

1 Captive-breeding and catch-and-release's effects on the reproductive success of

2 Atlantic salmon (*Salmo salar* L.)

3

4 Authors: Bouchard, R.^{1,2}, Wellband, K.², Lecomte, L.^{1,2}, Bernatchez, L.^{1,2}, & April, J.³.

5

6 ¹Département de Biologie, Université Laval, Québec, Canada

7 ²Institut de Biologie Intégrative et des Systèmes, (IBIS), Université Laval, Québec,

8 Canada

9 ³Direction de l'expertise sur la faune aquatique, Ministère des Forêts, de la Faune et

10 des Parcs du Québec, Québec, Canada

11

12

13

14

15

16

17

18

19

20

21

22 **Abstract**

23
24 Captive-breeding programs as well as and catch-and-release are among the most commonly
25 adopted conservation practices in recreational fisheries. However, risks and benefits associated
26 with their implementation are rarely evaluated. In the case of Atlantic Salmon, while previous
27 studies revealed that captive-bred fish show reduced fitness compared to their wild counterparts
28 in nature. Yet, few examined the extent and causes of their reduced reproductive success or
29 directly compared their contribution to enhance genetic diversity to that of wild fish, including
30 mature male parr. Furthermore, only one study specifically measured the reproductive success
31 of caught and released Atlantic salmon in natural settings, and no study to date evaluated if
32 released salmon are able to reproduce when released at temperature above 20°C which is
33 known to increase post-release mortality. Here, we use high-
34 throughput microsatellite sequencing of 38 loci to accurately assign 2500 offspring to a
35 comprehensive set of possible parents from a supplemented Atlantic salmon population in
36 Québec, Canada. The resolved molecular pedigree provided informative insight on the
37 reproductive pattern of both captive-bred salmon and caught-and-released salmon. Captive-
38 bred salmon had fewer partners than their wild conspecifics which lead to a significant reduction
39 of reproductive success relative to that of their wild counterparts. Supplementation of captive-
40 bred salmon significantly contributed to increase genetic diversity but mature male parr did so to
41 an even greater extent and significantly inflated the number of alleles found among offspring.
42 Moreover, our results showed that that at least 83% of caught-and-released salmon did
43 successfully reproduced although caught-and-released female salmon have a significantly
44 reduced reproductive success, averaging 73% of the reproductive output of non-caught salmon.
45 Reproductive success of released salmon was not influenced by water temperature over 20°C
46 which suggests either that the studied population is locally adapted to warm waters or that they
47 behaviorally regulated body temperature by accessing nearby thermal refugia. Our results

48 should help refining managers' ability to analyze the risks and benefits associated with captive-
49 breeding and catch-and-release, and thus, optimize conservation practices used for the
50 preservation of Atlantic salmon populations.

51

52 **Keywords:** Atlantic salmon, parentage assignment, reproductive success, mating success,
53 captive-breeding, supplementation, catch-and-release, conservation, recreational fishing

54 **Introduction**

55

56 In industrialized countries from temperate regions of the world, the rise of personal
57 wealth and leisure has generally shifted freshwater subsistence and commercial fisheries
58 towards recreational fisheries (Arlinghaus & Cooke, 2009) with an estimate of at least 220
59 million recreational fishers worldwide (FAO, 2018). This is more than five times the number of
60 commercial capture fishermen (Arlinghaus et al. 2015). Salmonids rank among the most
61 exploited species by recreational fishery despite numerous populations having experienced
62 worldwide decline over the past century (Post et al. 2002). Since recreational fisheries can have
63 negative impacts on exploited populations through overharvesting (Cooke & Cowx, 2004; Lewin
64 et al. 2006), careful management is needed in order to sustain this important socio-economic
65 sector (Arlinghaus et al. 2019). Two main practices currently exist to mitigate its impact, namely
66 captive-breeding programs for supplementation and catch-and-release fishing.

67 Captive-breeding programs are widely used for the conservation and restoration of
68 threatened and endangered species with the ultimate goal of maintaining wildlife biodiversity,
69 including genetic diversity and fitness within population (Fraser, 2008). Although this practice
70 has continuously adapted in parallel with increased knowledge, decades of studies have shown
71 that captive-breeding programs may cause a range of negative effects on stocked populations
72 (e.g. Ryman & Laikre, 1991; Hindar et al. 1991; Waples, 1991; Valiquette et al. 2014; Waples et
73 al. 2016; Hagen et al. 2020). For instance, captive rearing has been shown to induce genetic

74 and epigenetic changes which may be due either to unintentional domestication selection or
75 epigenetic reprogramming in hatchery environments (Christie et al. 2012; Le Luyer et al. 2017).
76 Genetic changes result from directional selective pressure in the hatchery which comes at the
77 expense of adaptation to the natural environment (Araki et al. 2008). Consequently, individuals
78 released in the wild have lower fitness compared to naturally produced conspecifics (Araki et al.
79 2007a). Increased understanding pertaining to (epi)-genetic domestication effects has led to the
80 recommendation that time spent in captivity should be minimized and to use naturally produced
81 fish as broodstock to avoid cumulative fitness decline (Willoughby et Christie, 2019).

82 Catch-and-release (C&R) angling is a promising complement to captive-breeding
83 programs which is generally applied and promoted to cope with high angling intensity
84 (Arlinghaus et al. 2007). Notably, C&R allows the social and economic benefits pertaining to
85 recreational fishery to persist, even when stock abundance is low (Cooke & Cowk, 2004).
86 Hence, properly applied C&R can provide a long-term management answer to potential angling-
87 induced impacts on fish population unlike captive-breeding. Nonetheless, the success of C&R
88 as a management tool will depend on the ability of the released fish to survive and contribute to
89 reproduction (Arlinghaus et al. 2007; Brownscombe et al. 2017). Indeed, C&R angling can
90 virtually affect or alter almost all biological processes that contribute to survival and an
91 organism's role in the community (Cooke & Sneddon, 2007). For instance, mortality rates can
92 be highly variable, ranging from 0% to 95% across a variety of marine and freshwater species
93 (Bartholomew & Bohnsack, 2005). While several studies documented survival of C&R fish, few
94 examined their reproductive success (Booth et al. 1995; Whoriskey et al. 2000; Thorstad et al.
95 2003; Richard et al. 2013). Other than the study by Richard et al. (2013), remaining studies only
96 provided indirect evidence of successful reproduction. Thus, further investigation in natural
97 settings is needed in order to more broadly evaluate the possible impacts of C&R on
98 reproduction.

99 Atlantic salmon (*Salmo salar*) is an emblematic species that supported subsistence
100 fisheries for thousands of years and commercial as well as recreational fisheries for decades
101 (MacCrimmon & Gots, 1979; Aas et al. 2010; ICES, 2019). Despite a generalised decline in
102 abundance across its range, which led to closures and restrictions of fisheries (ICES, 2019,
103 Atlantic salmon remains a highly prized game fish and is targeted by recreational anglers across
104 the North Atlantic during its upstream spawning migration (ICES, 2019). In Eastern Canada
105 alone, recreational fisheries targeting Atlantic salmon generates over \$100 million annually
106 which makes it a priority for conservation effort (ASF, 2011). Concerns about the specie's
107 conservation status led to the common adoption of C&R by fisheries managers (MFFP 2016,
108 ICES 2019). The total number of C&R salmon have increased substantially over the years; in
109 2018, over 162 000 salmon have been released around the North Atlantic (ICES, 2019).

110 Across North America and Europe, implementation of captive-breeding programs is also
111 used in combination with C&R to compensate decreasing recruitment on populations with
112 abundance below their appropriate conservation threshold (DFO, 2008; MFFP, 2016; NASCO,
113 2017; ICES 2019). As for C&R, very few studies have documented patterns of reproductive
114 success of captive-bred salmon (Milot et al. 2012; O'Sullivan et al. 2020). Previous research on
115 captive-bred salmon demonstrated that minimizing time spent in captivity would alleviate
116 unintentional domestication effect (Milot et al. 2012). Hence, there is a need to determine
117 whether current hatchery practices still produce salmon with reduced reproductive success to
118 assess the potential negative effect of those programs on targeted populations.

119 Global warming also necessitates involvement from Atlantic salmon managers to better
120 understand the potential impact of elevated river temperature on released salmon. Indeed,
121 previous studies have shown that the extent of post-release mortality varies with water
122 temperature and to a lesser extent also according to angler practices, gear and bait types,
123 angler experience (Cooke & Suski, 2005; Lennox et al. 2017). Although probability of post-
124 release mortality is low (<0.05) at water temperature ranging from 0 to 12°C, it increases with

125 warmer waters and expected to be as high as 0.35 at water temperatures ranging from 20 to
126 25°C (Van Leeuwen et al. 2020). Given the physiological impact of elevated river temperature
127 on released salmon, evaluating its consequences on reproductive success is crucial to
128 determine the long-term sustainability of C&R in the face of climate change (Gale et al. 2013).

129 Here, we evaluate relative reproductive success of captive-bred as well as C&R Atlantic
130 salmon from a wild anadromous population spawning in the Rimouski River, Québec, Canada.
131 This river has been targeted by several stocking programs since 1992. The current program is
132 now gradually ending since the population recently reach its appropriate conservation target
133 from 2017 to 2020 (MFFP, 2021). Captive-bred salmon are still present in this population, which
134 allowed comparing their reproductive success to that of their wild counterparts. We further
135 tested the contribution of captive-bred salmon to the population's genetic diversity and
136 compared its relative effect to the contribution of their wild counterparts, including mature male
137 parr, which are young salmon that sexually mature at very small size, roughly 200 times less
138 than that of anadromous males. These small males have previously been shown to significantly
139 contribute to preserve genetic diversity in salmon populations (Johnstone et al. 2013; Perrier et
140 al. 2014). Moreover, the exploitation of the Rimouski R. salmon population by recreational
141 anglers as well as C&R practice have increased over the last decades such that an average of
142 100 salmon are now released annually (MFFP, 2020). The Rimouski R. is also one of the
143 warmest rivers used by salmon in Quebec which frequently exceeds 20°C during fishing season
144 (MFFP, rivtemp.ca/mffp_qc/). Thus, this system allows assessing the contribution of C&R
145 salmon to the reproductive output of the population and their ability to reproduce when released
146 at elevated water temperature that are expected to increase post-release physiological impacts
147 and mortality.

148 Using novel microsatellite sequencing technology, we accurately quantified the
149 reproductive success of captive-bred Atlantic salmon and C&R salmon by linking putative
150 parents with their young-of-the-year progeny with molecular parentage analyses. The five goals

151 of this study were to; i) test whether current captive-breeding programs produce Atlantic salmon
152 with reduced reproductive success compared to their wild counterparts; ii) identify the possible
153 factors responsible for the discrepancy in their reproductive success; iii) compare the
154 contribution of captive-bred salmon and mature male parr to genetic diversity; iv) determine if
155 C&R salmon have a reduced reproductive success when compared to non-caught salmon; v)
156 evaluate the effect of temperature at release on reproductive success of C&R salmon.

157

158 **Material and Methods**

159

160 *Study site*

161 The Rimouski River is located on the South shore of the St. Lawrence Estuary, Québec,
162 Canada (48°44'N; 68°53'W). On average, 723 adult Atlantic salmon spawners returned to the
163 river annually from 2014 to 2018 (MFFP, 2020). A dam acting as a complete barrier to upstream
164 migration is located four km upstream to the river mouth, at the level of a natural impassable
165 waterfall. During their upstream migration, adult fish are trapped in a cage and transported 1 km
166 above the dam to be released upstream. Spawning grounds and suitable habitats for Atlantic
167 salmon juveniles extend over a stretch starting from the dam and ending 21 km upstream at a
168 second impassable waterfall. Spawning also occurs downstream of the dam, this minor section
169 of the river and the salmon that remained there are therefore not included in this study.

170

171 *Captive-breeding program of Rimouski River*

172 The captive-breeding program of Atlantic salmon in the Rimouski R. started in 1992 and
173 from 1992 to 2019, a total of 716 176 fry, 884 624 parr and 297 019 smolts have been stocked.
174 Starting in 2012, the broodstock was comprised of about 20 males and 20 females, with a semi-
175 factorial crossing design using a minimum of 3 females and 3 males. One third of the
176 broodstock held in captivity was replaced on an annual basis and no individual spawned more

177 than three times. For this stocking program, the number of juveniles to be stocked annually
178 (about 60 000) was determined based on a mathematical model described by Bernatchez
179 (2009) in order to result in at least a 15% increase in abundance while limiting the effective
180 population size reduction at less than 10%. Broodstock were collected from the Rimouski R.
181 each year and crossed at the Québec Government hatchery located in Tadoussac. None of
182 these captive breeders were born in the hatchery and kept all its life in captivity. However, some
183 returning adult trapped at the dam and brought to the hatchery each year to maintain the pool of
184 breeders may have been themselves offspring from captive-born fish that had been released as
185 fry, parr or smolt in the Rimouski R. during past supportive breeding years, when stocked
186 salmon were not marked. From 2012 to 2017, stocked salmon were young-of-the-year
187 weighting 3.21 to 3.54 g. Adipose fins were removed from stocked salmon for future
188 identification purposes.

189

190 *Atlantic salmon recreational fishery in the Rimouski River*

191 Recreational Atlantic salmon angling on Rimouski R. is restricted to summer months
192 beginning June 15th and closing September 30th. Anglers have to register at the Rimouski's ZEC
193 (Area of Controlled Exploitation) which monitors recreational fishing activities on the river.
194 Provincial regulation allows angler to keep up to two grilse (salmon < 63 cm in fork length) or to
195 catch and release 3 salmon, whichever quota is reached first. All large salmon (> 63 cm) must
196 be release.

197

198 *Sampling*

199 *Adult sampling and stocked fish identification* - Measurements and fin samples were
200 taken on all anadromous adults crossing the dam in 2018 when fish were released across the
201 dam. The genetic sex of every returning adult was determined using King & Stevens (2019)

202 PCR-amplification based method. Adult were identified as hatchery born using the
203 presence/absence of adipose fin which was clipped on captive-bred fish.

204 *Caught and released fish sampling* –During the 2018 fishing season, angler participation
205 was requested to collect tissue samples on their C&R salmon (punch of 5mm diameter of
206 adipose fin) and to gather information on the C&R event. To facilitate the sampling process,
207 anglers received punch pliers coupled with a kit that contained a 1.5 ml Eppendorf filled with
208 95% ethanol to preserve the adipose punch and a water-proofed sheet to record information on
209 the C&R event. After each C&R event, anglers recorded date, time of the day, the pool number,
210 the length of the fight (from hooking to landing), the kind of hook used (single or double, barb or
211 barbless), the hooking location on the fish, the presence of bleeding and approximate air
212 exposure duration. Temperature data loggers were placed in all frequently visited river pools.
213 Given the information collected by the anglers, we could record the water temperature for each
214 C&R event. Angler participation was not mandatory; however, the scientific team was present
215 every fishing day on the main river pools to promote the project and eventually assist anglers
216 during the sample collection.

217 *Fry sampling* – From July 15th to August 15th 2019, young-of-the-year (or fry, age 0+)
218 born in the river were sampled using electrofishing over a stretch starting from the dam and
219 ending 21 km upstream at an impassable waterfall. The very small tributaries of this river stretch
220 do not provide known spawning grounds or significant habitat for juveniles because of their
221 limited accessibility. Fry sampled were conserved in a 15 ml Falcon tubes filled with 95%
222 ethanol. Within every 1 km reach, we selected 12 electrofishing sites (mean area 100 m²) given
223 their fry habitat suitability index which was provided by the Québec Minister of Forests, Wildlife
224 and Parks (MFFP). Each site was electro-fished once to maximise the amount of site sampled
225 in a single day. To assess the effect of the number of offspring sampled on the potential for
226 detection of anadromous parents, we sub-sampled 50 to 2381 offspring by steps of 50, with

227 each step being subsampled 1000 times. In the case where enough offspring were sampled, the
228 number of identified parents should reach a plateau.

