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Reduced fitness of Atlantic salmon released in the wild after one generation of captive breeding

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Abstract

Salmonids rank among the most socioeconomically valuable fishes and the most targeted species by stocking with hatchery-reared individuals. Here, we used molecular parentage analysis to assess the reproductive success of wild- and hatchery-born Atlantic salmon over three consecutive years in a small river in Québec. Yearly restocking in this river follows a single generation of captive breeding. Among the adults returning to the river to spawn, between 11% and 41% each year were born in hatchery. Their relative reproductive success (RRS) was nearly half that of wild-born fish (0.55). RRS varied with life stage, being 0.71 for fish released at the fry stage and 0.42 for fish released as smolt. The lower reproductive success of salmon released as smolt was partly mediated by the modification of the proportion of single-sea-winter/multi-sea-winter fish. Overall, our results suggest that modifications in survival and growth rates alter the life-history strategies of these fish at the cost of their reproductive success. Our results underline the potential fitness decrease, warn on long-term evolutionary consequences for the population of repeated stocking and support the adoption of more natural rearing conditions for captive juveniles and their release at a younger stage, such as unfed fry.

Introduction

Supplementation of wild populations with captive-bred individuals is a common practice, particularly so in salmonid species. However, such practices have been widely criticized for both their low efficiency in preventing wild population declines and their potential contribution to fitness reduction (Aprahamian et al. 2003; Araki et al. 2008; Fraser 2008; McClure et al. 2008). Even though captive breeding practices have been improved, for example, through the release of young individuals (i.e., fry or smolt) produced using yearly caught local wild breeders, to minimize domestication and loss of local adaptation, significant fitness decrease in hatchery-reared relative to wild fish persists (Araki et al. 2007b, 2009; Thériault et al. 2011; Anderson et al. 2012; Christie et al. 2012). The achievement of successful management and conservation practices thus requires documenting the fate of hatchery-reared individuals released in the wild.

Different selection regimes in hatcheries than in the wild may result in relatively low reproductive success of hatchery-reared fish released in the wild (Fleming and Eimers 1997; McGinnity et al. 2003; Araki et al. 2007b, 2009; Hutchings and Fraser 2008; McLean et al. 2008; Thériault et al. 2010, 2011). First, nonrandom sampling or artificial breeding can cause unintentional selection on particular traits. Second, the disruption of natural mate choice and hence of sexual selection mechanisms may have important genetic implications for the next generation (Wedekind 2002; Neff et al. 2008; Anderson et al. 2012). Third, mortality patterns and hence viability selection during life in the hatchery may differ from the wild (Ford 2002; Mignon-Grasteau et al. 2005; Frankham 2008). Therefore, selection may decrease the fitness of hatchery-reared fish once they are released in the wild (Araki et al. 2007b; Thériault et al. 2011). Moreover, Christie et al. (2012) showed that the lifetime reproductive success of first-generation hatchery steelhead was twice higher than that of wild-born fish bred in hatchery, which was a clear demonstration of adaptation to captivity. Ultimately, heritable traits selected in the hatchery that are disadvantageous in nature may have long-lasting evolutionary impacts on the fitness of
Captive rearing can also induce plastic phenotypic responses that may result in environmental carryover effects on their life-history traits once released in the wild. Carryover effects have been defined as the nonlethal influence on individual performance of a previous (environmental) event in its life (Harrison et al. 2011). Hatchery and wild environments differ by many aspects including fish density, spatial and temporal heterogeneity of physical environment, intra- and interspecific interactions, and food availability that may lead to plastic phenotypic divergence among wild and captive fish, including growth rate, morphology, and behavior (Metcalfe et al. 2003; Kostow 2004; Blanchet et al. 2008; Hawkins et al. 2008). For instance, hatchery-reared salmonids fed *ad libitum* generally have higher growth rates than wild conspecifics (McDonald et al. 1998; Berejikian et al. 2000). Such modifications may later affect the life history of stocked salmonids, notably a reduction in their average number of winters at sea compared with wild-born fish (Kostow 2004; Jonsson and Jonsson 2006; Kallio-Nyberg et al. 2011; but see McGinnity et al. 2003). Ultimately, their reproductive success in the wild may be affected (Weir et al. 2005; Theriault et al. 2010, 2011) partly because spawner body size is affected by time spent at sea and correlates with fecundity (Fleming 1996). Theriault et al. (2011) notably showed that the reproductive success of coho salmon (*Oncorhynchus kisutch*) released as fry was similar to that of wild fish, whereas salmon released as smolts performed worse, suggesting important carryover effects of hatchery environment on the reproductive success of smolt-stocked fish. The wild progeny of such stocked individuals may moreover also experience a reduced reproductive success originating from genetic carryover effects (Araki et al. 2009). Introgressive hybridization could thus magnify these effects and result in negative evolutionary change on wild populations.

