between events were 3 and

5 days, respectively. Both managed to cross the fish ladder and produced, respectively, 38 and 25 fry.

From the 36 salmon that were C&R in pool #3, 31 crossed the fish ladder. As the failure to cross the fish ladder after being C&R could be due to C&R but also to many other factors, the impact of C&R on the capacity of large salmon to produce at least one offspring (see Access to reproduction below) was assessed with and without those five salmon. Mean total length of C&R salmon for the 35 salmon that crossed the fish ladder was 78.1 cm (SD = 6.3 cm), which is not different from the noncaught large salmon (78.2, SD = 5.7, $n = 160$) (Welch two sample t-test, $P = 0.96$). Mean water temperature during C&R events was 16.0 °C (min = 10.5, max = 19.1). Fifteen C&R salmon were reported to have been kept in the water (0 s out of water), 11 C&R salmon were kept out of the water for 1 –10 s, whereas 13 salmon were air-exposed for more than 10 s.

Genetic and parentage analyses

Genotypes were obtained for all adults and for 2548 of the 2577 offspring. The reanalysis of all 2009 adult samples revealed an error rate of 0.003% for loci MST-3 and SsaD71 and a null error rate for others. The 12 loci were highly polymorphic with a number of alleles per locus ranging from 8 to 33 (mean = 20.5) and observed heterozygosity ranging from 0.69 to 0.96. Only Ssa197 had a significant, albeit modest, F_{IS} value (0.056) in adults but not among offspring. We think that the deficit of heterozygotes for Ssa197 has very small effect on our analyses results. We rerun the parentage analysis performed on CERVUS (because it is fast and easy to run) without this marker, and the results were the same for 99.15% of offspring. The probability that the multilocus genotypes did not differ between two randomly chosen individuals (identity nonexclusion probability) was 2.31×10^{-20}. For parentage assignment, the combined identity nonexclusion probability across all loci for the first parent was 5×10^{-6}.

Description of the mating system

We assigned at least one fry to 245 of the 268 anadromous salmon that entered the river. Given that the sex of an individual was determined on the basis of its inferred mate, the sex of the 23 salmon for which no fry were assigned remains unknown. Of the 245 sexed salmon, 144 were females (142 large, two grilse) and 101 were males (37 large, 64 grilse).

For females, the number of inferred fry ranged between 1 and 77 [mean = 17.7, variance (Var) = 229.5]. For males, the number of fry assigned to an anadromous individual ranged from 1 to 80 (mean = 14.2, Var = 211.3). If we consider fry assigned to mature male parr, then the minimum and the maximum number of fry assigned to a male remained unchanged, but the mean number of offspring per male was reduced to 4.5 with a variance of 58.7. Figure 2 shows the distribution of the number of inferred fry per anadromous individual when both sexes are pooled together (A) and when males and females are treated separately (B).

Males and females were mostly polygamous, but apparent monogamy was more frequent in males than in females (respectively, 10/101 and 1/144, Fisher's exact test P-value < 0.001). Among males, the odds of monogamy were the same for grilse or large salmon (respectively, 8/64 and 2/37, Fisher's exact test P-value = 0.21), but all males that had nine or more mates were large salmon. For females, the total number of inferred mates ranged from 1 to 34 (mean = 9.5, Var = 44.3). If we consider only their anadromous mates, females had between zero and seven mates
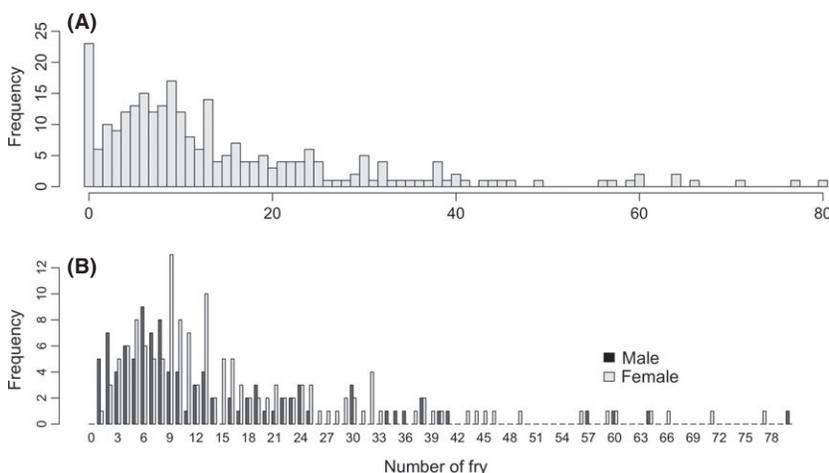