229

230 *Molecular analyses*

231 DNA was extracted from adult's adipose fin tissue and fry's caudal fin tissue using salt
232 extraction method described by Aljanabi and Martinez (1997). Fifty-two microsatellite loci were
233 then amplified by PCR in two multiplexes previously developed by Bradbury et al. (2018) (panel
234 1a and 2a). Locus amplification followed the protocol of Zhan et al. (2017); two sets of
235 polymerase chain reactions (PCRs) were used, a multiplex PCR and an index PCR. Each
236 multiplex PCR was performed using Qiagen Multiplex Master Mix. Each oligonucleotide in the
237 multiplex reaction was tailed with Illumina sequencing primer sequence and served as oligo-
238 binding sites in the subsequent index PCR. PCR multiplex conditions were the same for the two
239 multiplexes and included 5 ul Qiagen Multiplex Master Mix, 10 ng DNA, 2.4 ul Oligo Mix for a
240 total volume of 25 ul. Thermal reaction conditions included 95°C, 25X (94°C 30s, 65°C 3m,
241 72°C 30s) 72°C 30s. Multiplex-PCR products were pooled (per sample) in equal volume
242 amounts, cleaned using Quanta-Bio SparQ Puremag Beads, and then used as template for the
243 index PCR. Libraries were sequenced at 10–12 pM concentration at the genomic platform of the
244 Institut de Biologie Intégrative et des Systèmes (IBIS), Université Laval, Québec
245 (<http://www.ibis.ulaval.ca/>). Sequencing was performed using Illumina MiSeq (Illumina) and the
246 MiSeq Reagent Kit V3 with 150 cycles in one direction and dual indexing. Indexed individuals
247 were demultiplexed with the Miseq Sequence Analysis software. Allelic sizes were then scored
248 using MEGASAT (Zhan et al. 2017) setting minimum depth (per sample per locus) at 20 reads;
249 i.e. alleles with less than 20 reads were not called. Examination of histogram outputs (depth vs
250 allele size) from MEGASAT confirmed allele scores, and we adjusted scores when necessary.

251 Loci with more than 10% missing data were removed from the dataset to insure precision to our
252 parentage analysis.

253

254 *Parental allocation of fry*

255 Parentage allocation was conducted using Cervus v 3.0 (Kalinowski et al. 2007; Marshall
256 et al. 1998) and Colony2 (Jones & Wang, 2010) that differ in their approach to parentage
257 assignment. Cervus3 uses simulated parents and offspring to determine cut-off points of log-
258 likelihood (LOD) scores for true parents, which are then used to identify parent-offspring pairs in
259 empirical data. Cervus3 was first used to find the most probable mother-offspring and father-
260 offspring dyad. As mentioned above, Rimouski R. is known for harboring mature male parr.
261 Those males were not sampled in 2018; thus, the full likelihood approach implemented in
262 Colony2 (Jones and Wang, 2010) was used to infer their genotypes from the pedigree analysis.
263 Briefly, Colony2 uses a group-wise method to find the most likely configuration of full-sib and
264 half-sib families in the data. Since we sampled every mother in our system, grouping offspring
265 into full-sib and half-sib families allowed us to infer the genotype of mature male parr given the
266 genotype of the mother when the offspring was not already assigned to an anadromous father.

267

268 *Detection of first generation (F_0) migrant*

269 Mobley et al. (2019) have shown that local Atlantic salmon exhibit higher fitness in their
270 native river compared to dispersers. Therefore, we conducted a first generation (F_0) migrant
271 detection analysis with GeneClass2 (Piry et al. 2004) to remove those potential dispersers from
272 downstream analysis. Since we had no genotypic reference of potential source populations with
273 this microsatellite panel, we computed the likelihood of individual genotype within the Rimouski
274 population (L_home). To do so, we used the frequency-based method of Paetkau et al. (1995)
275 and the Monte Carlo resampling algorithm developed by Paetkau et al. (2004) simulating 10 000
276 individuals to estimate the probability of an observed multi-locus genotype. Individuals that had

277 a probability below 0.01 (type I error) were considered as F_0 migrant, and thus removed from
278 downstream analyses.

279

280 *Analysis of relative reproductive success (RRS) of hatchery and C&R fish*

281 We estimated relative fitness of hatchery-born fish and C&R fish to that of wild-born fish
282 and uncaught fish, respectively. To do so, we used the number of offspring assigned to a given
283 spawner as a measure of reproductive fitness. This measure is necessarily partial because not
284 all offspring of a given spawner were collected. Then, we computed the ratio of reproductive
285 fitness of the hatchery/wild fish and the C&R/non-caught fish which gives a measure of relative
286 reproductive success (RRS) using Eq. 14 of Araki & Blouin (2005). RRS calculations were
287 conducted independently for single-sea-winter (1SW) males, multi-sea-winter (MSW) males and
288 females. Analyses were performed separately for each sex since they may respond differently
289 to the hatchery environment and C&R events (Christie et al. 2014). To test for statistical
290 significance, we perform non-parametric one-tailed permutations to test the hypothesis that
291 captive-bred and catch-and released fish have lower fitness than that of wild and uncaught fish,
292 respectively (i.e. whether $RRS < 1.0$). Briefly, numbers of offspring assigned to each parent
293 were permuted

294 1 000 000 times (without replacement) and the probability of obtaining a value equal or larger
295 than the observed fitness difference was evaluated (see Araki & Blouin 2005 for details). One-
296 tailed test were chosen as we had an *a priori* expectation for lower RRS in captive-bred based
297 on previous work.

298 Following Araki & Blouin (2005) approach, we used the maximum-likelihood method
299 developed by Kalinowski & Taper (2005) to calculate confidence intervals for RRS estimates.
300 Their method is appropriate for our study because it assumes that the frequencies of hatchery
301 and wild fish are known exactly and that the only uncertainty in the estimate of RRS comes from
302 sampling a finite number of offspring. Considering this set of assumptions, maximising the

303 number of offspring sampled allowed us to obtain more precise estimates of the realized RRS
304 regardless of the adult sample size.

305 Reduced RRS in captive-bred fish can generally be explained by reduced survival of
306 their offspring in the wild because of transgenerational effects of the hatchery on offspring
307 phenotypes via genetic or epigenetic inheritance. To rule out the possibility that hatchery fish
308 could simply have lower spawning success or, in the case of females, a higher rates of egg
309 retention, we tested whether a higher fraction of captive-bred fish would have a reproductive
310 success equal to zero due to spawning failure. Thus, using the `prop.test` function implemented
311 in R, we tested if there was a higher proportion of zero reproductive success in hatchery fish
312 compared to wild fish.

313

314 *Effects of captive-breeding on components of reproductive success*

315 Then, we assessed the captive-breeding effects on two components of reproductive
316 fitness, namely the number of offspring assigned and the number of mates. The main idea was
317 to evaluate which of the two components was significantly different between captive-bred and
318 wild salmon. Results from this analysis would therefore help better understand significant
319 deviation from one in RRS estimates. We performed this analysis separately for females and
320 males using a zero-inflated negative binomial model (ZINB). We applied a ZINB model because
321 estimates of number of offspring assigned and mating success contained a high proportion of
322 individuals without any offspring, which hampers the possibility to identify their mates. Zero-
323 inflated mixture models consisted of a binomial model for the frequency of zeros, and
324 conditional on this, a count model using a negative binomial distribution. For females, we
325 performed individual analysis per mate type, that is alternative reproductive tactics (mature male
326 parr, 1SW and MSW males). For each model explaining the number of offspring assigned to
327 female, we built a global ZINB model using origin (i.e. captive-bred/wild), fork length and
328 number of mates. For the analysis pertaining to the number of mates, we built a global ZINB

329 models using origin and fork length. To analyse the factors influencing the number of offspring
330 assigned to males, we built a global ZINB model using origin, number of years spent at sea (one
331 (1SW) or more (MSW)) and number of mates as well as the interaction between time at sea and
332 origin and between time at sea and number of mates. For the analysis pertaining to the number
333 of mates for males, we built a global ZINB models using origin, time spent at sea and number of
334 mates and the interaction between time at sea and origin.

335 For all models, we assessed the fit of the global model by visualizing quantile-quantile
336 residuals distribution and rootogram which graphically compares empirical frequencies with
337 fitted frequencies from a given probability model with the package `countreg` in R (Zeileis &
338 Kleiber, 2018). Then, we built a set of models made of all models nested within the global model
339 (i.e. all combinations of including or excluding each variable) plus a null model (intercept only).
340 Those models were ranked according to their AICc (a corrected measure of AIC for small
341 samples), and ΔAICc (AICc of the model minus the AICc of the best model) was computed for
342 each model. Following this procedure, we built a confidence set of models with all models with a
343 $\Delta\text{AICc} < 4$ (according to Hurvich & Tsai, 1989). Finally, we quantified the effect of variables
344 appearing in the top models with multi-model inference using the shrinkage method (Burnham
345 and Anderson 2002). Every model was build using the 'pscl' package in R 3.4.4.

346

347 *Genetic estimates of the effect of captive-bred fish on the effective number of breeders* 348 *(Nb)*

349 To investigate the contribution of captive-bred fish on the effective number of breeders
350 (Nb), this parameter was estimated for three different datasets corresponding to parent-fry
351 assignments implicating (i) wild anadromous breeders ($n = 916$), (ii) wild and captive-bred
352 anadromous breeders ($n = 1560$) and (iii) wild anadromous breeders and mature male parr ($n =$
353 1544). To do so, we used the LDNe program (Waples & Do 2008) to estimate Nb and the
354 contribution of wild and captive-bred fish to Nb. We used a threshold of 0.05 as the lowest allele

355 frequency that gives the least biased results according to Waples & Do (2010). Since the
356 sample of parent-fry assignment to wild breeders only was smaller than that also including the
357 contribution of mature male parr, we subsampled these latter datasets using the same number
358 of fry as that of the wild breeders dataset. In this way, the threshold on the lowest allele
359 frequency has the same effect on each dataset. Hence, we subsampled the parent-fry
360 assignment of data sets ii) and iii) 1000 times and calculated Nb on each subsampling step.
361 Finally, we compared value of Nb obtained in group i) with the distribution generated with group
362 ii) and iii).

363

364 *Estimate of the effect of mature male parr and captive-bred salmon on offspring's* 365 *genetic diversity*

366 To contrast the contribution of mature male parr to allelic richness to that of captive-bred
367 males, we compared the total number of alleles found among progeny assigned to i) wild
368 anadromous pairs, ii) wild and captive-bred anadromous pairs and iii) wild anadromous female
369 and mature male parr for an increasing number of offspring sampled. We subsampled from 50
370 to 1500 fry, by steps of 50, 1000 times for each step, and estimated the total number of alleles
371 found among fry assigned to the aforementioned groups of parents. We represented the
372 differences in the number of alleles among these three groups with a Loess regression of the
373 mean value of the total number of alleles found for each number of fry sampled considered, as
374 well as the 95% distribution of values.

375

376 *Effect of temperature and air exposure time on reproductive success of C&R salmon*

377 To assess the effect of the variable of the C&R event on the reproductive output of MSW
378 adults, we used a negative binomial model since it describes count data that shows
379 overdispersion. Because we had data for a limited number of C&R salmon only, we limited the

380 number of predictor variables included in the model. Therefore, we tested the relationship
381 between the effect of temperature during the C&R event, the air exposure time and their
382 interaction on RS since they are variables known to affect RS of C&R fish (Richard et al. 2013).
383 To do so, we built a global negative binomial model using the aforementioned variables with the
384 pscl package in R (Jackman, 2020). To assess the fit of the global model, we visualized
385 quantile-quantile residuals distribution and rootogram which graphically compares empirical
386 frequencies with fitted frequencies from a given probability model with the package countreg in
387 R (Zeileis & Kleiber, 2018). Then, we built a set of models made of all models nested within the
388 global model plus a null model (intercept only). We ranked the best models using AICc
389 (corrected measure of AIC for small samples), and we computed $\Delta AICc$ for each model (AICc of
390 the model minus the AICc of the best model). This step allowed to build a confidence set of
391 models with every model that had a $\Delta AICc < 4$ (as suggested by Hurvich & Tsai, 1989). Finally,
392 we quantified the effect of variables appearing in the top models with multi-model inference
393 using the shrinkage method (Burnham & Anderson, 2002).

394 **Results**

395 **Adult population of Rimouski River**

396 From June 15th and October 30th of 2018, 475 anadromous Atlantic salmon (273 males
397 and 202 females) were transported above the dam, of which 26 % were from the captive-
398 breeding program ($n = 126$) (Table 1). The anadromous population was composed of 57 % ($n =$
399 271) salmon > 63 cm which are considered as MSW and of 43% ($n = 204$) salmon < 63 cm
400 which were considered 1SW salmon. The proportion of MSW and 1SW was significantly
401 different between wild and captive-bred salmon ($\chi^2 = 7.58$, p -value = 0.005) with the former
402 having 186 (53%) MSW for 160 (45%) 1SW and the latter having 85 (67%) MSW for 41 (33%)
403 1SW. Eight individuals were identified as first-generation migrant, of which two were MSW
404 females and six were SSW males. In total, Colony 2 estimated that 432 mature male parr

405 fathered 750 offspring with a mean reproductive success of 1.69 offspring per mature parr. The
406 presence of mature parr highly skewed the sex ratio which was of 1 female to 1.43 male before
407 accounting for them and of 1 female to 3.7 males when accounting for them.

408

409 *Caught-and-released salmon during 2018 angling season*

410 A total of 33 fish out of 89 C&R salmon were successfully sampled by anglers. Most of
411 those C&R events were done below the dam (31/33), three km upstream from the mouth of the
412 river and one km downstream from the dam. Identity analysis between salmon that crossed the
413 dam and C&R salmon revealed that 18 of those salmon successfully crossed the dam after
414 being released (Table 1). Thus, we obtained a reproductive success measurement for a total of
415 13 MSW female (mean \pm sd length = 78.1 \pm 5.6 cm), 4 MSW male (length = 76.1 \pm 4.79 cm)
416 and 1 SSW male (length = 55 cm).

417

418 *Parental allocation*

419 After filtering for loci with more than 10% missing data on both parents and offspring
420 data set, 38 polymorphic microsatellite loci were retained for subsequent analyses. The number
421 of alleles ranged from 3 to 13 per locus (average = 7) and observed heterozygosity ranged from
422 0.024 to 0.8396 with an average of 0.55. Average F_{is} was -0.005 (95% CI: -0.01-0.0091) thus
423 indicating the absence of within-river Wahlund effect.

424 For the 475 adults transported above the dam, we obtained a complete genotype of 468
425 individuals that was then used for parental allocation (Table 1). A total of 2495 fry were sampled
426 during July and August in 2019, genotyped and assigned to putative parents that spawned
427 above the dam during fall 2018. We unambiguously assigned the paternity of 1617 and the
428 maternity of 2495 offspring samples to anadromous adults and the paternity of 750 offspring to

429 mature parr. The remaining 128 fry were assigned to mature parr with a probability lower than
430 0.8 and were thus excluded from subsequent analyses.

431

432 *Description of the mating system*

433 The number of inferred offspring to females ranged from 0 to 67 (mean = 5.6, variance =
434 76.3) for mature male parr mates, from 0 to 29 (mean = 3.5, variance = 22.7) for 1SW mates
435 and from 0 to 33 (mean = 4.4, variance = 33.5) for MSW mates. For males, the number of
436 inferred offspring ranged from 1 to 8 (mean = 1.7, variance = 0.9) for mature male parr, from 0
437 to 23 (mean = 3.7, variance = 21.9) for 1SW salmon and from 0 to 56 (mean = 11.6, variance =
438 173) for MSW salmon.