Atlantic salmon (*Salmo salar*) is one of the most socioeconomically important fish species, through recreational fishing, fisheries, and aquaculture. Over the last decades, wild Atlantic salmon populations have been widely impacted by various anthropogenic pressures, resulting in the common use of supportive breeding to compensate decreasing recruitment (Aprahamian et al. 2003; Jonsson and Jonsson 2009). Here, we studied a small anadromous Atlantic salmon population spawning in the Malbaie River, Québec, which has been subjected for 20 years to a supportive breeding program releasing fry and smolt fish produced using local adults yearly caught in the river. We used molecular parentage analyses to quantify and compare the reproductive success in the wild of wild-born and of fry and smolt-stocked hatchery-born Atlantic salmon. We thus tested three hypotheses: (i) hatchery-reared individuals will have a lower reproductive success relative to wild-born fish because of detrimental selective and carryover effects of the hatchery environment, (ii) fish stocked as fry will have a higher reproductive success than those stocked 1 year later as smolt, as a result of stronger selective and environmental carryover effects in the latter, and (iii) smolt-stocked salmon returning to spawn will differ from wild and fry-stocked fish in their proportion of multi-sea-winter fish (MSW) as an effect of longer time spent in hatchery on their subsequent life history. We then discuss the potential role of mechanisms such as selection and environmental carryover effects of a single generation of captive breeding in causing the observed fitness reduction in hatchery-born salmon released in the wild and the implications for stocking practices.

### Materials and methods

#### Study site

The Malbaie River is located on the North shore of the St. Lawrence estuary, Québec, Canada (47°67′N; 70°16′W), and harbors a small anadromous spawning population of Atlantic salmon. On average, 283 adult spawners annually returned to the river from 1997 to 2004 (Table S1), a number reaching only 20% of the appropriate conservation threshold for this population (Minister of Natural Resources and Wildlife, Québec). A dam acting as a complete barrier to upstream migration is located eight kilometers upstream to the river mouth. During the upstream migration from the St. Lawrence to the Malbaie River, adult fish are trapped in a cage and transported just above the dam to be released upstream. Spawning grounds and suitable habitats for Atlantic salmon juveniles extend over a stretch starting from the dam and ending 35 km upstream.

#### Supportive breeding

Supportive breeding began in 1992 when a number of returning adults were first caught at the dam and transferred to the provincial hatchery at Tadoussac, located approximately 60 km downstream of the Malbaie River estuary along the St. Lawrence River. The pool of breeders coming from the wild has been maintained at almost 20 individuals, about half of them being renewed each year by adding new breeders caught at the dam. No fish born in the hatchery was kept all its life in captivity and used as a captive breeder. However, there is a possibility that some returning adult trapped at the dam and brought to the hatchery each year to maintain the pool of breeders were themselves hatchery-born fish that had been released as fry or smolt in the Malbaie River during supportive breeding efforts. Breeders were mated in captivity and the progeny reared in indoor tanks at density of about 500 fish/m³ until being stocked either as fry or smolt, respectively, after four years.
and fifteen months following hatching. From 1992 to 2002, a total of 133 579 eggs, 890 489 fry and 323 923 smolts have been stocked on the spawning grounds of the Malbaie River (Table S1).