Fig. 2 Observed distribution of the number of inferred offspring (reproductive success) in the Escoumins River for the 2009 spawning season when (A) males and females are pooled together and (B) when males (black) and females (grey) are separated. The sex of salmon with no reproductive success remains unknown.
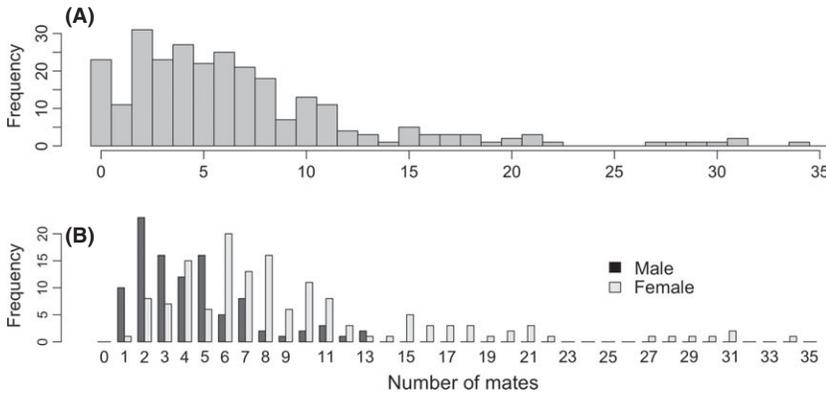
Fig. 3 Observed distribution of the number of mates in the Escoumins River for the 2009 spawning season when (A) males and females are pooled together and (B) when males (black) and females (grey) are separated. The sex of salmon with no reproductive success, and thus with no mate, remains unknown.

(mean = 3.0, Var = 2.1). Mature male parr successfully reproduced with anadromous females, and the mean number of parr mates per female was 6.5 (range 0–31). A small number of females mated only with parr (5/144). The successful mature male parr that were identified by COLONY spawned with one to six females (mean = 2.0, Var = 0.4), while the anadromous males had between one to 13 mates (mean = 4.3, Var = 8.0). Figure 3 shows the distribution of the inferred number of mates for all anadromous salmon pooled together (A) and for anadromous males and females treated separately (B).

Mature parr fathered 1115 of the 2548 offspring (43.8%) that were included in the parentage analysis. COLONY identified 462 different parr, which fathered a mean of 2.4 fry (range 1–10). Thus, when considering identified mature parr, the total number of potential spawners increases by 2.7 times, from 268 to 730. Mature parr also skewed the sex ratio of the population from 1:1.4 (males:females) in the anadromous fish to 3.9:1 when taking mature parr into account. Those values are underestimated as we only considered mature parr that were identified by COLONY, that is, a parr that produced at least one fry included in our analysis.

Determinants of the reproductive success

Access to reproduction. The odds for a grilse to access reproduction (66 of the 77 grilse have at least one inferred offspring in the parentage analysis) were lower than for large salmon (179/191) (Fisher's exact test, P-value = 0.034). For large salmon, the global model was not informative, as the second best model in the AIC_c table was the null model (with a $\Delta AIC_c = 0.58$). Moreover, none of the predictors had a significant effect on access to reproduction. Assuming that the five salmon that never entered the river after being C&R did not cross the fish ladder because of resulting mortality, injury and/or change in migratory behaviour due to C&R, we measured a significant negative effect on large

salmon access to reproduction reducing their chance to reproduce by 12% (GLM, binomial distribution, P-value = 0.015).