439 Females were highly polyandrous with three females that mated with one male only. The
440 total number of mates per female ranged from 0 to 33 (mean = 7, variance = 38.0). Mature male
441 parr mates per female ranged from 0 to 26 (mean = 3.6, variance = 16.9), 1SW mates per
442 female ranged from 0 to 7 (mean = 1.6, variance = 2.8), MSW mates per female ranged from 0
443 to 8 (mean = 1.6, variance = 3.0). Males were polygamous but to a lesser extent than females:
444 57 males mated with only one female of which 47 were 1SW males. The number of mates for
445 mature male parr ranged from 1 to 5 (mean = 1.4, variance = 0.4), for 1SW it ranged from 0 to 7
446 (mean = 1.64, variance = 2.43) and for MSW it ranged from 0 to 16 (mean = 4.2, variance =
447 16.9).

448

449 *Relative reproductive success (RRS) of captive-bred versus wild and C&R versus non-* 450 *caught Atlantic salmon*

451 Estimates of RRS for captive-bred versus wild and C&R versus non-caught salmon are
452 shown separately for males and females and time spent at sea (1SW, MSW) in Table 2. Our
453 results show that captive-bred salmon had a reduced fitness compared to their wild

454 counterparts. Thus, the RRS of MSW hatchery-reared females was of 0.805; this value was
455 significantly lower one ($p < 0.01$) given our permutation test and our maximum-likelihood
456 confidence interval estimation (Figure 1). For MSW hatchery-reared males, RRS was of 0.828;
457 likewise, this value was significantly lower than one ($p < 0.01$) given both our permutation test
458 and our maximum-likelihood confidence interval estimation (Figure 1). The RRS of captive-bred
459 1SW males was of 0.649 which again was significantly lower than one ($p < 0.01$) wild born 1SW
460 males.

461 For C&R fish, C&R MSW females had a RRS of 0.732 which was significantly lower ($p <$
462 0.01) than one given our permutation test and our maximum-likelihood confidence interval
463 estimation. C&R MSW males had a RRS of 0.797 but this value was not significantly different
464 than one given both our permutation test and maximum-likelihood confidence interval estimation
465 (Figure 1). Hence, our results show that C&R tend to have a reduce fitness compared to non-
466 caught salmon, but this reduction was only significant for females.

467

468 *Effect of origin and male reproductive tactics on components of reproductive success*

469 The number of offspring assigned to females increased with the number of mates for all
470 three male alternative reproductive tactics (Table 3, Figure 2, A)). However, as expected,
471 mating with mature male parr increased the number of offspring assigned at a lower rate than
472 for 1SW and MSW mates. Female length had a significant positive effect on the number of
473 offspring assigned when mating with MSW males, however its effect size was negligible
474 compared to the effect of number of MSW mates. The number of offspring assigned to wild and
475 captive-bred females did not differ significantly, suggesting that the survival rate of offspring
476 from captive-bred females was comparable to that of wild females. Females' mating success
477 showed a positive relationship with length for all three types of male alternative reproductive
478 tactics (Figure 2, B)). There was no difference between the number of mature male parr and

479 MSW mates between captive-bred females and wild females. However, captive-bred females
480 had significantly less 1SW mates than wild females. Therefore, the observed reduction of RRS
481 of captive-bred females was apparently mainly caused by a lower mating success with 1SW
482 mates compared to wild females.

483 MSW males had a higher number of offspring assigned than the 1SW salmon (Table 4,
484 Figure 3, A)). Moreover, both 1SW and MSW males increased their number of offspring by
485 mating with multiple females but 1SW males did so more rapidly than MSW males. As for
486 captive-bred females, captive-bred males did not show a significant reduction in offspring
487 assigned relative to their wild counterparts. 1SW males had fewer mating partners than MSW
488 males and both 1SW and MSW captive-bred males showed a significant reduction in their
489 mating success compared to their wild counterpart (Figure 3, B)). Hence, the previously
490 observed reduction of RRS for both 1SW and MSW captive-bred males was apparently mainly
491 caused by a lower mating success compared to wild males.

492

493 *Estimation of the effect of captive-bred anadromous salmon and of mature male parr on*
494 *genetic diversity of offspring*

495

496 Using LDNe to estimate N_b from the genetic data, we obtained values of 114 (CI: 110.8-
497 121.7) for wild anadromous salmon only, of 146 (CI: 136.8-154.9) for wild and captive-bred
498 anadromous salmon combined and of 173 (CI: 160.5-185.6) for all wild anadromous salmon and
499 mature male parr (Figure 4). Thus, captive-bred salmon increased the effective number of
500 breeders by 28% which is significantly less compared to mature male parr which inflated it by
501 52%. Global estimate of N_b obtained from COLONY, including wild, captive bred and mature
502 male parr was of 271 (CI: 231-323).

503

504 Captive-bred anadromous salmon and mature male parr both contributed to increase the
total number of alleles in the population relative to considering wild anadromous fish only

505 (Figure 5). Fry produced by pairs of anadromous females and mature male parr had a higher
506 number of alleles than fry produced by pairs of wild anadromous salmon and by wild and
507 captive-bred anadromous salmon. For instance, sampling 1000 offspring 1000 times in each
508 dataset, the average number of alleles was 252 (CI: 252-259) for wild anadromous salmon, 258
509 (CI: 254-262) for wild and captive bred anadromous salmon and 265 (CI: 265-272) for wild
510 anadromous salmon and mature male parr.

511

512 *Impact of C&R conditions on reproductive success*

513 The best model was the null model which provided the lowest AICc whereas the global
514 model had the highest value. This result indicates that neither air exposure nor water
515 temperature had a significant effect on the number of produced offspring. The effect of
516 temperature on reproductive success of C&R salmon is shown on Figure 6. Surprisingly, the
517 C&R event that occurred at the higher water temperature was associated with the highest
518 observed reproductive success among fish manipulated by anglers. These results must be
519 interpreted cautiously given the small sample size that was available for this part of our study.

520

521 **Discussion**

522 Most wild populations of Atlantic salmon have experienced a sharp decline in abundance
523 over the past century. As a consequence, captive-breeding programs for fish supplementation
524 and adoption of catch-and-release in recreational fisheries have generally been implemented as
525 a mean to preserve ecosystem integrity, enhance declining populations, and sustain fisheries. In
526 this study, we evaluated the efficiency of these practices by means of molecular parental
527 assignment in a wild population of Atlantic salmon from the Rimouski River, Québec. We
528 demonstrate that captive-bred males and females displayed lower RRS than their wild
529 counterparts mainly because captive-bred salmon had a lower mating success. Yet, captive-

530 bred salmon contributed to increase genetic the effective number of breeders in the wild
531 population, albeit to a lesser extent than mature male parr which also contributed to increase
532 allelic diversity. Finally, we provide evidence that caught-and-released males and females have
533 reduced RRS compared to salmon that have not been caught, but we found no evidence that
534 elevated water temperature has an effect on their reproductive output. Below we underline the
535 evolutionary and conservation implications of these results which should contribute to guide
536 future directions for management of Atlantic salmon populations.

537

538 *Atlantic salmon mating system in the Rimouski River*

539 *Female reproductive and mating success* – Female reproductive success was highly
540 variable and best explained by their number of mates. All females mated with multiple
541 anadromous males and mature parr which reflects the well documented male-biased
542 operational sex-ratio in this species (Fleming et al. 1996). In such conditions, display of
543 aggressive behavior by MSW males has a low reproductive pay-off because the high relative
544 number of male competitors decrease the probability of successfully defend spawning females
545 (Fleming & Gross, 1994). Hence, multiple male spawning event occurs, and sperm deposition is
546 usually in order of dominance status (Fleming et al. 1996, 1997). Accordingly, female
547 reproductive success increased more rapidly for MSW mates than for 1SW and mature parr
548 mates which adopt a sneaking strategy (Fleming & Einum, 2011).

549 Interestingly, length was also a significant, albeit weak predictor of female reproductive
550 success when mating with MSW males. Potential egg production of female closely tracks
551 increase in body size (Fleming, 1996); yet several studies also found a weak effect of female
552 length on their reproductive success (Taggart et al. 2001; Garant et al. 2001, 2003; Richard et
553 al. 2013). This is not completely unexpected since environmental heterogeneity in time and
554 space plays an important role in determining offspring survival (Gibson & Myers, 1988). Rivers

555 draining on the south shore of the St. Lawrence River watershed are generally characterized by
556 lower annual minimum flows which is a known abiotic factor that reduce survival of juvenile
557 salmon (Assani et al. 2006). Low river discharge is associated with a reduction in subsurface
558 flow, and therefore oxygen supply in the gravel substrate, which in turns have negative effects
559 on developing eggs and embryos (Gibson & Myers, 1988). Such stochasticity in abiotic factor is
560 expected to decrease the relationship between body size and reproductive success among
561 females (Chapman, 1988).

562 Polyandry has been reported in several studies on Atlantic salmon and our study
563 confirms that it is the main reproductive strategy in the Rimouski R. Such mating pattern has
564 direct genetic benefits for female; for example, Garant et al. (2005) found that females with a
565 higher number of mates also had more outbred offspring, and that both of these characteristics
566 increased their reproductive success. Moreover, in environmentally heterogeneous systems,
567 such as the Rimouski R., polyandry could also have potential ecological benefits. Female
568 Atlantic salmon can reduce variance of fitness by adopting multiple-reds strategy depending on
569 temporal and spatial variation in offspring survival (Barlaup et al. 1994). Admittedly, without
570 behavioural observation, we cannot tell whether multiple matings occurred at different nest sites
571 rather than at a specific redd. Nonetheless, we found a spatial distribution of families that is
572 highly heterogeneous with half-siblings from the same mother frequently collected more than 5
573 km apart (Bouchard, pers. obs.). These observations have also been reported in Garant et al.
574 (2001) and strongly suggests that females might have constructed multiple redds since fry
575 generally have low dispersal ability (< 1.5 km, Eisenhauer et al. 2020).

576 *Male reproductive and mating success* – As for females, there was high interindividual
577 variance in reproductive success among males which was best explained both by number of
578 mates and the number of years spent at sea. This is in accordance with the fact that Atlantic
579 salmon males do not provide any parental care, making their offspring production an increasing
580 function of mating success (see Arnold & Duvall, 1994). However, our results showed that the

581 relationship between mating and reproductive success differs among alternative reproductive
582 tactics. Although MSW males are typically dominant on the spawning territories and achieve
583 higher reproductive and mating success than 1SW males (Garant et al. 2003), they exhibit
584 courtship behavior, actively fight and defend nesting site against other males which in turn,
585 increase the cost of mating with multiple females (Fleming, 1996). On the other hand, 1SW
586 males are much smaller than MSW salmon, and behave like subordinate males on the
587 spawning grounds (Fleming, 1998). Instead of fighting, these males have to cruise between
588 multiple females to increase their chances of successful mating. Our results thus suggest that
589 achieved reproductive success of MSW males may represent a trade-off between investing into
590 courtship and active defense of nests and the benefits gained from mating with multiple
591 females. In contrast, 1SW increased their fitness more rapidly with multiple matings which
592 reflects the benefits of their reproductive tactics when operational sex-ratio is highly male
593 biased.

594 *Mature male parr* – We identified 432 mature parr male which fathered 30% of all
595 offspring sampled. This is in broad accordance with previous studies which reported proportions
596 varying between 22 and 65% (Garcia-Vazquez et al. 2001; Taggart et al. 2001; Saura et al.
597 2008; Weir et al. 2010). Compared to a previous study performed in Les Escoumins R. draining
598 on the North shore of the St. Lawrence River in Québec, mean reproductive success of mature
599 parr was lower (1.7 vs 2.4; Richard et al. 2013). Because the aggressive behaviour of
600 anadromous males can restrain the participation of mature parr in reproduction (Jones &
601 Hutchings, 2001; Tentelier et al. 2016), it seems plausible that the spawning success of male
602 parr was reduced by the larger proportion of anadromous males in our study (57% vs 41% in
603 Richard et al. 2013).

604

605 *Reduced fitness of captive-bred Atlantic salmon after one generation of captivity*

606 The reduced RRS of captive-bred Atlantic salmon corroborates results from Christie et
607 al. (2014) who quantitatively synthesised the results of five studies that used genetic parentage
608 analysis to estimate the fitness of first-generation hatchery-born adults and wild-born adults
609 spawning in the wild in various salmonid species. In 46 out of 51 estimates, adults born in a
610 hatchery had lower fitness than wild-born adults. However, compared to the one previous study
611 on Atlantic salmon (Milot et al. 2013), captive-bred salmon from the Rimouski R. had a higher
612 RRS. Here, captive-bred MSW females and males averaged ~80% while 1SW males averaged
613 65% of the reproductive success of their wild counterparts compared to Milot et al. (2013) which
614 reported an average relative reproductive success of 50% for both sexes. Furthermore, our
615 ZINB model showed that captive-breeding did not directly affect the number of offspring per
616 mating event but instead the number of mating events. Thus, the number of offspring per
617 captive-bred females was not significantly reduced when controlling for mating success and
618 length which suggests they were able to find suitable spawning sites and display level of
619 fecundity similar than that of wild females. However, captive-bred females had fewer 1SW
620 mates than their wild counterparts. Fleming & Gross (1993) previously reported that captive-
621 bred females were less competitive in their ability to acquire a nesting territory during direct
622 competition with wild females which constrained them to build fewer nests (Fleming &
623 Petersson, 2001). If captive-bred females did build fewer nests than wild females, MSW males
624 could more readily defend their redds which would decrease their probability of getting fertilized
625 by 1SW males. Again, behavioral observation would be required to confirm this hypothesis.

626 As observed for females, the number of offspring assigned to captive-bred males did not
627 differ from that of their wild counterparts when controlling for mating success and time spent at
628 sea, suggesting that their ability to fertilize female's eggs is similar to that of wild males. Yet,

629 both MSW and 1SW captive-bred males showed a significantly reduced mating success which
630 affected 1SW to a greater extent. Reduced aggressiveness of captive-bred males has
631 previously been documented in Atlantic salmon (Fleming et al. 1996). However, if captive-bred
632 males displayed reduced aggression during spawning season, we would expect MSW salmon
633 to be more affected since they are actively competing for access to females. A more plausible
634 hypothesis could be that captive-bred males display more aggression than their wild
635 counterparts. A previous study on captive-bred Atlantic salmon reported that progeny resulting
636 from captive-breeding practices to be more aggressive than wild-born conspecifics (Blanchet et
637 al. 2008) and that this behavioral syndrome can hold years after being released in nature
638 (Fleming et al. 1997). Male and female salmon invest more than 50% of their total energy to
639 reproduction, but 90% of the male loss is in somatic investments (Jonsson, 1991; Hendry &
640 Beall, 2004). During spawning, combat between MSW is an energetically costly behavior that
641 may terminate quickly with a bite after rushing at an opponent or intensify into a fight that results
642 in several wounds (Jones, 1959). Engaging in too many prolonged combats could be
643 detrimental for males as they can be reproductively active for about two months (Webb and
644 Hawkins, 1989, Fleming et al. 1996). Being parsimonious with engaging in fight is therefore
645 crucial for MSW males, and it can most probably pay to be careful and exhibit subordinate
646 postures when meeting superior competitors (Fleming, 1996; Fleming et al. 1996). This would
647 be particularly true for 1SW males which have better chances to furtively gain access to females
648 rather than engaging into combat. Accordingly, reduced mating success affected their RRS to a
649 greater extent compared to MSW males.

650 Although we do not have behavioral data to support this hypothesis, a previous study on
651 Atlantic salmon controlling for the genetic background revealed that the environmental effects of
652 hatchery-rearing up to the smolt stage (juvenile migrating at sea) could be significant on male
653 behavior (Fleming et al. 1997). Whereas captive-bred males had similar levels of aggression,
654 they were involved in more prolonged aggressive encounters and incurred greater wounding

655 and mortality than wild males. As a consequence, those males were less able to monopolize
656 spawning and obtained a mating success 51% that of wild males. Reduction of mating success
657 was less striking in our study, but captive-bred salmon were stocked in the Rimouski R. at the
658 fry stage which significantly reduced exposure to the hatchery environment and may have
659 contributed to increased RRS compared to salmon stocked at the smolt stage (Milot et al.
660 2013).