Sampling

Scale and fin samples were taken on all anadromous adults returning to the river between 2002 and 2004, as well as on all breeders at the Tadoussac hatchery. The sex of 69% of returning to the river between 2002 and 2004, as well as on all breeders at the Tadoussac hatchery. The sex of 69% of the fish was determined with some confidence using secondary sexual characters when possible (Maise and Bagliniere 1986). Age, that is, number of years in river, and secondary sexual characters when possible (Maise and Bagliniere 1986). Age, that is, number of years in river + number of years at sea, was determined from scale growth patterns (Lund and Hansel 1991; Stokesbury and Lacroix 1997). Scale growth patterns also allowed identifying returning adults that were born in hatchery and released at the smolt stage (Auclair E., Bernatchez L., Dodson J.J., unpublished data). During the summers of 2003, 2004, and 2005 and before the stocking of hatchery-born fry each year, fry born in the river were randomly sampled using electrofishing over a stretch starting from the dam and ending 35 km upstream. All 136 breeders present at the Tadoussac hatchery from 2000 to 2002, all of the 876 returning adults that were caught in 2002, 2003, and 2004, and 1141 fry caught in 2003, 2004, and 2005 were genotyped (Table 1).

Molecular analyses

DNA was extracted from fin tissue using the salt extraction method described by Aljanabi and Martinez (1997) and amplified by PCR at eight microsatellite loci: SsaD71, SsaD144, SsaD85, SsaD170 (King et al. 2005), Ssa197 (Oreilly et al. 1996), Sso417 (Slettan et al. 1995), Sspp2201 and Sspp2213 (Paterson et al. 2004). PCR products were run on an ABI 3100 automated capillary sequencer (Applied Biosystems). Allelic sizes were scored using GENOTYPER™ v.3.7NT software (Applied Biosystems, Foster City, CA, USA).

Table 1. Details of the genotyped adult and juveniles Atlantic salmon. The samples include the 876 returning adults caught at the Malbaie River dam from summer 2002 to 2004 and the juveniles caught on the Malbaie R. spawning grounds during spring 2003 to 2005.

| Number of individuals per spawning year | 2002 | 2003 | 2004 | Total |
|-----------------------------------------|------|------|------|-------|
| Adults transported above dam            | 153  | 324  | 399  | 876   |
| Adults used for assignments*            | 136  | 287  | 362  | 785   |
| Adults with known origin                | 135  | 253  | 348  | 736   |
| Born in the river (wild origin)         | 120  | 167  | 206  | 493   |
| Born in the Tadoussac hatchery          | 15   | 86   | 142  | 243   |
| Stocked at the smolt stage              | 14   | 70   | 51   | 135   |
| Stocked at the fry stage                | 1    | 16   | 91   | 108   |
| Returning as SSW                        | 108  | 204  | 204  | 516   |
| Returning as MSW                        | 28   | 73   | 154  | 255   |
| Fry assigned                            | 226  | 421  | 494  | 1141  |

*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 (see text).
2005). It is important to mention that the error rate entered in PASOS does not affect the allocation of real offspring, but only affects the simulations. Thus, assuming a (too) high error rate is conservative in the sense that it will lead to an underestimation of the expected rate of correct allocation.

Adults with incomplete genotypes were discarded from the analyses because PASOS requires complete genotypes. The number of missing parents for each year (potentially mature parrs and adults with incomplete genotypes) as estimated from cumulative allocation was entered in the simulations. A thousand ‘pseudo-offspring’ were generated from virtual parents created by resampling with replacement of alleles based on empirical frequencies. Ten iterations were performed for each year separately, and the average of correct assignments was used as a point estimate of correctness rate.