For grilse, the model predicts that all individuals that entered the river early in the summer did reproduce, but grilse that entered the river later in the season had a reduced (50% less) chance of mating (Fig. 4). The global logistic model fits the data reasonably well (Hosmer–Lemeshow test, P-value = 0.77). With a predictor weight of 1, there was strong support for the importance of the date of river entrance (DRE) relative to the two other predictors, length and the interaction of DRE and length (predictor weight of 0.37 and 0.09, respectively) (Table 1). Moreover, the DRE model-averaged estimate was the only one of the three estimates for which the unconditional 95% CI did not include 0.
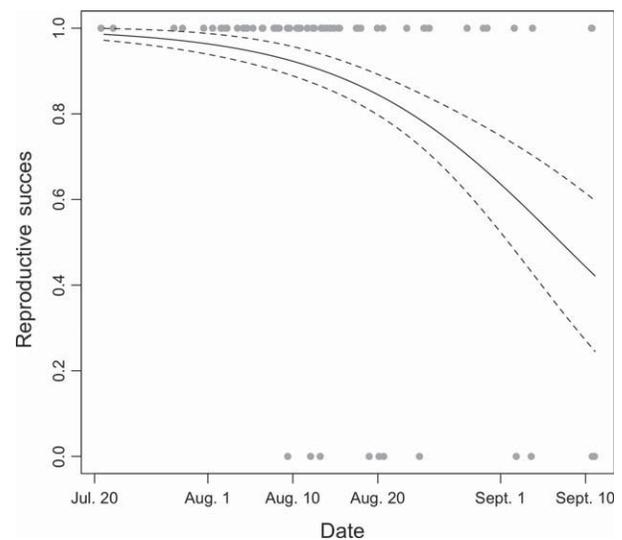

Fig. 4 Model-averaged predictions (solid line) and their associated unconditional standard errors (dashed lines) of grilse chances to access reproduction (i.e. to produce at least one offspring) as a function of the date of river entrance. Real observations are plotted in grey.

Table 1 Parameter estimates for each of the models in the confidence set of logistic models for grilse access to reproduction. When a variable is not part of a model, the corresponding cell is left blank. Models are ranked by AIC_c. For each model, the number of parameter (k), the ΔAIC_c and the Akaike weight are shown. Also shown for each parameter is the model-averaged estimate, its 95% unconditional CI and its importance weight. In bold is the only parameter (date of river entrance) with a significant effect on the grilse capacity to produce at least one offspring

	Model no.	Intercept	DRE	Length	DRE:Length*	k	AICc	ΔAICc	Akaike weight
	1	6.98	**−0.088**			2	57.33	0.00	0.63
	2	3.96	**−0.087**	0.055		3	59.01	1.68	0.27
	3	7.18	**−0.135**	−0.007	0.0009	4	61.21	3.88	0.09
Model-averaged estimate			**−0.088**	0.055	0.0009				
95% CI inf			**−0.146**	−0.100	−0.0102				
95% CI sup			**−0.030**	0.210	0.0121				
Importance weight			**1.000**	0.366	0.0913				

*Colon (:) indicates the interaction between two variables.

Number of offspring produced. A strong fit of the global negative binomial model was observed after the exclusion of two outliers from the analysis (pseudo-R^2 = 0.83, Pearson's goodness-of-fit test χ^2 = 183.32, residual d.f. = 166, P-value = 0.17). One of the two outliers (a male) was the salmon that had produced the most offspring, whereas the other excluded individual (a female) was the third most successful individual. Both individuals had a near average number of mates. When included in the analysis, the model did not fit the data (Pearson's goodness-of-fit test P-value = 0.02). Subsequent analyses were thus made without these two fish, and the results must be interpreted accordingly. The confidence set of models contained 33 models (Table 2 shows the 10 best models).