661 Early environment is a deterministic factor that acts on later performance in fish
662 (Jonsson & Jonsson, 2014). Although differences in fitness between hatchery-reared and wild
663 salmon were previously thought to be genetically based only, mounting evidence also points
664 toward an epigenetic basis associated with the effect of hatchery environment on epigenetic
665 reprogramming of the progeny produced in captivity (Christie et al. 2016; Le Luyer et al. 2017;
666 Gavery et al. 2018; Wellband et al. 2021; Leitwein et al. 2021). Of particular interest is the study
667 of Rodriguez Barreto et al. (2019) which showed that early-life hatchery exposure changed the
668 pattern of methylation of Atlantic salmon males and that corticotropin-releasing factor receptor
669 1-like was one of the differentially methylated regions in hatchery fish. This gene is involved in
670 increased aggression and activity in another salmonid, the Arctic charr, *Salvelinus arcticus*
671 (Backström et al. 2015). Results from their study also demonstrated that those changes were
672 inheritable which raises concern about the potential negative long-term consequences of
673 captive-breeding. In our case, hatchery-rearing clearly reduced mating success of both females
674 and males and further study should investigate whether a causal relationship exists between
675 epigenetic modifications and aggressiveness of captive-bred Atlantic salmon.

676

677 *Contribution of captive-bred salmon and mature male parr to the effective number of*
678 *breeders (Nb) and their influence on genetic diversity*

679 It is generally accepted that genetic diversity both within and between populations is
680 important to conserve, and it is relevant to ask whether captive breeding programs effectively
681 maintain genetic diversity (Fraser, 2008). In this study, captive-bred salmon significantly
682 contributed to a 1.28-fold increase in the effective number of breeders. These results are in line
683 with those of Araki et al. (2007b) which demonstrated that the use of local broodstock for
684 stocking contributed to a 1.73-fold increase in Nb over two generations. The contribution of
685 captive-bred salmon to increase Nb is encouraging from a conservation perspective since
686 contemporary captive-breeding programs for Atlantic salmon generally aim to help population
687 retain 90% of their genetic diversity over 100 years by maintaining a Nb of at least 100 (Waples,
688 1990). Although mature male parr fathered 30% of the fry that were genotyped, their
689 contribution to reproduction led to a 1.52-fold increase in Nb. This is in broad agreement with a
690 similar study performed in another salmon population from the Malbaie R. on the North shore of
691 the St. Lawrence River where mature male parr resulted in a 1.79-fold increase in Nb compared
692 to a Nb estimate without considering their contribution to reproduction (Perrier et al. 2014).
693 Moreover, we demonstrate that the number of alleles found in pairs of wild anadromous female
694 salmon and mature male parr was higher than that of wild and captive-bred anadromous
695 salmon. Hence, mature male parr most likely buffer against reduction of genetic diversity in
696 populations with relatively small census size and as such, could contribute to enhance their
697 evolutionary potential and ultimately, the long-term persistence of fisheries.

698

699 *Effect of catch-and-release on the reproductive success of Atlantic salmon*

700 *Reduced reproductive success of released salmon* - We found that the catch-and-
701 release events reduced the reproductive success of female and male salmon by 28% and 20%

702 respectively, although the reduction was significant for females only. Although released males
703 did not have a significantly reduced reproductive success compared to uncaught males, there is
704 a possibility that the qualitative difference was real, but that the statistical power of our analysis
705 was limited by the small sample size for this part of the study (Christie et al. 2012).

706 The mechanism causing the reduced reproductive success of C&R salmon could be
707 manifold. C&R event has various physiological consequence for fish (Gale et al. 2013). From
708 hooking to landing, levels of extracellular acidosis increase conjointly with blood and muscle
709 lactate causing a decreasing content of extracellular pH, plasma bicarbonate, ATP and
710 glycogen which considerably reduce likelihood of recovery following release (Wilkie et al. 1996;
711 1997; Thorstad et al. 2003; reviewed in Gale et al. 2013). Coupled to exhaustive exercise is the
712 production of “stress hormones” which result in a suite of physiological and biochemical
713 alterations to the internal physiology of fish to maintain performance during exercise. This
714 causes a shift of investment of energy from anabolic process (i.e., growth and reproduction) to
715 catabolic activities (i.e., energy mobilization and restoration of homeostasis) (Bonga, 1997). This
716 physiological cascade can lead to mortality in some cases but when it does not, it can result in
717 so-called sub-lethal consequences (Schreck 2010). For instance, C&R can lead to disrupted
718 gametogenesis because of reallocation of energy during reproductive maturation in sockeye
719 salmon (Patterson et al. 2004) and to altered courting and mating behavior in smallmouth bass
720 (Cooke et al. 2002). Given this, it is difficult to pinpoint the exact cause of the reduction of
721 fitness of released salmon. Previous studies convincingly demonstrated that C&R does not
722 affect gamete or fry quality in Atlantic salmon (Davidson et al. 1994; Booth et al. 1995).
723 Nonetheless, recent simulation-based study on Atlantic salmon documented shortened
724 migration distances in caught salmon relative to their non-caught counterparts, which likely
725 arose from the stress and exhaustion experience after release (Lennox et al. 2016; but see
726 Thorstad et al. 2003). This suggests that this prolonged stress and exhaustion could influence
727 breeding success since it is highly linked to physiological condition on spawning grounds

728 (Hendry and Beall, 2004). Ultimately, if hindered migration after release reflects reduced activity
729 during spawning season, there could be fewer reproductive encounters or nests built by
730 released salmon which would decrease overall fitness.

731 *Effect of temperature on reproductive success of released salmon* - This is the first study
732 attempting to document reproductive success of released salmon above their optimal
733 temperature for aerobic scope which is estimated at ~20°C in Eastern Canada (DFO, 2012).
734 Admittedly, our results must be interpreted cautiously given the small sample size that was
735 available for this part of our study. Yet, our results suggest that increasing temperature did not
736 affect the reproductive output of released fish. High temperature reduces dissolved oxygen
737 concentration in water, while increasing the metabolic rate and thus the oxygen demand of fish.
738 Ultimately, when oxygen consumption becomes less than oxygen demand, the fish physiology
739 uniquely relies on anaerobic energy pathway. When the C&R event is paired with high water
740 temperatures their impacts are synergistic, and the complete exhaustion of aerobic and
741 anaerobic muscular fuels are possible (Wilkie et al. 1996). Consequently, survival of released
742 salmon is highly dependent on water temperature and probability of mortalities can be as low as
743 5% at cool river temperature (<12°C) but range from 7% and 33% between 18 and 20°C (Lenox
744 et al. 2018; Van Leeuwen et al. 2020). As mortality increases with water temperature, we would
745 expect sublethal effects on released fish to increase as well. For instance, Richard et al. (2013)
746 reported that increasing temperature negatively impacted reproductive success of salmon
747 between 12-19°C. The fact that we find no such correlation might be related to the availability of
748 thermal refugia (i.e. colder body of water) in our system. During high temperature events,
749 Atlantic salmon often engage in behavioral thermoregulation by moving within available thermal
750 refugia to alleviate physiological stress (Breau et al. 2011). All the released salmon in our study
751 were caught close to a known thermal refugium which probably gave them the opportunity to
752 escape high water temperature and to enhance restorative processes.

753 Another non-exclusive hypothesis is that this could be locally adapted to high water
754 temperatures. Rimouski river frequently warm up to temperature higher than the Atlantic salmon
755 lethal limit (>28°C) during practically every summer while sustaining a viable salmon population
756 that support an angling fishery. Local adaptation for higher temperature tolerance has previously
757 been demonstrated in other salmonids by shifting the temperature at which maximum heart rate
758 ceases to increase (Eliason et al. 2011; Antilla et al. 2014). This would increase the amount of
759 anaerobic energy available to face C&R at high water temperature; therefore, increasing survival
760 and minimizing sub-lethal effects.

761

762 *Evolutionary and practical consequences of captive-breeding and catch & release on*
763 *wild populations*

764 This study provides a comprehensive overview of the potential benefits and
765 consequences of captive-breeding and catch-and-release as management practices and raises
766 issues pertaining to the conservation of wild Atlantic salmon populations. First, our results
767 revealed that mating success was the main factor explaining the reduction in relative
768 reproductive success of first-generation captive-bred salmon. A growing body of literature
769 suggests that breeding in captivity generates epigenetic modifications in captive-bred salmon
770 which may underly observed decrease of fitness of captive-bred fish. If such epigenetic
771 modifications are inheritable, as suggested in a recent study (Leitwein et al. 2021) captive-
772 breeding could have a cumulative negative effect on the reproductive success of spawners via
773 introgressive hybridization of hatchery and wild stocks (Willoughby & Christie 2019). Further
774 research should investigate whether epigenetic modifications truly underly the decrease in
775 breeding success in Atlantic salmon. Meanwhile, we suggest that implementation of captive-
776 breeding programs should be limited to the short-term (<10 years; Willoughby & Christie, 2019)
777 when possible.

778 Second, we also showed that mature male parr contribute importantly to maintain
779 genetic diversity. Anglers and managers generally pay little attention to the potential importance
780 of mature male parr, either from a demographic or genetic standpoint. In fact, their presence
781 has even been seen as having a negative effect on recruitment to fishery and on harvestable
782 biomass (Myers, 1984). However, several studies now support their key role in maintaining the
783 long-term genetic diversity within salmon populations (Araki et al. 2007; Perrier et al. 2014;
784 Johnstone et al. 2013) and to reduce inbreeding (Perrier et al. 2014). Indeed, those males
785 constitute a reservoir that can compensate for variations in the number of anadromous males
786 returning from sea migration. This phenomenon, referred to as genetic compensation, is
787 responsible for limiting the decrease of N_e when few anadromous male breeders survive until
788 breeding (Araki et al. 2007b). Although we demonstrate that captive-breeding programs
789 contributed to increase N_b in the Rimouski R. salmon population, it does so to a lesser extent
790 than the contribution of mature male parr. Therefore, we suggest that the contribution of mature
791 male parr to genetic diversity should always be considered and evaluated when managing
792 Atlantic salmon populations.

793 Third, despite the fact that released salmon experienced reduced reproductive success
794 (RRS) relative to that of their wild counterparts, it is noteworthy that a minimum of 83% of them
795 successfully reproduced. These results corroborate studies showing that mandatory C&R
796 resulted in a 2.3-fold increase in the number of spawning redds in Norway (Thorstad et al. 2003)
797 and in higher parr and fry densities in Russia (Whoriskey et al. 2000). Moreover, we
798 demonstrate that salmon released at river temperature above 20°C are able to successfully
799 reproduce suggesting that those salmon were able to find thermal refugia or that the studied
800 population is locally adapted to high water temperature. From a management and conservation
801 perspective, these results provide evidence that mandatory C&R successfully increase
802 sustainability of exploited fish population since released fish contribute to the reproductive
803 output of the population and that this benefit might hold in the face of global warming.

804
805

806 Raw data used for this study is available at the Dryad digital repository: to be completed after
807 manuscript is accepted for publication.

808 **Acknowledgments**

809 This study was funded by the Ministère des Forêts, de la Faune et des Parcs du Québec
810 (MFFP) and the Canadian Research Chair in genomics and conservation of aquatic resources.
811 R.B. was supported by scholarship from Fonds de Recherche du Québec - Nature et
812 Technologies. We thank Stéphane Forest, William Cayer-Blais, Arnaud Benoit-Pépin, Félix-
813 Antoine Picard, Juliette Bherer, Jerome Doucet-Caron and Cécilia Hernandez for field and
814 laboratory assistance. Finally, we thank employees from ZEC Rimouski, Gilles Schooner from
815 BORALEX and fishermen of the Rimouski River without whom this project would have been
816 impossible. This project is part of the research program of Ressources Aquatiques Québec
817 (RAQ).

818

819

820

821

822

823

824

825

826

827

828 **References**

- 829 Akaike, H. (1987) Factor analysis and AIC. *Psychometrika*, 52, 317–332.
830 <https://doi.org/10.1007/BF02294359>
- 831 Aljanabi, S., & Martinez, I. (1997). Universal and rapid salt-extraction of high quality genomic
832 DNA for PCR- based techniques. *Nucleic Acids Research*, 25(22), 4692–4693.
833 <http://doi.org/10.1093/nar/25.22.4692>
- 834 Anttila, K., Couturier, C.S., Øverli, Ø., Johnsen, A., Marthinsen, G., Nilsson, G.E. & Farrell, A.P.
835 (2014). Atlantic salmon show capability for cardiac acclimation to warm temperatures. *Nature*
836 *communications*, 5, 42-52. <http://doi.org/10.1093/10.1038/ncomms5252>
- 837 Araki, H., Berejikian, B., Ford, M., & Blouin, M.S. (2008). Fitness of hatchery-reared salmonids
838 in the wild. *Evolutionary Applications*, 1, 342-355. [http://doi.org/10.1111/j.1752-](http://doi.org/10.1111/j.1752-4571.2008.00026.x)
839 [4571.2008.00026.x](http://doi.org/10.1111/j.1752-4571.2008.00026.x)
- 840 Araki, H. & Blouin, M.S. (2005). Unbiased estimation of relative reproductive success of different
841 groups: evaluation and correction of bias caused by parentage assignment errors. *Molecular*
842 *Ecology*, 14(13), 4097-4109. <https://doi.org/10.1111/j.1365-294X.2005.02689.x>
- 843 Araki, H., Cooper, B., & Blouin, M.S. (2007). Genetic effects of captive breeding cause a rapid,
844 cumulative fitness decline in the wild. *Science*, 318, 100-103.
845 <https://doi.org/10.1126/science.1145621>
- 846 Araki, H., Waples, R.S., Ardren, W.R., Cooper, B., & Blouin, M.S. (2007b). Effective population
847 size of steelhead trout: Influence of variance in reproductive success, hatchery programs, and
848 genetic compensation between life-history forms. *Molecular Ecology*, 16, 953-966.
849 <https://doi.org/10.1111/j.1365-294X.2006.03206.x>
- 850 Arlinghaus, R., & Cooke, S. (2009). Recreational Fisheries: Socioeconomic Importance,
851 Conservation Issues and Management Challenges. In *Recreational Hunting, Conservation and*

- 852 *Rural Livelihoods: Science and Practice*, Blackwell Publishing Ltd, pp. 39-58. [https://doi-](https://doi.org/10.1002/9781444303179.ch3)
853 [org/10.1002/9781444303179.ch3](https://doi.org/10.1002/9781444303179.ch3)
- 854 Arlinghaus, R. et al. (2007). Understanding the Complexity of Catch-and-Release in
855 Recreational Fishing: An Integrative Synthesis of Global Knowledge from Historical, Ethical,
856 Social, and Biological Perspectives. *Reviews in Fisheries Science*, 15, 75-167.
857 <https://doi.org/10.1080/10641260601149432>
- 858 Arlinghaus, R., Tillner, R., & Bork, M. (2015). Explaining participation rates in recreational
859 fishing across industrialised countries. *Fisheries Management Ecology*, 22,45–55.
860 <https://doi.org/10.1016/j.jhydrol.2006.01.015>
- 861 Arlinghaus, R. et al. (2019). Opinion: Governing the recreational dimension of global fisheries.
862 *Proceedings of the National Academy of Sciences of the United States of America*. 116, 5209–
863 5213. <https://doi.org/10.1073/pnas.1902796116>
- 864 Arnold, S.J., & Duvall, D. (1994). Animal mating systems: a synthesis based on selection theory.
865 *American Naturalist*, 143, 317-348. <https://doi.org/10.1093/jhered/92.2.137>
- 866 Assani, A.A., Tardif, S., & Lajoie, F. (2006). Statistical analysis of factors affecting the spatial
867 variability of annual minimum flow characteristics in a cold temperate continental region
868 (southern Québec, Canada). *Journal of Hydrology*, 328, 3-4, 753-763.
869 <https://doi.org/10.1016/j.jhydrol.2006.01.015>
- 870 Backström, T., Heynen, M., Brännäs, E., Nilsson, J., Winberg, S., & Magnhagen, C. (2015).
871 Social stress effects on pigmentation and monoamines in Arctic charr. *Behav Brain Res*.
872 291,103–107. <https://doi.org/10.1016/j.bbr.2015.05.011>
- 873 Barlaup, B.T., Lura, H., Saegrov, H., & Sundt, R.C. (1994). Inter- and intra-specific variability in
874 female salmonid spawning behavior. *Canadian Journal of Zoology*, 72(4), 636-642.
875 [https://doi.org /10.1139/z94-086](https://doi.org/10.1139/z94-086)