Origin of spawners

To estimate the genetic contribution of stocked salmon to the reproductive output in the Malbaie River, we first classified returning adults from the 2002, 2003, and 2004 spawning runs according to their origin (wild born or hatchery born). Smolt-stocked fish were not adipose fin clipped, but the growth pattern of scales easily allows identifying hatchery-born adults that had been released in the river at the smolt stage (Lund and Hansel 1991; Stokesbury and Lacroix 1997). Identification of fish released at the fry stage was performed by parental allocation with PASOS following the procedure described previously and using the returning adults as offspring to be assigned. For these fish, only the pool of captive breeders from Tadoussac was included as potential parents. We did not estimate the correct allocation rate by simulation as we did for fry because the parents of wild-born returning adults were necessarily unknown. Hence, we could not simulate pseudo-offspring from these unknown parents. Consequently, performing simulations only based on Tadoussac genotypes was not warranted because it would not provide any estimate of correctness for wild-born returning adult neither an estimate of misallocations for hatchery-born spawners. We thus used the following criteria to filter allocations. An adult was considered as stocked from the hatchery at the fry stage if (i) the scale growth pattern did not identify it as released at the smolt stage, (ii) if it was allocated to two Tadoussac (hatchery) parents, and (iii) it had at most one incompatible allele with the identified parents.

The genotypes for the breeders in hatchery were known only for those individuals present at Tadoussac from 2000 onwards. Therefore, adults of hatchery origin returning to spawn in the Malbaie River in 2002 were more likely to remain unallocated than those from 2003 because the former had a higher probability to have been born before 2000, that is, from Tadoussac parents not included in this study. This was also the case for 2003 relative to 2004 spawners. Consequently, it was expected that an increasing proportion of returning adults would be successfully identified as being stocked as fry with increasing year, and this was considered in all subsequent result interpretations.

Analysis of reproductive success

We used the number of fry caught in the river allocated to a given spawner as a proxy for its reproductive success (RS) in the wild. Although this measure is partial (i.e., not all offspring of a spawner were collected), it allowed estimating the success of hatchery-born fish relative to that of wild-born fish (RRS) by computing the ratio in RS of the former over the latter. Confidence intervals around the RRS of stocked fish for the 3 years pooled were estimated by bootstrapping. As the proportion of repeat spawners is low in Atlantic salmon (e.g., <10%; Fleming and Reynolds 2004) and as there was to our knowledge no study reporting any difference in iteroparity rate between wild-born and hatchery-born fish, the RRS in a given year was considered as proxy for the lifetime RRS.

To further disentangle the factors affecting reproductive success, we used generalized linear models (GLMs) to test for the effect of origin/stocking stage (STOCKSTAGE, with possible values ‘wild’, ‘fry’, and ‘smolt’), sex, and number of winters spent at sea (SEAWINTER, with possible values ‘SSW’ and ‘MSW’ corresponding respectively to only one or several (mainly two) winters at sea). We also controlled for among-year variability in fry sampling effort by including year as a fixed factor. As reproductive success is a count of offspring, the GLMs assumed a Poisson distribution (i.e., we used a log link function). Models were fit using the GLM function in R Development Core Team (2012). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org/. We first ran a general model (Model 1) with first-order interactions among SEAWINTER, STOCKSTAGE and SEX. We then fitted two reduced models: a simple additive model (model 2) (i.e., without interactions) including the four variables and a model (model 3) in which we removed sex because its determination by external morphology may not be totally reliable and the sex was in fact uncertain for a number of individuals (Table 1). Models fit to the data were compared by chi-square analysis of deviance.

Results

Parental allocation

In 2002, 2003, and 2004, a total of 153, 324, and 399 returning anadromous adults were transported above the
Two studies were conducted to assess the lower reproductive success of hatchery-reared fish compared to wild-born fish. The first study involved the assignment of hatchery-originated offspring to their parents using genotyping methods. The researchers found that the reproductive success of hatchery-reared fish was significantly lower than that of wild-born fish, indicating a potential bias favoring wild-born parents. The study also showed that the assignment of offspring to their parents was more accurate for wild-born fish than for hatchery-reared fish, suggesting that the different environments and selection pressures between the two groups could contribute to these differences.