Based on the interpretation of the unconditional 95% CI, four predictors had a significant effect on the number of produced fry: sex, number of mates, the interaction between sex and number of mates and the interaction between C&R and length. For C&R salmon, the predicted number of fry declined with an increase in the total length of the fish (Fig. 5A). This suggests that C&R has a more important effect on the reproductive success of larger relative to that of smaller salmon in multi-sea-winter fish. Yet, the overlap of the prediction's standard errors probably reflects the relatively weaker importance of the interaction between C&R and length (predictor weight = 0.33) compared with other predictors such as the number of mates, the sex and their interaction (respective predictor weight = 1,1 and 0.97). Model predictions revealed that an increase in the number of mates translated into an increase in the number of produced fry for both males and females, but at a steeper rate for males than for females (Fig. 5B).

Impact of C&R conditions. The global negative binomial model fits the data moderately well (pseudo-R^2 = 0.23,

Pearson's goodness-of-fit test χ^2 P-value = 0.49). The global model provided the lower AIC_c, but the null model ranked second, only 1.06 AIC_c apart from the best model. The air exposure time and the water temperature interaction was the only predictor that had a significant effect on the number of produced offspring. The averaged model predicted that for salmon that were kept in water prior to release, the number of produced offspring is inversely proportional to water temperature. For salmon that were either exposed to air for a short ($\leq$10 s) or a long (>10 s) period of time, the number of produced offspring was slightly influenced by water temperature whereby they produced more offspring if released in warmer water than in cooler water. For water temperature below 17 °C, the number of predicted offspring produced by nonexposed salmon was greater than for salmon exposed to air for a short period of time, which, in turn, was greater than for salmon kept out of the water for more than 10 s (Fig. 6).

Discussion

This is the first study to sample every breeding anadromous adult in a wild natural population of Atlantic salmon in North America. The complete sampling of anadromous putative parents contributed greatly to improve the accuracy of our parentage analysis and enabled us to estimate the reproductive contribution of all spawners, including mature male parr. Furthermore, the high ratio of assigned offspring to the number of anadromous parents of both sexes (female 2548/144 = 17.7, male 1433/101 = 14.2) implies that we collected enough juveniles to adequately represent the true distribution of reproductive success (Anderson *et al.* 2011).

Anderson *et al.* (2011) highlighted that a key theme emerging from work on fish reproductive success is

Table 2 Parameters of the 10 best negative binomial models for the number of produced offspring by large salmon. For each model, parameter estimates are given for included quantitative variables, whereas inclusion of a qualitative variable is represented by a '+'. When a variable is not part of a model, the corresponding cell is left blank. Models are ranked by AIC_c. For each model, the number of parameter (k), the ΔAIC and the Akaike weight (ω) are shown. Also shown for each parameter is the model-averaged estimate, its 95% unconditional CI, as well as its importance weight. In bold are the parameters with a significant influence on the number of produced offspring for large salmon

Model no.	Intercept	Sex:Nbr of mate*	Sex: Length	Sex: DRE	C&R: Sex	C&R: Length	C&R (Noncaught)	Sex (Male)	Number of mate	Length	DRE	k	AICc	ΔAICc	ω
1	1.80	+						+	0.0910			4	1187.32	0.00	0.14
2	1.83	+			+		+	+	0.0909			6	1188.23	0.91	0.09
3	3.33	+			+	+	+	+	0.0904	−0.0193		8	1188.44	1.12	0.08
4	3.34	+				+	+	+	0.0906	−0.0204		7	1188.47	1.15	0.08
5	1.50	+						+	0.0906	0.0039		5	1189.04	1.72	0.06
6	1.75	+					+	+	0.0911			5	1189.08	1.76	0.06
7	1.76	+						+	0.0909		0.0010	5	1189.22	1.90	0.05
8	1.61	+			+		+	+	0.0906	0.0030		7	1190.16	2.84	0.03
9	1.79	+			+		+	+	0.0908		0.0010	7	1190.18	2.86	0.03
10	3.31	+				+	+	+	0.0905	−0.0206	0.0013	8	1190.33	3.01	0.03
Model-averaged estimate		**0.0614**	0.0081	−0.0017	0.3377	**0.0304**	0.0533	**0.5958**	**0.0948**	0.0036	0.0012				
95% CI inf		**0.0180**	−0.0188	−0.0161	−0.0810	**0.0011**	−0.1286	**0.4186**	**0.0843**	−0.0088	−0.0032				
95% CI sup		**0.1048**	0.0350	0.0127	0.7563	**0.0596**	0.2353	**0.7731**	**0.1054**	0.0161	0.0056				
Importance weight		**0.97**	0.14	0.06	0.35	**0.33**	0.65	**1**	**1**	0.56	0.31				