- 876 Bartholomew, A., & Bohnsack, J. (2005). A review of catch-and-release angling mortality with
877 implications for no-take reserves. *Rev. Fish Biol. Fish.*, 15, 129–154.
878 <https://doi.org/10.1007/s11160-005-2175-1>
- 879 Bernatchez, L. (2009). Plan de reproduction du saumon atlantique. Stratégie de compromis
880 entre considérations génétiques et démographiques. Étude réalisée pour le compte du
881 ministère des Ressources naturelles et de la Faune, Direction de l'expertise sur la faune et ses
882 habitats, 40 p.
- 883 Blanchet, S., Páez, D., Bernatchez, L., & Dodson, J. (2008). An integrated comparison of
884 captive-bred and wild Atlantic salmon (*Salmo salar*): Implications for supportive breeding
885 programs. *Biological Conservation*, 141, 1989-1999.
886 <https://doi.org/10.1016/j.biocon.2008.05.014>
- 887 Bradbury, I. R., Wringe, B. F., Watson, B., Paterson, I., Horne, J., Beiko, R., Lehnert, S.,
888 Clement, M., Anderson, E. C., Jeffery, N. W., Duffy, S., Sylvester, E., Robertson, M., & Bentzen,
889 P. (2018). Genotyping- by-sequencing of genome-wide microsatellite loci reveals fine-scale
890 harvest composition in a coastal Atlantic salmon fishery. *Evolutionary Applications*, 11, 918–
891 930. <https://doi.org/10.1111/eva.12606>
- 892 Bonga, S.E.W. (1993). The stress response in fish. *Physiological reviews*, 77, 591-625.
893 <https://doi.org/10.1152/physrev.1997.77.3.591>
- 894 Booth, R., Kieffer, J., Davidson, K., Bielak, A., & Tufts, B. (1995). Effects of late-season catch
895 and release angling on anaerobic metabolism, acid-base status, survival, and gamete viability in
896 wild Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences*, 52,
897 283–290. <https://doi.org/10.1139/f95-029>
- 898 Burnham, K.P., & Anderson, D.R. (2002). Model Selection and Multimodel Inference: A Practical
899 Information-Theoretic Approach, 2nd edn. Springer, Berlin.

- 900 Breau, C., Cunjak, R.A., & Peake, S.J. (2011). Behaviour during elevated watertemperatures:
901 can physiology explain movement of juvenile Atlantic salmon to cool water? *Journal of Animal*
902 *Ecology*, 80, 844–853. <https://doi.org/10.1111/j.1365-2656.2011.01828.x>.
- 903 Brownscombe, J. W., Danylchuk, A. J., Chapman, J. M., Gutowsky, L. F. G., & Cooke, S. J.
904 (2017). Best practices for catch-and-release recreational fisheries – Angling tools and tactics.
905 *Fisheries Research*, 186, 693–705. <https://doi.org/10.1016/j.fishres.2016.04.018>
- 906 Cooke, S.J., Schreer, J.F., Wahl, D.H., & Philipp, D.P. (2002). Physiological impacts of catch-
907 and-release angling practices on largemouth bass and smallmouth bass. Black Bass 2000
908 Symposium: Ecology, Conservation, and Management. *American Fisheries Society*, St. Louis,
909 MO.
- 910 Cooke, S., & Sneddon, L. (2007). Animal welfare perspectives on recreational angling. *Applied*
911 *Animal Behaviour Science*, 104(3-4), 176-198.
- 912 Chapman, D. W. (1988). Critical review of variables used to define effects of fines in redds of
913 large salmonids. *Trans. Am. Fish. Soc.*, 117, 1–21. [https://doi.org/10.1577/1548-](https://doi.org/10.1577/1548-8659(1988)117<0001:CROVUT>2.3.CO;2)
914 [8659\(1988\)117<0001:CROVUT>2.3.CO;2](https://doi.org/10.1577/1548-8659(1988)117<0001:CROVUT>2.3.CO;2)
- 915 Christie, M., Ford, M., & Blouin, M.S. (2014). On the reproductive success of early-generation
916 hatchery fish in the wild. *Evolutionary Applications*, 7, 883-896.
917 <https://doi.org/10.1111/eva.12183>
- 918 Christie, M., Marine, M., Fox, S.E., French., R.A., & Blouin, M.S. (2016) A single generation of
919 domestication heritably alters the expression of hundreds of genes. *Nature communications*, 7,
920 10676. <https://doi.org/10.1038/ncomms10676>
- 921 Christie, M., Marine, M., French, R. & Blouin, M.S. (2012). Genetic adaptation to captivity can
922 occur in a single generation. *Proceedings of the National Academy of Sciences of the United*
923 *States of America*, 109(1), 238-242. <https://doi.org/10.1073/pnas.1111073109>

- 924 Cooke, S., & Cowx, I. (2004). The role of recreational fishing in global fish crises. *BioScience*,
925 54(9), 857-859. [https://doi.org/10.1641/00063568\(2004\)054\[0857:TRORFI\]2.0.CO;2](https://doi.org/10.1641/00063568(2004)054[0857:TRORFI]2.0.CO;2)
- 926 Cooke, S., & Suski, C. (2005). Do we need species-specific guidelines for catch-and-release
927 recreational angling to effectively conserve diverse fishery resources? *Biodiversity and*
928 *Conservation*, 14, 1195–1209. <https://doi.org/10.1007/s10531-004-7845-0>
- 929 David, P., Pujol, B., Viard, F., Castella, V., & Goudet, J. (2007). Reliable selfing rate estimates
930 from imperfect population genetic data. *Molecular Ecology*, 16(12), 2474–2487.
931 <https://doi.org/10.1111/j.1365-294X.2007.03330.x>
- 932 Davidson, K., Hayward, J., Hambrook, M., Bielak, A.T., & Sheasgreen, J. (1994). The effects of
933 late-season angling on gamete viability and early fry survival in Atlantic salmon. *Can. Tech.*
934 *Rep. Fish. Aquat. Sci.*, 1982, 1–12.
- 935 DFO (Fisheries and Oceans Canada). (2008). Evaluation of Captive Breeding Facilities in the Context of
936 their Contribution to Conservation of Biodiversity. *DFO Can. Sci. Advis. Sec. Sci. Advis. Rep.* 2008/027.
- 937 DFO (Fisheries and Oceans Canada). (2012). Temperature threshold to define management strategies
938 for Atlantic salmon (*Salmo salar*) fisheries under environmentally stressful conditions. *DFO Can. Sci.*
939 *Advis. Sec. Sci. Advis. Rep.* 2012/019.
- 940 Eisenhauer, Z., Christman, P., Matte, J.-M., Arden, W., Fraser, D. & Grant, J. (2020). Revisiting the
941 restricted movement paradigm: the dispersal of Atlantic salmon fry from artificial redds. *Canadian*
942 *Journal of Fisheries and Aquatic Sciences*. <https://doi.org/10.1139/cjfas-2020-0162>
- 943 Eliason, J.E., Clark, T.D., Hague, M.J., Hanson, L.M., Gallagher, Z.S., Jeffries, K.M., Gale,
944 M.K., Patterson, D.A., Hinch, S.G., & Farrell, A.P. (2011). Differences in thermal tolerance
945 among sockeye salmon populations. *Science*, 332, 109-112.
946 <https://doi.org/10.1126/science.1199158>

- 947 FAO. (2018). The State of World Fisheries and Aquaculture (Food and Agricultural Organization
948 of the United Nations, Rome).
- 949 Fleming, I.A. (1996). Reproductive strategies of Atlantic salmon: ecology and evolution.
950 *Reviews in Fish Biology and Fisheries*, 6, 379-416.
- 951 Fleming, I.A., & Gross, M.R. (1993). Breeding success of hatchery and wild coho salmon
952 (*Oncorhynchus kisutch*) in competition. *Ecological Applications*, 3, 230–245.
953 <https://doi.org/10.2307/1941826>
- 954 Fleming, I.A. & Gross, M.R. (1994). Breeding competition in a Pacific salmon (coho:
955 *Oncorhynchus kisutch*) in competition. *Ecological Application*, 3, 230-245.
956 <https://doi.org/10.2307/2410475>
- 957 Fleming, I.A., Jonsson, B., Gross, M.R., & Lamberg, A. (1996). An experimental study of the
958 reproductive behaviour and success of farmed and wild Atlantic Salmon (*Salmo salar*). *Journal*
959 *of Applied Ecology*, 33, 905. <https://doi.org/10.2307/2404960>
- 960 Fleming, I.A., Lamberg, A., & Jonsson, B. (1997). Effects of early experience on the
961 reproductive performance of Atlantic salmon. *Behavioral Ecology*, 8, 470-480.
962 <https://doi.org/10.1093/beheco/8.5.470>
- 963 Fleming, I.A., & Petersson, E. (2001). The ability of release, hatchery salmonids to breed and
964 contribute to the natural productivity of wild populations. *Nordic Journal of Freshwater*
965 *Research*, 75, 71-98. <https://doi.org/10.1111/j.1752-4571.2008.00026.x>
- 966 Fleming, I.A. (1998). Pattern and variability in the breeding system of Atlantic salmon (*Salmo*
967 *salar*), with comparisons to other salmonids. *Canadian Journal of Fisheries and Aquatic*
968 *Sciences*, 55, 59-76. <https://doi.org/10.1139/d98-009>

- 969 Fraser, D. (2007). How well can captive breeding programs conserve biodiversity? A review on
970 salmonids. *Evolutionary Applications*, 1, 535- 586. [https://doi.org/0.1111/j.1752-](https://doi.org/0.1111/j.1752-4571.2008.00036.x)
971 [4571.2008.00036.x](https://doi.org/0.1111/j.1752-4571.2008.00036.x)
- 972 Gale, M., Hinch, S. & Donaldson, M. (2013). The role of temperature in the capture and release
973 of fish. *Fish and Fisheries*, 14, 1-33. <https://doi.org/10.1111/j.1467-2979.2011.00441.x>
- 974 Garant, D., Dodson, J.J., & Bernatchez, L. (2001). A genetic evaluation of mating system and
975 determinants of individual reproductive success in Atlantic salmon (*Salmo salar* L.). *Journal of*
976 *Heredity*, 92, 137-145. <https://doi.org/10.1093/jhered/92.2.137>
- 977 Garant, D., Dodson, J.J., & Bernatchez, L. (2003). Differential reproductive success and
978 heritability of alternative reproductive tactics in wild Atlantic salmon (*Salmo salar* L.). *Evolution*,
979 57, 1333-1141. <https://doi.org/10.1111/j.0014-3820.2003.tb00322.x>
- 980 Garcia-Vazquez, E., Moran, P., Martinez, J.L., et al. (2001). Alternative mating strategies in
981 Atlantic salmon and brown trout. *Journal of Heredity*, 92, 146–149.
982 <https://doi.org/10.1093/jhered/92.2.146>
- 983 Gavery, M.R., Nichols, K.M., Goetz, G.W., Middleton, M.A., & Swanson, P. (2018).
984 Characterization of genetic and epigenetic variation in sperm and red blood cells from adult
985 hatchery and natural-origin steelhead, *Oncorhynchus mykiss*. *G3*, 8,3723–3736.
986 <https://doi.org/10.1534/g3.118.200458>
- 987 Gibson, R.J., & Myers, R.A. (1988). Influence of seasonal river discharge on survival of juvenile
988 Atlantic salmon, *Salmo salar*. *Can J Fish Aquat Sci*, 45,344–348. <https://doi.org/10.1139/f88-040>
- 989 Grueber, C.E., Nakagawa, S., Laws, R.J., & Jamieson, I.G. (2011). Multi-model inference in
990 ecology and evolution: challenges and solutions. *Journal of Evolutionary Biology*, 24, 699–711.
991 <https://doi.org/10.1111/j.1420-9101.2010.02210.x>

- 992 Hagen, I. J., Ugedal, O., Jensen, A. J., Lo, H., Holthe, E., Bjørn, B., Florø-Larsen, B., Sægvog, H., Skoglund, H., & Karlsson, S. Evaluation of genetic effects on wild salmon populations from
993 stock enhancement. *ICES Journal of Marine Science*, 1-10.
994 <https://doi.org/10.1093/icesjms/fsaa235>.
- 996 Hendry, A.P., & Beall, E. (2004). Energy use in spawning Atlantic salmon. *Ecology of*
997 *Freshwater Fish*, 13, 185-196. <https://doi.org/10.1111/j.1600-0633.2004.00045.x>
- 998 Hindar, K., Ryman, N., & Utter, F. (1991). Genetic effects of cultured fish on natural fish
999 populations. *Can. J. Fish Aquat Sci.*, 48, 945-957. <https://doi.org/10.1139/f91-111>
- 1000 Hurvich, C.M. & Tsai, C.-L. (1989). Regression and time series model selection in small
1001 samples. *Biometrika*, 76, 297– 307. <https://doi.org/10.1093/biomet/76.2.297>
- 1002 ICES (2019). Working Group on North Atlantic Salmon (WGNAS). *ICES Scientific Reports*, 1,
1003 368.
- 1004 Jackman, S. (2020). *pscl: Classes and Methods for R Developed in the Political Science*
1005 *Computational Laboratory*. United States Studies Centre, University of Sydney. Sydney, New
1006 South Wales, Australia. R package version 1.5.5. URL <https://github.com/atahk/pscl/>
- 1007 Johnstone, D.L., O'Connell, M.F., Palstra, F.P., & Ruzzante, D.E. (2013). Mature male parr
1008 contribution to the effective size of an anadromous Atlantic salmon (*Salmo salar*) population
1009 over 30 years. *Molecular Ecology*, 22, 2394– 2407. <https://doi.org/10.1111/mec.12186>
- 1010 Jones, J.W. (1959). *The salmon*. London: Collins. 192 pp.
- 1011 Jones, M.W., & Hutchings, J.A. (2001). The influence of male parr body size and mate
1012 competition on fertilization success and effective population size in Atlantic salmon. *Heredity*,
1013 86, 675–684. <http://doi.org/10.1046/j.1365-2540.2001.00880.x>.