The second study focused on the reproductive success of individual fish. It was found that the reproductive output of hatchery-reared fish was significantly lower than that of wild-born fish, which could be due to various factors including environmental differences and selection pressures. The study concluded that the lower reproductive success of hatchery-reared fish is likely due to the different evolutionary histories and selective pressures experienced by individuals from these two environments.
success of 1.28 (Table 2, Figure S1). For wild-born fish, from 0 to 34 fry were assigned per individual, for an average reproductive success of 2.34. Thus, the overall RRS of hatchery-reared fish was 0.55 (CI: 0.35–0.82) when all individuals were pooled. The weighted geometric mean of hatchery-reared fish RRS for the 3 years was 0.53. While the RRS of hatchery-reared fish increased from 2002 to 2004, it remained far below 1 for all years: 0.30 in 2002, 0.45 in 2003, and 0.64 in 2004 (Table 2). Overall, the RRS of fish released as smolt was 0.42 (CI: 0.20–0.74), which was lower than that of fish released as fry, 0.71 (CI: 0.42–1.22) (Table 2). Individual reproductive success of females was about twice higher than that of males for both wild- and hatchery-born fish (Table 2). Also, the reproductive success of SSW individuals was much lower than the RS of MSW individuals, both for wild-born (1.14 vs 4.25, respectively) and hatchery-born fish (0.87 vs 2.77, respectively). The RRS of hatchery-born fish was of 0.76 (CI: 0.48–1.18) for SSW (i.e., when compared with SSW wild-born fish), which was slightly higher than that of MSW fish, namely 0.65 (CI: 0.28–1.19) when compared with MSW wild-born fish. Considering adults returning in 2004, the RRS of hatchery-born fish was on average 0.64, that is, 0.34 for smolt-stocked fish and 0.80 for fry-stocked fish.

Generalized linear models (GLMs) results are reported in Table 3, and the RS values predicted by the best model for the different groups of fish are shown in Fig. 1. The best model was the general model (1) including the four variables and interactions among seawinter, stockstage, and sex. A purely additive model (2) or the model with sex removed (3) did not fit the data as well (Table 3). In all models, spawning year had a significant effect on reproductive success, reflecting the among-year variation in sampling effort/success. The factor having the most marked effect on reproductive success in all models was seawinter, with SSW salmon performing less than MSW salmon. Importantly, the differences between hatchery-reared and wild-born fish were relatively small within groups defined by sex and seawinter.

**Table 2. Reproductive success (RS) of Atlantic salmon spawning in the Malbaie River as estimated from parental allocation using PASOS based on microsatellites markers. relative reproductive success (RRS) is the reproductive success of hatchery-reared fish relative to that of wild-born fish belonging to the same category (e.g., SSW, female and fry stocked). A dash indicates that no fish among those sampled entered in a particular category, while ‘n.a.’ means ‘not applicable’. For the RRS of fish for all years pooled, we report the 95% confidence intervals estimated by bootstrapping 10,000 times.**