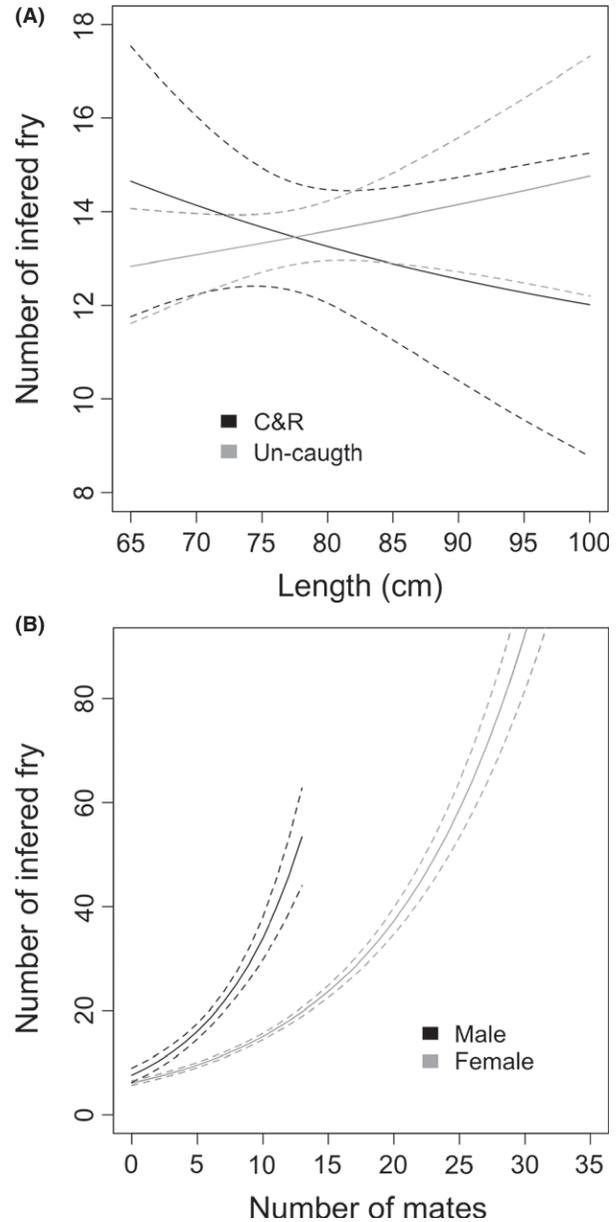*Colon (:) indicates the interaction between two variables.

Fig. 5 (A) The effect of the interaction between C&R and size on the number of inferred fry as illustrated by the model-averaged predictions (solid lines) and their associated unconditional standard errors (dashed lines) for C&R (black) and noncaught (grey) salmon. Plotted predictions are for females that entered the river in the late July and who mated with nine partners. (B) Model-averaged predictions (solid lines) and their associated unconditional standard errors (dashed lines) of the number of inferred offspring for male (black) and female (grey) uncaught salmon of 78 cm that entered the river in the late July.