- 1014 Jones, O., & Wang, J. (2010). COLONY: a program for parentage and sibship inference from
1015 multilocus genotype data. *Molecular Ecology*, 10, 551-555. <http://doi.org/10.1111/j.1755->
1016 [0998.2009.02787.x](http://doi.org/10.1111/j.1755-0998.2009.02787.x)
- 1017 Jonsson, N., Jonsson, B., & Hansen, L.P. (1991). Energetic cost of spawning in male and
1018 female Atlantic salmon (*Salmo salar* L.). *Journal of Fish Biology*, 39, 739–744.
1019 <https://doi.org/10.1111/j.1095-8649.1991.tb04403.x>
- 1020 Kalinowski, S. T., & Taper M. L. (2005). Likelihood-based confidence intervals of relative fitness
1021 for a common experimental design. *Canadian Journal of Fisheries and Aquatic Sciences*, 62,
1022 693–699. <https://doi.org/10.1139/f04-239>
- 1023 Kalinowski, S.T., Taper, M.L., & Marshall, T.C. (2007) Revising how the computer program
1024 CERVUS accommodates genotyping error increases success in paternity assignment.
1025 *Molecular Ecology*, 16, 1099-1106. <http://dx.doi.org/10.1111/j.1365-294x.2007.03089.x>
- 1026 King, R., & Stevens J. (2019). An improved genetic sex test for Atlantic salmon (*Salmo salar* L.).
1027 *Conservation Genetics Resources* 12, 191-193. <https://doi.org/10.1007/s12686-019-01094-y>
- 1028 Lehnert, S. J., Kess, T., Bentzen, P., Kent, M. P., Lien, S., Gilbey, J., Clément, M., Jeffery, N.
1029 W., Waples, R. S., & Bradbury, I. R. (2019). Genomic signatures and correlates of widespread
1030 population declines in salmon. *Nature Communications*, 10, 2996.
1031 <https://doi.org/10.1038/s41467-019-10972-w>
- 1032 Leitwein, M., Laporte, M., Le Luyer, J., Mohns, K., Normandeau, E., Withler, R., & Bernatchez,
1033 L. (2021). Epigenomic modifications induced by hatchery rearing persist in germ line cells of
1034 adult salmon after their oceanic migration. *Evolutionary Applications*.
1035 <https://doi.org/10.1111/eva.13235>
- 1036 Lennox, R.J., Cooke, S.J., Diserud, O.H., Havn, T.B., Johansen, M.R., Thorstad, E.B.,
1037 Whoriskey, F.G., & Uglem, I. (2016). Use of simulation approaches to evaluate the

- 1038 consequences of catch-and-release angling on the migration behaviour of adult Atlantic salmon
1039 (*Salmo salar*). *Ecological Modelling*, 333, 43-50.
1040 <https://doi.org/10.1016/j.ecolmodel.2016.04.010>
- 1041 Le Luyer, J., Laporte, M., Beacham, T.D., Kaukinen, K.H., Withler, R.E., Leong, J.S., Rondeau,
1042 E.B., Koop, B.F., & Bernatchez, L. (2017). Parallel epigenetic modifications induced by hatchery
1043 rearing in a Pacific Salmon. *Proceedings of the National Academy of Sciences of the United*
1044 *States of America*, 49, 12964–12969. <https://doi.org/10.1073/pnas.1711229114>
- 1045 Lennox, R. J., Cooke, S. J., Davis, C. R., Gargan, P., Hawkins, L. A., Havn, T. B., Johansen, M.
1046 R., Kennedy, R. J., Richard, A., Svenning, M., Uglem, I., Webb, J., Whoriskey, G. G., &
1047 Thorstad, E. B. (2017). Pan-Holarctic assessment of post-release mortality of angled Atlantic
1048 salmon, *Salmo salar*. *Biological Conservation*, 209, 150–158.
1049 <https://doi.org/10.1016/j.biocon.2017.01.022>
- 1050 Lewin, W.-C., Arlinghaus, R., & Mehner, T. (2006). Documented and potential biological impacts
1051 of recreational fishing: Insights for management and conservation. *Reviews in Fisheries*
1052 *Science*, 14, 305–367. <https://doi.org/10.1080/10641260600886455>
- 1053 Marshall, T.C., Slate, J., Kruuk, L.E.B., & Pemberton, J.M. (1998) Statistical confidence for
1054 likelihood-based paternity inference in natural populations. *Molecular Ecology*, 7, 639-655.
1055 <http://dx.doi.org/10.1046/j.1365-294x.1998.00374.x>
- 1056 MacCrimmon, H.R., & Gots, B.L. (1979). World distribution of Atlantic salmon, *Salmo salar*.
1057 *Journal of Fisheries Research Board of Canada*, 36, 422–457. <https://doi.org/10.1139/f79-062>
- 1058 Milot, E., Perrier, C., Papillon, L., Dodson, J.J., & Bernatchez, L. (2013). Reduced fitness of
1059 Atlantic salmon released in the wild after one generation of captive breeding. *Evolutionary*
1060 *Applications* 6, 472–485. <https://doi.org/10.1111/eva.12028>

- 1061 Ministères des Forêts, de la Faune et des Parcs. (2016). Plan de gestion du saumon atlantique
1062 2016-2026, ministère des Forêts, de la Faune et des Parcs, Direction générale de l'expertise
1063 sur la faune et ses habitats, Direction de la faune aquatique, Québec, 40 p.
- 1064 Ministères des Forêts, de la Faune et des Parcs. (2020). Bilan de l'exploitation du saumon au
1065 Québec en 2019, ministère des Forêts, de la Faune et des Parcs, Secteur de la faune et des
1066 parcs, 302 p.
- 1067 Ministères des Forêts, de la Faune et des Parcs, Direction de l'expertise sur la faune aquatique.
1068 *Système d'information sur la faune aquatique (IFA), Suivi de la température de l'eau.*
1069 http://rivtemp.ca/mffp_qc/
- 1070 Mobley, K.B., Granroth-Wilding, H., Ellmen, M., Vähä, Aykanat, T., Johnston, S.E., Orell, P.,
1071 Erkinaro, J & Primmer, C.R. (2018). Home ground advantage: selection against dispersers
1072 promotes cryptic local adaptation in wild salmon. *Science*, 5, eaav1112.
1073 <https://doi.org/10.1126/sciadv.aav1112>
- 1074 Myers, R.A.(1984). Demographic consequences of precocious maturation of Atlantic salmon
1075 (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences*, 41, 1349– 1353.
1076 <https://doi.org/10.1139/f84-165>
- 1077 Nakagawa, S., & Freckleton, R.P. (2010). Model averaging, missing data and multiple
1078 imputation: a case study for behavioural ecology. *Behavioral Ecology Sociobiology*, 65, 103–
1079 116. <https://doi.org/10.1007/s00265-010-1044-7>.
- 1080 North Atlantic Salmon Conservation Organization. (2017). Understanding the risks and benefits
1081 of hatchery and stocking activities to wild Atlantic salmon populations. 2017. Report of a Theme-
1082 based Special Session of the Council of NASCO. *CNL*, 17, 61-116pp

- 1083 O'Sullivan, R.J. et al. (2020). Captive-bred Atlantic salmon released into the wild have fewer
1084 offspring than wild-bred fish and decrease population productivity. *Proc. R. Soc. B* 287,
1085 20201671. <http://dx.doi.org/10.1098/rspb.2020.1671>
- 1086 Paetkau, D., Calvert, W., Stirling, I., & Strobeck, C. (1995). Microsatellite analysis of population
1087 structure in Canadian polar bears. *Molecular Ecology*, 4, 347–354.
1088 <https://doi.org/10.1111/j.1365-294x.1995.tb00227.x>
- 1089 Paetkau, D., Slade, R., Burden, M., & Estoup, A. (2004). Genetic assignment methods for the
1090 direct, real-time estimation of migration rate: a simulation-based exploration of accuracy and
1091 power. *Molecular Ecology*, 13, 55–65. <https://doi.org/10.1046/j.1365-294X.2004.02008.x>
- 1092 Patterson, D.A., Macdonald, J.S., Hinch, S.G., Healey, M.C., & Farrell, A.P. (2004). The effect
1093 of exercise and captivity on energy partitioning, reproductive maturation and fertilization success
1094 in adult sockeye salmon. *Journal of Fish Biology* 64, 1039–1059. [https://doi.org/10.1111/j.1095-](https://doi.org/10.1111/j.1095-8649.2004.0370.x)
1095 [8649.2004.0370.x](https://doi.org/10.1111/j.1095-8649.2004.0370.x)
- 1096 Perrier, C., Normandeau, E., Dionne, M., Richard, A., & Bernatchez, L. (2014). Alternative
1097 reproductive tactics increase effective population size and decrease inbreeding in wild Atlantic
1098 salmon. *Evolutionary Applications*, 7, 1094-1106. <https://doi.org/10.1111/eva.12172>
- 1099 Piry, S., Alapetite, A., Cornuet, J.-M., Paetkau, D., Baudouin, L., & Estoup, A. (2004).
1100 GeneClass2: A Software for Genetic Assignment and First-Generation Migrant Detection.
1101 *Journal of Heredity*, 95, 536-539. <https://doi.org/10.1093/jhered/esh074>
- 1102 Post, J., Sullivan, M., Cox, S., Lester N., Walters, C., Parkinson, E., Paul, A., Jackson, L., &
1103 Shuter, B. (2002). Canada's Recreational Fisheries: The Invisible Collapse? *Fisheries*, 27(1), 6-
1104 17. [http://doi.org/10.1577/15488446\(2002\)027<0006:CRF>2.0.CO;2](http://doi.org/10.1577/15488446(2002)027<0006:CRF>2.0.CO;2)

- 1105 Richard, A., Dionne, M., Wang, J., & Bernatchez, L. (2013). Does catch and release catch-and-
1106 release affect the mating system and individual reproductive success of wild Atlantic salmon
1107 (*Salmo salar* L.)? *Molecular Ecology*, 21, 187–200. <https://doi.org/10.1111/mec.12102>
- 1108 Rodriguez-Barreto, D., Garcia de Leaniz, C., Verspoor, E., Sobolewska, H., Coulson, M., &
1109 Consuegra, S. (2019). DNA Methylation Changes in the Sperm of Captive-Reared Fish: A
1110 Route to Epigenetic Introgression in Wild Populations. *Molecular Biology and Evolution*, 36,
1111 2205-2211. <https://doi.org/10.1093/molbev/msz135>
- 1112 Saura, M., Caballero, A., Caballero, P., & Moran, P. (2008). Impact of precocious male parr on
1113 the effective size of a wild population of Atlantic salmon. *Freshwater Biology*, 53, 2375–2384.
1114 <https://doi.org/10.1111/j.1365-2427.2008.02062.x>
- 1115 Schreck, C.B. (2010). Stress and fish reproduction: The roles of allostasis and hormonesis.
1116 *General and Comparative Endocrinology*, 165, 549-556.
1117 <https://doi.org/10.1016/j.ygcen.2009.07.004>.
- 1118 Stoffel, M.A., Esser, M., Kardos, M., Humble, E., Nichols, H., David, P., & Hoffman, J.I. (2016).
1119 inbreedR: An R package for the analysis of in- breeding based on genetic markers. *Methods in*
1120 *Ecology and Evolution*, 7(11), 1331–1339. <https://doi.org/10.1111/2041-210X.12588>
- 1121 Szulkin, M., & David, P. (2011). Negative heterozygosity-fitness correlations observed with
1122 microsatellites located in functional areas of the genome. *Molecular Ecology*, 20(19), 3949–
1123 3952. <https://doi.org/10.1111/j.1365-294X.2011.05277.x>
- 1124 Taggart, J.B., McLaren, I.S., Hay, D.W., Webb, J.H. & Youngson, A.F. (2001). Spawning
1125 success in Atlantic salmon (*Salmo salar* L.): a long-term DNA profiling-based study conducted in
1126 a natural stream. *Molecular Ecology*, 10, 1047-1060. <https://doi.org/10.1046/j.1365-294X.2001.01254.x>
- 1127

- 1128 Tentelier, C., Lepais, O., Larranaga, N., Manicki, A., Lange, F. & Rives, J. (2016). Sexual
1129 selection leads to a tenfold difference in reproductive success of alternative reproductive tactics
1130 in male Atlantic salmon. *Sci. Nat.* 103, 47. <https://doi.org/10.1007/s00114-016-1372-1>
- 1131 Thorstad, E., Naesje, T., Fiske, P., & Finstad, B. (2003). Effects of hook and release on Atlantic
1132 salmon in the River Alta, northern Norway. *Fisheries Research*, 60, 293–307.
1133 [https://doi.org/10.1016/S0165-7836\(02\)00176-5](https://doi.org/10.1016/S0165-7836(02)00176-5)
- 1134 Valiquette, E., Perrier, C., Thibault, I., & Bernatchez, L. (2014). Loss of genetic integrity in wild
1135 lake trout populations following stocking: insights from an exhaustive study of 72 lakes from
1136 Québec, Canada. *Evolutionary Applications*, 7, 625–644. <https://doi.org/10.1111/eva.12160>
- 1137 Van Leeuwen, T.E., Dempson, J.B., Burke, C. M., Kelly, N.I., Robertson, M.J., Lennox, R.J.,
1138 Havn, T.B., Svenning, M.-A., Hinks, R., Guzzo, M.M., Thorstad, E.B., Purchase, C.F., & Bates,
1139 A.E. (2020). Mortality of Atlantic salmon after catch and release angling: Assessment of a
1140 recreational Atlantic salmon fishery in a changing climate. *Canadian Journal of Fisheries &
1141 Aquatic Sciences*, 77(9), 1–11. <https://doi.org/10.1139/cjfas-2019-0400>
- 1142 Vuong, Q.H. (1989). Likelihood ratio tests for model selection and non-nested hypotheses.
1143 *Econometrica*. <https://doi.org/10.2307/1912557>
- 1144 Waples, R.S. (1990). Conservation genetics of Pacific salmon. II. Effective population size and
1145 the rate of loss of genetic variability. *Journal of Heredity*, 81, 267–276.
1146 <https://doi.org/10.1093/oxfordjournals.jhered.a110989>
- 1147 Waples, R.S. (1991). Genetic interactions between wild and hatchery salmonids: lessons from
1148 the Pacific Northwest. *Can. J. Fish. Aquat. Sci.* 48, 124-133. <https://doi.org/10.1139/f91-311>
- 1149 Waples, R., Punt, A.E., & Cope, J.M. (2008). Integrating genetic data into management of
1150 marine resources: how can we do it better? *Fish and Fisheries*, 9, 423–449.
1151 <https://doi.org/10.1111/j.1467-2979.2008.00303.x>

- 1152 Waples, R., & Do, C. (2010). Linkage disequilibrium estimates of contemporary Ne using highly
1153 variable genetic markers: a largely untapped resource for applied conservation and evolution.
1154 *Evolutionary Applications*, 3, 244–262. <https://doi.org/10.1111/j.1752-4571.2009.00104.x>
- 1155 Webb, J.H., & Hawkins, A.D. (1989). The movements and spawning behaviour of adult salmon
1156 in the Girnock Bum, a tributary of the Aberdeenshire Dee, 1986. *Scott. Fish. Res. Rep. No*, 40,
1157 42.
- 1158 Wedekind, C. (2002). Sexual selection and life-history decisions: Implications for supportive
1159 breeding and the management of captive populations. *Conservation Biology*, 16, 1204–1211.
1160 <https://doi.org/10.1111/10.1111/j.1365-294X.2011.05058.x>
- 1161 Weir, L.K., Breau, C., Hutchings, J.A., & Cunjak R.A. (2010). Multiple paternity and variance in
1162 male fertilization success within Atlantic salmon *Salmo salar* redds in a naturally spawning
1163 population. *Journal of Fish Biology*, 77, 479–493. [https://doi.org/10.1111/j.1095-](https://doi.org/10.1111/j.1095-8649.2010.02690.x)
1164 [8649.2010.02690.x](https://doi.org/10.1111/j.1095-8649.2010.02690.x)
- 1165 Wellband, K., Roth, D., Linnansaari, T., Curry, A., & Bernatchez, L. (2021). Environment-driven
1166 reprogramming of gamete DNA methylation occurs during maturation and influences offspring
1167 fitness in salmon. bioRxiv. <https://doi.org/10.1101/2020.11.25.396069>
- 1168 Whoriskey, F., Prusov, S., & Crabbe, S. (2000). Evaluation of the effects of catch-and-release
1169 angling on the Atlantic salmon (*Salmo salar*) of the Ponoï River, Kola Peninsula, Russian
1170 Federation. *Ecology of Freshwater Fish*, 9, 118–125. [https://doi.org/10.1034/j.1600-](https://doi.org/10.1034/j.1600-0633.2000.90114.x)
1171 [0633.2000.90114.x](https://doi.org/10.1034/j.1600-0633.2000.90114.x)
- 1172 Willoughby, J. & Christie, M. (2019). Long-term demographic and genetic effects of releasing
1173 captive-born individuals into the wild. *Conservation Biology*, 33, 377–388.
1174 <https://doi.org/10.1111/cobi.13217>