that a significant proportion of the breeders, particularly males, produce no offspring. Here, we inferred zero offspring for 9% of the anadromous breeders. The sex of the salmon that failed to reproduce is unknown, but
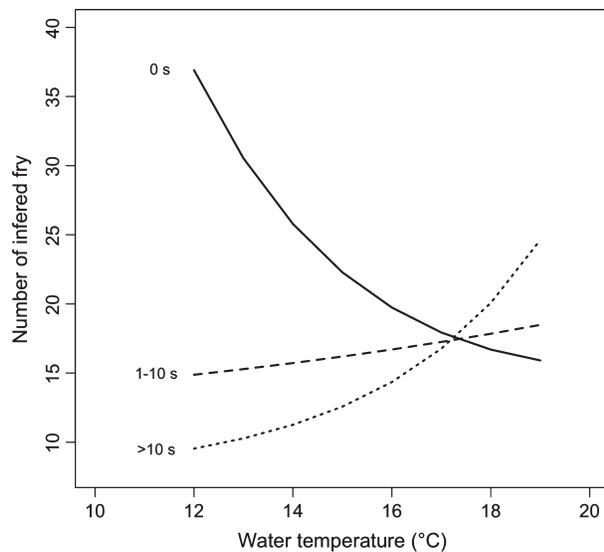
Fig. 6 Model-averaged predictions of the number of inferred fry for C&R salmon that were exposed to air for 0 (solid line), 1–10 s (dashed line) and >10 s (dotted line) across the 12–19 °C range of water temperature.

we could infer the number of winters they spent at sea by their body size. Grilse were significantly overrepresented in the zero-offspring-inferred group. Grilse are mainly males (97% in the sexed fish) and typically adopt a sneaking strategy to access to ovipositing females that are controlled by larger dominant males (Fleming 1996). This strategy results in a lower reproductive success than that of larger males, which is counterbalanced by a higher probability of surviving the marine feeding migration given that grilse are at sea for a shorter period of time and do not migrate as far as large salmon (Garant *et al.* 2003). Moreover, our model highlighted that the date of river entrance was a good predictor of mating opportunities for grilse but had no effect for large salmon. These observations indicate that most anadromous salmon that apparently did not reproduce were grilse that had limited access to reproduction either because of male–male competition with large salmon or because of their late arrival in the river.

Female mating pattern

Female reproductive success was highly variable, and their number of mates was the best predictor of their fitness. All but one female were confirmed to mate with two or more males. Females can take advantage of polyandry in many ways [see Garant *et al.* (2001)]. Furthermore, Garant *et al.* (2005) showed that females with a higher number of mates produced more outbred offspring and that both of these factors increased their

fitness. Thus, females should aim to mate with a large number of males, which may explain why female salmon tend to spawn asynchronously, a behaviour that results in a male-biased operational sex ratio (i.e. the number of sexually active males to females) favourable to polyandry (Fleming & Reynolds 2004). On the other hand, females are also known to be aggressive towards anadromous males and have been observed leaving their nest while waiting for male dominance to be (re)established (Fleming 1998). Females thus seem to express preference towards dominant anadromous males. Nevertheless, most (93%) of the females mated with mature male parr, and all females did not seem to deliberately avoid parr as five of them mated with parr in the absence of any anadromous male.

Body size effect

Even though body size is thought to be the primary trait under selection in salmonid species (Fleming & Gross 1994), we found only a weak positive relationship between body size and the number of produced offspring for both large males and large females. Such a weak relationship has also been reported by Garant *et al.* (2001) and could result from different factors. One of these is the physical environment of the river. In the middle of the summer, the Escoumins River water flow is low (6 m^3/s) and long sections of the river show extremely low water levels, conditions that could disfavour larger individuals, as has been shown for Atlantic salmon (Jonsson *et al.* 1991; Mitchell & Cunjak 2007) and for sockeye salmon (*Oncorhynchus nerka*) spawning in shallow creeks (Lin *et al.* 2008). The weak correlation between fitness and body size could also arise if that latter trait is a weak predictor of male status as reported in Pacific salmon (Quinn & Foote 1994), or if heritability is low for this trait.

Anadromous male mating pattern

As for females, anadromous male reproductive success was highly variable and the number of mates was the best predictor of the number of produced offspring. Anadromous males were mainly polygamous, but the proportion (10%) of them apparently mating with a single partner was 14 times greater than within females (Fisher's exact test, *P*-value = 0.001). Among males, the capacity to mate with a high number of females could be related to the reproductive strategy adopted because all anadromous males that had the highest number of mates (more than nine) were all multi-sea-winter salmon. In accordance with sexual selection theory (Bateman 1948; Andersson 1994), an increase in the number of mates was more beneficial for males than for females

(Fig. 5B). Mature male parr presence may, in part, drive this difference because they generally produce less offspring than anadromous males. However, when excluding mature parr, there was still a stronger correlation between the number of anadromous mates and the number of inferred offspring in males than in females ($r = 0.64$ P-value < 0.001 and $r = 0.45$ P-value < 0.001, respectively). Standardized variance ($\sigma^2/mean^2$) (Wade & Arnold 1980) in reproductive success is thus expected to be greater for males than for females (Shuster & Wade 2003), as we observed here. However, with only anadromous males being considered, males and females standardized variances in reproductive success did not differ as much but was still higher in males (respectively, 1.05 and 0.73) and were comparable with values reported for anadromous Atlantic salmon by Fleming et al. (1997) (between 0.3 and 1.35) and by Garant et al. (2001) in a stream section without any sexually mature parr (0.53 males and 0.59 for females).

Mature male parr

The proportion of progeny attributed to mature parr reported in recent genetic studies on Atlantic salmon reproduction performed in natural streams ranged from 22% to 65% (Garcia-Vazquez et al. 2001; Taggart et al. 2001; Saura et al. 2008; Weir et al. 2010). The sole study performed in a North American river (Weir et al. 2010) reported that parr fathered 22% of the eggs analysed when an assumption was made that the three most successful males in a nest were anadromous. Here, parr fathered 44% of the studied fry, a result that is consistent with those reported previously. Individually, each male parr produced less offspring than their anadromous counterpart (mean number of sired offspring: 2.4 vs. 14.2). This reduced fitness is counterbalanced by a higher rate of survival to breeding age, because they mature earlier and do not undertake sea migration (Hutchings & Myers 1994). Altogether, parr increased the number of successful breeding males by a factor of 5.5, and their presence strongly skewed the sex ratio, such that when considering mature parr, there were four times more males than females in the river.

Impact of catch and release

This study demonstrated that C&R salmon represented 20% of the multi-sea-winter population and were one of the parents for 22% of the genotyped offspring, hence playing an important role in the reproductive output of the whole population. Our results thus confirm the role played by released salmon in the observed higher redd and parr density that followed the inception of C&R fishing on the Ponoi River in Russia and

on the Alta River in Norway (Whoriskey et al. 2000; Thorstad et al. 2003). Thus, C&R is an effective conservation and management tool towards maintaining the socio-economic benefits from recreational fishing while ensuring a minimal impact on the exploited population, pending appropriate practices (see below). In Canada, annual economic value for wild Atlantic salmon has been estimated at $255 million and 3872 full-time equivalent jobs are directly created annually because of wild Atlantic salmon, most of which (86%) are related to recreational fishing (ASF 2011). Furthermore, in this study, as well as in other previous studies (Whoriskey et al. 2000; Thorstad et al. 2003), a small proportion (namely, 5%, 11% and 4%) of salmon were caught and released more than once in the fishing season, thus increasing the value of each fish and the economic benefits of C&R.