1175 Wilkie, M.P., Davidson, K., Brobbel, M.A., Kieffer, J.D., Booth, R.K., Bielak, A.T. & Tufts, B.L.
1176 (1996). Physiology and survival of wild Atlantic salmon following angling in warm summer
1177 waters. *Trans. Am. Fish. Soc.* 125: 572–580. [10.1577/1548-](https://doi.org/10.1577/1548-8659%281996%29125%3C0572%3APASOWA%3E2.3.CO%3B2)
1178 [8659%281996%29125%3C0572%3APASOWA%3E2.3.CO%3B2](https://doi.org/10.1577/1548-8659%281996%29125%3C0572%3APASOWA%3E2.3.CO%3B2)

1179 Wilkie, M.P., Brobbel, M.A., Davidson, K.G., Forsyth, L. & Tufts, B.L. (1997). Influences of
1180 temperature upon the postexercise physiology of Atlantic salmon (*Salmo salar*). *Can. J. Fish.*
1181 *Aquat. Sci.* 54: 503–511. <https://doi.org/10.1139/f96-305>

1182 Zeileis, A., & Kleiber, C. (2018). countreg: Count Data Regression. R package version 0.2-1.
1183 URL <http://R-Forge.R-project.org/projects/countreg/>

1184 Zhan, L., Paterson, I.G., Fraser, B.A., Watson, B., Bradbury, I.R., Nadukkalam Ravindran, P., &
1185 Bentzen, P. (2017). Megasat: Automated inference of microsatellite genotypes from sequence
1186 data. *Molecular Ecology Resources*, 17(2), 247–256. <https://doi.org/10.1111/1755-0998.12561>

1187

1188

1189

1190

1191

1192

1193

1194

1195

1196

1197

1198

1199 **Table 1:** Details of the genotyped adults and juveniles Atlantic salmon. The samples include all the
1200 returning adults caught at the Rimouski River dam from summer 2018 and the juveniles caught on the
1201 Rimouski River spawning grounds during spring 2019.

	Number of individuals
Adult transported above dam	475
Adult used for assignments *	468
Born in the river (wild origin)	349
Born in the Rimouski hatchery	126
Returning as SSW	204
Returning as MSW	271
C&R fish	33
C&R fish transported above dam	18
Fry assigned	2495

* Difference between the number of adults used for assignment and the number transported above the dam is due to fish with missing or partial genotypes.

1202

1203

1204

1205

1206

1207

1208

1209

1210

1211

1212

1213 **Table 2:** Relative reproductive success (RRS) of naturally spawning F_1 parent. (nF_1 is the sample size for
 1214 naturally spawning captive-bred (C-B), wild (W), caught-and-released (C&R) and non-caught (N-C)
 1215 parent; nF_2 is the number of offspring assigned to each group of parents. RS is the reproductive success
 1216 measured as the mean number of offspring assigned per parent. Variance is the average of the squared
 1217 differences from the mean reproductive success. RRS is calculated as the RS of captive-bred fish over
 1218 the RS of wild-origin fish and RS of C&R fish over the RS of non-caught fish, associated P-values are
 1219 based on one-tailed permutation tests. Statistical power is the RRS value that would be significant with
 1220 80% and 95% probability).

Sex/ Winter at sea	$n F_1$ (C- B/W)	$n F_2$ (H/W)	RS Captive- bred	Variance Captive- bred	RS Wild	Variance Wild	RRS	P- value	80%/95% Power
Female MSW	53/133	607/1860	11.5	101	14.0	238	0.805	< 0.01	0.963/0.929
Male MSW	28/51	286/620	10.2	160	12.2	183	0.828	< 0.01	0.943/0.897
Male 1SW	40/146	105/593	2.62	11.8	4.06	24.3	0.649	< 0.01	0.919/0.853
	$n F_1$ (C&R/ N-C)	$n F_2$ C&R/N-C)	RS C&R	Variance C&R	RS Wild	Variance Wild	RRS	P- value	80%/95% Power
Female MSW	13/174	124/2362	9.54	77.8	13.5	206	0.732	< 0.01	0.932/0.868
Male MSW	4/75	37/869	9.25	236	11.6	173	0.797	0.07 41	0.754/0.866

1221

1222

1223

1224

1225

1226 **Table 3:** Summaries of ZINB model testing the effect of number of mates, length and origin (wild/captive-
1227 bred) and the effect of length and origin on the number of offspring assigned to females and mating
1228 success respectively. The “zero inflation” term accounts for the large number of adults with zero
1229 reproductive success and mating success in our sample.

1230

1231

1232

1233

1234

1235

1236

1237

1238

1239

1240

1241

1242

1243

1244

1245

1246

1247

1248

1249

1250

1251

1252

1253

1254

1255

1256

1257

1258

1259

1260

1261

1262

1263

1264

Number of offspring												
		Mature pair					1SW				MSW	
Parameter	Estimate ± SE	z- score	p-Value	Estimate ± SE	z-score	p-Value	Estimate SE	z-score	p-Value	Estimate ± SE	z-score	p-Value
Number of mates	0.24 0.02	± 10.65 8	< 0.01	0.67 0.05	± 12	< 0.01	0.69 ± 0.06	-11.789	< 0.01	0.69 ± 0.06	-11.789	< 0.01
Length	-0.18 0.16	± -1.11	0.267	-0.027 0.167	± -1.075	0.282	0.03 ± 0.01	2.349	0.019	0.03 ± 0.01	2.349	0.019
Origin (Wild)	-0.02 0.01	± -1.85	0.063	0.02 0.17	± -0.165	0.869	0.30 ± 0.17	1.716	0.086	0.30 ± 0.17	1.716	0.086
Zero Inflation	-12.10 ±90.06	-0.134	0.893	-12.97 84.27	± -0.154	0.878	-11.43 43.51	± -0.263	0.793	-11.43 43.51	± -0.263	0.793
Mating success												
Length	0.046 0.05	± 9.410	< 0.01	0.037 0.009	± 4.053	< 0.01	0.0187 0.08	± 2.256	0.024	0.0187 0.08	± 2.256	0.024
Origin (Wild)	0.057 0.102	± 0.561	0.575	0.396 0.180	± 2.204	0.028	-0.0243 0.157	± -0.154	0.878	-0.0243 0.157	± -0.154	0.878
Zero Inflation	-0.989 ±0.179	-5.52	< 0.01	-1.56 0.45	± -3.464	< 0.01	-0.784 0.204	± -3.838	< 0.01	-0.784 0.204	± -3.838	< 0.01

1265

1266

1267

1268 **Table 4:** Summaries of ZINB model testing the effect of number of mates, sea age, and origin
1269 (wild/captive-bred) and the effect of sea age and origin on the number of offspring and mating success
1270 respectively. The “zero inflation” term accounts for the large number of adults with zero reproductive
1271 success and mating success in our sample.

1272

Parameter	Number of offspring		
	Estimate \pm SE	z-score	p-Value
Intercept	0.74 \pm 0.18	4.23	< 0.01
Number of mates	0.28 \pm 0.03	10.59	< 0.01
Sea age (1SW)	-0.90 \pm 0.21	-4.37	< 0.01
Sea age (1SW) : Number of mates	0.36 \pm 0.06	6.18	< 0.01
Origin (Wild)	-0.01 \pm 0.13	-0.08	0.93
Zero inflation	-12.27 \pm 78.35	-0.157	0.876

Parameter	Mating success		
	Estimate \pm SE	z-score	p-Value
Intercept	1.44 \pm 0.13	10.97	< 0.01
Sea age (SSW)	-1.06 \pm 0.12	-8.67	< 0.01
Origin (Wild)	0.28 \pm 0.14	2.08	0.038
Zero inflation	-1.90 \pm 0.33	-5.79	< 0.01

1273

1274

1275

1276

1277

1278

1279

1280

1281

1282 **Figure legends**

1283 **Fig 1.** Maximum-likelihood estimates of relative reproductive success (RRS) and their associated 95% confidence
1284 intervals for captive-bred vs wild fish and caught-&-released vs non-caught Atlantic salmon. If captive and wild or
1285 C&R and non-caught salmon had equal fitness, then RRS would be equal to 1 (dashed red line). Filled and empty
1286 circles represent RRS that were significantly different at the 95% confidence interval given the permutation test.

1287

1288 **Fig 2.** A) Relationship between the number of offspring (No. offspring) and mating success (No. mates) for female
1289 Atlantic salmon for three alternative reproductive tactics (Mature parr, 1SW and MSW). Coloured lines represent
1290 ZINB model prediction for captive-bred (blue) and wild (yellow) females, grey areas and hatched lines represent 95%
1291 confidence intervals (CI) obtained by bootstrap. Circles show individual data points. B) Relationship between mating
1292 success (No. mates) and length of female Atlantic salmon for three alternative reproductive tactics (Mature parr, 1SW
1293 and MSW). Coloured lines represent ZINB model prediction for captive-bred (blue) and wild (yellow) females, grey
1294 areas and hatched lines represent 95% confidence intervals (CI) obtained by bootstrap. Circles show individual data
1295 points.

1296

1297 **Fig 3.** A) Relationship between number of offspring (No. offspring) and mating success (No. mates) for 1SW and
1298 MSW male Atlantic salmon. Lines represent ZINB model prediction for captive-bred (blue) and wild (yellow) 1SW and
1299 MSW males, grey areas represent 95% confidence intervals (CI) obtained by bootstrap. B) Relationship between
1300 mating success (No. mates) and winters at sea (Sea winters) \times in male Atlantic salmon. Large circles with error bars
1301 represent the model prediction \pm 95% confidence interval (CI) obtained by bootstrap while small circles show
1302 individual data points. Captive-bred males had significantly less mates than wild males ($p < 0.038$).

1303

1304 **Fig 4.** Distribution of genetic (LDNe) estimates of effective number of breeders (N_b) considering either only wild
1305 anadromous salmon, both wild and captive-bred anadromous salmon or both wild anadromous salmon and mature
1306 male parr. The distribution of N_b calculated for wild anadromous salmon only was obtained directly from NeEstimator
1307 2 (Do et al. 2014) whereas the distribution for wild and captive-bred anadromous salmon or wild anadromous salmon
1308 and mature male parr was obtained by subsampling 916 fry from the parent-fry assignment of wild and hatchery
1309 breeders 1000 times and calculating N_b on each subsampling step. The 2.5% and 97.5% tails of the distribution are
1310 indicated in red.

1311

1312 **Fig 5.** Loess regression of the mean value of the number of alleles over all genotyped microsatellite loci calculated
1313 for 50 to 1500 fry fathered by wild anadromous male, wild and captive-bred anadromous male combined and all wild
1314 anadromous male and mature male parr. Each estimate was bootstrapped 1000 times. Five to 95% interval
1315 distribution of the data were given around the mean value.

1316

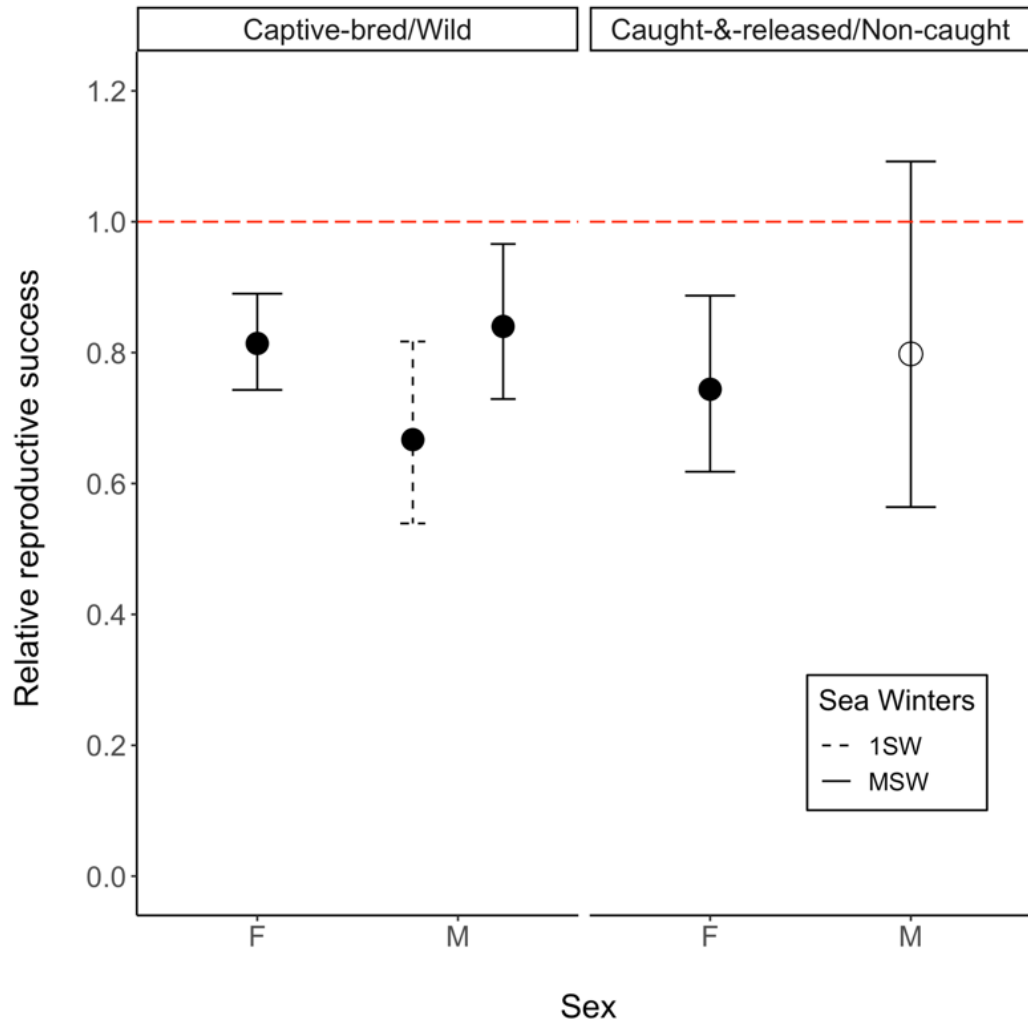
1317 **Fig 6.** Reproductive success (estimated by number of fry assigned) for the group of caught-and-released Atlantic
1318 salmon ($n = 18$) with increasing water temperature.