At an individual scale, if we exclude from the analysis the five C&R salmon that did not pass through the fish ladder, C&R salmon had the same probability of reproduction as noncaught salmon. On the other hand, when taking the fish that did not pass the ladder into account, C&R impaired access to reproduction of multi-sea-winter salmon, reducing their chances of mating by 12%. Several reasons may explain why these salmon never crossed the dam. Indeed, although all except one were reported to be in excellent condition, these salmon could have died or aborted migration as a result of C&R. However, these salmon could also have come in the first pools of the river as visitors before returning to the sea. This is plausible based on migrant detection in other Atlantic salmon studies (Jonsson et al. 2003; Dionne et al. 2008). Based on the previous studies and on the fact that we do not have data on the behaviour of noncaught salmon in those downstream pools, we then suggest that C&R does not significantly impair the access to reproduction of large salmon.

Within the group of large salmon for which at least one offspring was assigned, C&R had a significant, albeit weak, impact on the number of offspring inferred and that effect was dependent on fish length. Thus, while smaller fish fitness did not seem to be impaired by C&R, larger C&R salmon produced significantly less offspring than same size noncaught salmon. Previous studies of the effect of size on salmonids post-release mortality have led to mixed conclusions (Bartholomew & Bohnsack 2005). However, size has been identified as an important source of variability to the physiological disturbance of rainbow trout captured by angling as larger fish showed higher level of plasma cortisol, glucose and lactate levels (Meka & McCormick 2005). In Atlantic salmon, angled salmon showed decreased plasma concentration of calcium and pH and a higher plasma concentration of glucose, lactate, osmolarity,

chloride and sodium than nonangled fish and the magnitude of the disequilibrium for plasma concentration of calcium, lactate and pH was positively correlated with body length (Thorstad *et al.* 2003). Larger fish take longer to land and that could explain why they suffer more important physiological disturbance and reduced fitness from C&R (Thorstad *et al.* 2003; Meka 2004). Fishermen should thus minimize the time elapsed between hooking and landing to minimize the impact of C&R.

Water temperature has been identified as a major predictor of salmonid survival rate (Muoneke & Childress 1994; Thorstad *et al.* 2003; Boyd *et al.* 2010), explaining 72% of the variation in survival from Atlantic salmon C&R angling (Dempson *et al.* 2002). Air exposure is also associated with C&R-related physiological disturbance (Ferguson & Tufts 1992; Schreer *et al.* 2005), and studies recently showed that there are interactive effects of air exposure duration and water temperature on survival and physiological disturbances of C&R fish (Gingerich *et al.* 2007; Gale *et al.* 2011). Here, water temperature negatively impacted reproductive success of salmon kept in the water, but in the temperature range of 12–17 °C, air exposure time had a greater negative impact on fitness than water temperature. Depending on the temperature, reproductive success can be up to two or three times higher for salmon kept in the water compared with those exposed to air for ≤ 10 s and with those exposed to air for >10 s, respectively. Predictions obtained for water temperature above 17 °C, where a longer air exposure seems beneficial in terms of fitness, as well as the positive relation between water temperature and the number of produced offspring for the long exposure time group, could be explained by the fact that high water temperatures may enhance the recovery of exercised Atlantic salmon (Wilkie *et al.* 1997). Thus, the conditions in which C&R is conducted influence the success of the practice in terms of conservation. Consequently, precaution must be taken to limit C&R in warm water periods and avoid air exposure prior to release.

Overall, this study measured the impact of C&R on individual reproductive success and allowed an evaluation of its sustainability for an exploited fish population. Nevertheless, our study suffers from limitations that should be considered to improve further studies of this type. First, ideally such studies should include more than 1 year of data because other similar studies showed that patterns of reproductive success and selection gradients can change substantially from year to year (Ford *et al.* 2008). Secondly, reproductive success was evaluated at the fry stage only, and consequently, comparison of the production of offspring that survive to reproduce would be warranted in future studies.

Finally, there is a need to perform similar studies in other populations to bring stronger support to our statements about the general merits of this management strategy.

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Data accessibility

Genotypes of all sampled fish as well as individual information for adult, offspring and C&R salmon are accessible through Dryad doi:10.5061/dryad.m2m8f.

Supporting information

Additional supporting information may be found in the online version of this article.

Table S1 PCR recipes for the two multiplex.

Data S1 Sexing methodology.