1319

1320

1321

1322



1323

1324

1325

1326

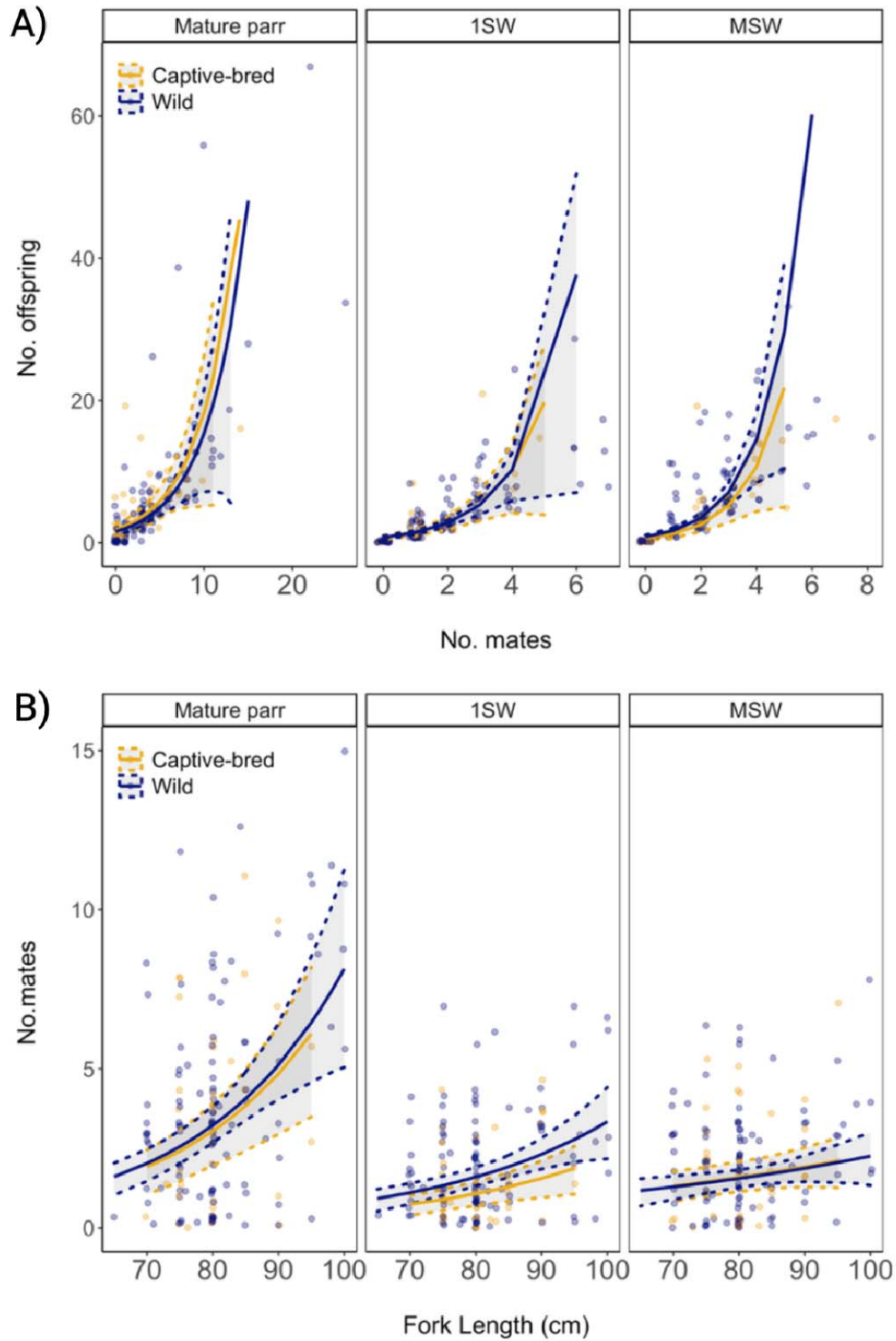
1327

1328

1329

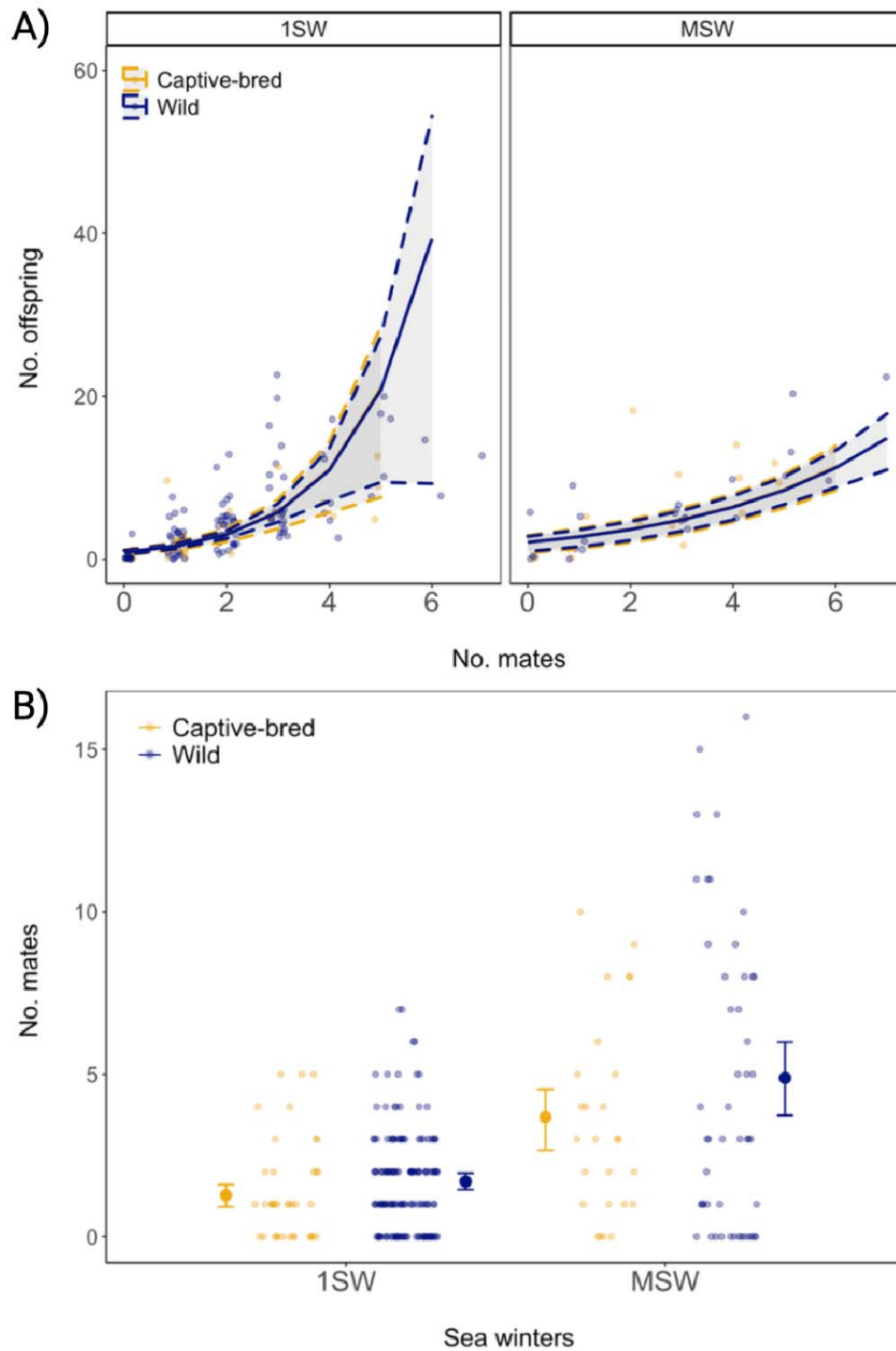
1330

1331



1332

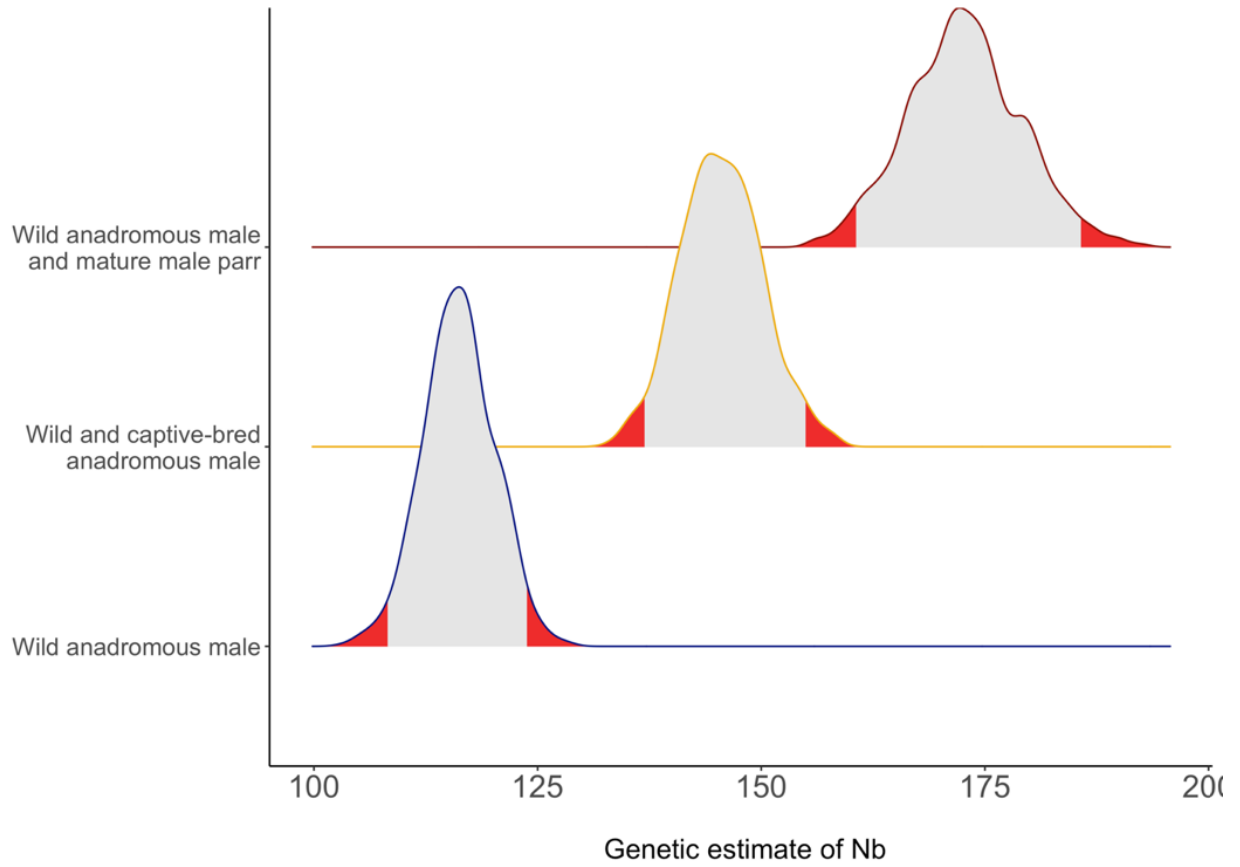
1333



1334

1335

1336



1337

1338

1339

1340

1341

1342

1343

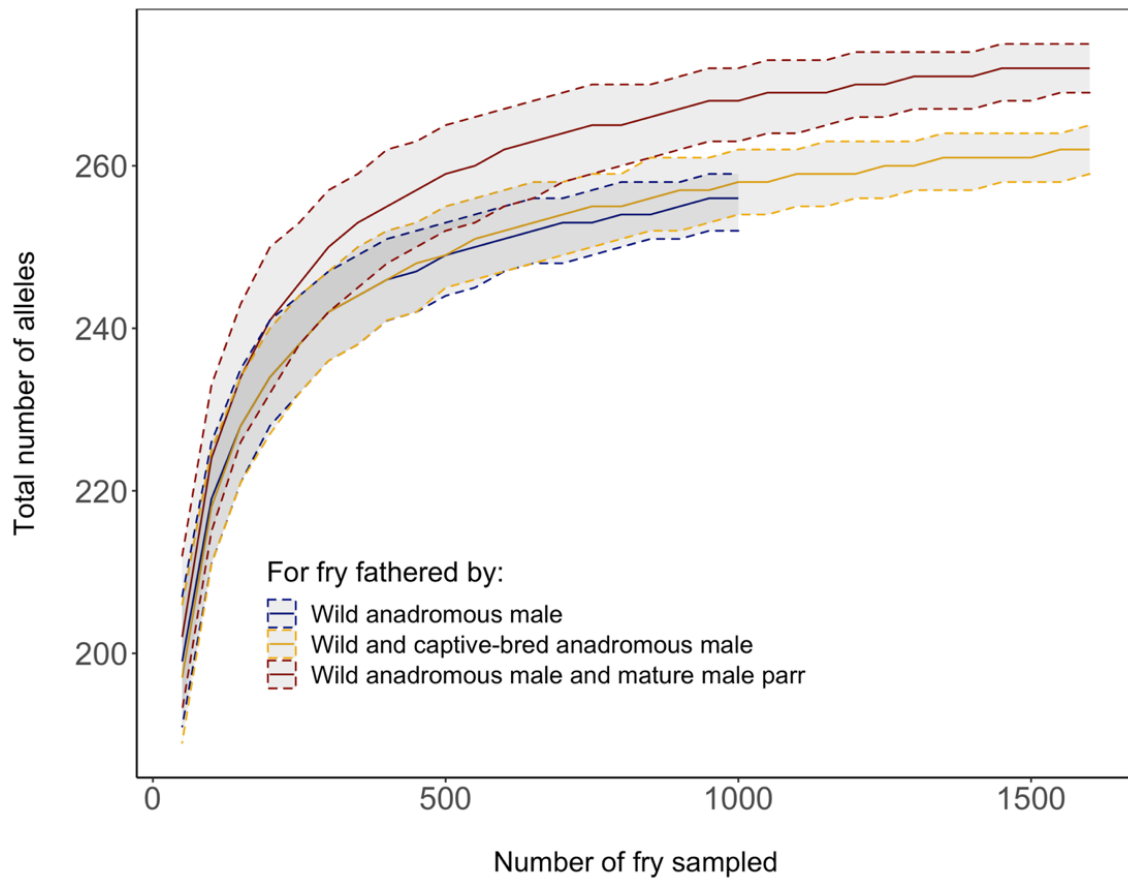
1344

1345

1346

1347

1348



1349

1350

1351

1352

1353

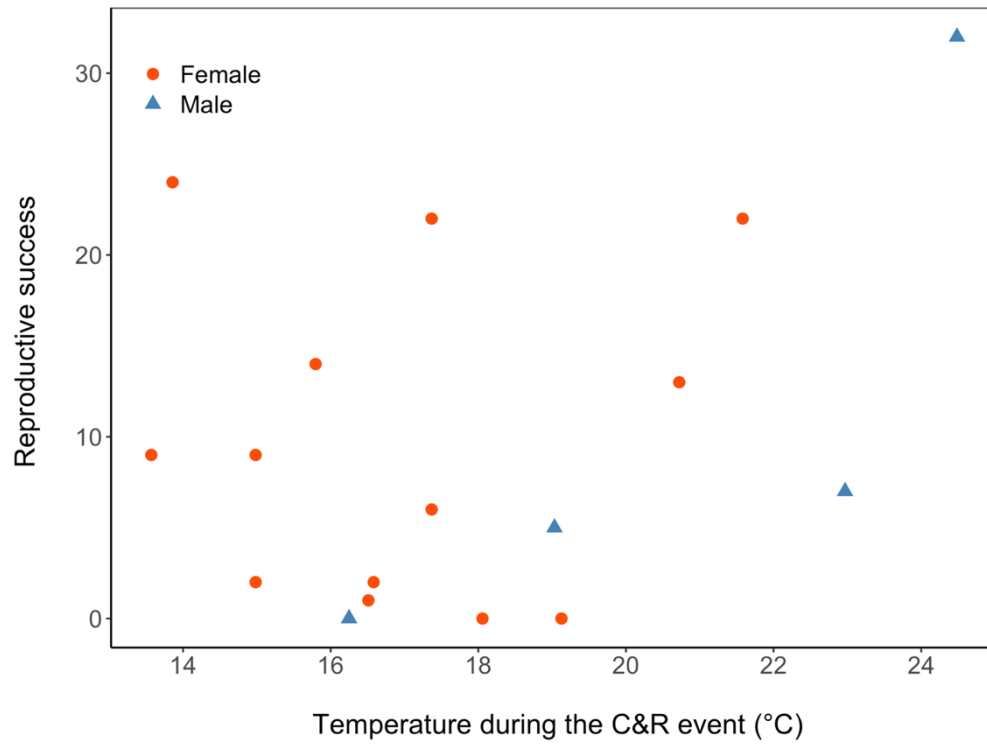
1354

1355

1356

1357

1358



1359