| Origin | Measurement Year | Time at sea | Sex | Stage stocked | Total |
|--------|-----------------|-------------|-----|----------------|-------|
|        |                 | SSW        | MSW | FEMALE         | MALE  |
| Wild   | 2002            | 1.28       | 5.69| 3.82           | 2.23  | 1.66      | n.a. | n.a. | 2.13 |
|        | 2003            | 1.12       | 5.08| 4.41           | 4.48  | 1.54      | n.a. | n.a. | 2.58 |
|        | 2004            | 1.02       | 3.41| 2.26           | 2.2   | 1.42      | n.a. | n.a. | 2.26 |
|        | All years       | 1.14       | 4.25| 3.49           | 3     | 1.53      | n.a. | n.a. | 2.34 |
| Hatchery | 2002         | 0.71       | –   | –              | 0.8   | 0.67      | –    | 0.67 | 0.63 |
|        | 2003            | 0.81       | 7.2 | 4.63           | 0.81  | 0.83      | 1    | 1.19 | 1.15 |
|        | 2004            | 0.94       | 2.43| 1.3            | 1.93  | 1.11      | 1.81 | 0.77 | 1.44 |
|        | All years       | 0.87       | 2.77| 2.1            | 1.61  | 0.95      | 1.66 | 0.98 | 1.28 |
| Hatchery | RRS*         | 0.56       | –   | –              | 0.36  | 0.4       | –    | 0.31 | 0.3  |
|        | 2003            | 0.72       | 1.42| 1.05           | 0.18  | 0.54      | 0.39 | 0.46 | 0.45 |
|        | 2004            | 0.92       | 0.71| 0.58           | 0.88  | 0.78      | 0.8  | 0.34 | 0.64 |
|        | All years       | 0.76       | 0.65| 0.6            | 0.54  | 0.62      | 0.71 | 0.42 | 0.55 |

*The RRS of fry- and smolt-stocked fish is relative to all categories of wild-born fish.
Table 3. Effects of spawning year, time spent at sea (SEAWINTER), stage at stocking (STOCKSTAGE), and sex on the reproductive success (RS) of adult Atlantic salmon returning in the Malbaie River to spawn between 2002 and 2004. RS was obtained from parental allocation analysis based on microsatellites and modeled as a Poisson distribution. The middle part shows a model comparison based on a chi-square analysis of deviance. The lower part of the table reports partial regression coefficients (±SE) for each factor tested by fitting generalized linear models (GLMs) to salmon data (n = 539 adults). Coefficients were fitted relative to 2002 MSW female fish stocked as fry. A ‘×’ denotes a second-order interaction term.

| Model description | Model 1 | Model 2 | Model 3 |
|-------------------|---------|---------|---------|
| Deviance          | 1980.69 | 2009.9  | 1995.47 |
| df                | 527     | 532     | 531     |
| P                 | n.a.    | <0.001  | <0.001  |
| YEAR: 2003        | -0.18 (0.09) | -0.13 (0.09) | -0.17 (0.09) |
| YEAR: 2004        | -0.66 (0.10) *** | -0.65 (0.10) *** | -0.66 (0.10) *** |
| SEAWINTER: SSW    | -1.06 (0.32) *** | -1.24 (0.08) *** | -0.69 (0.19) *** |
| STOCKSTAGE: SMOLT | 0.69 (0.27) *    | -0.48 (0.15) ** | 0.34 (0.23) |
| STOCKSTAGE: WILD  | 0.52 (0.21) *    | -0.09 (0.11)     | 0.26 (0.16) |
| SEX: MALE         | 0.36 (0.29)      | -0.20 (0.08) **  | n.a.    |
| SSW × SMOLT       | -0.69 (0.38)     | n.a.              | -1.33 (0.29) *** |
| SSW × WILD        | -0.34 (0.27)     | n.a.              | -0.68 (0.21) ** |
| SSW × MALE        | 0.17 (0.21)      | n.a.              | n.a.    |
| SMOLT × MALE      | -1.05 (0.41) *   | n.a.              | n.a.    |
| WILD × MALE       | -0.62 (0.30) *   | n.a.              | n.a.    |

n.a., not applicable.

*0.05 > P > 0.01; **0.01 > P > 0.001; ***P < 0.001.

†Second-order interactions are included for variables in brackets. For instance, model 1 expands to YEAR + SEAWINTER + STOCKSTAGE + SEX + SEAWINTER + STOCKSTAGE + SEX + STOCKSTAGE × SEX.

Figure 1 Average number of fry assigned per adult fish as predicted from a generalized linear model (GLM) (our model 1) fitted to salmon data. Predicted values are for the 2004 spawning run, that is, the year when the proportion of adults born in hatchery is best estimated (see text). Values are shown separately for males and females returning after a single year (SSW; black bars) or multiple years (MSW; gray bars) at sea and, within each of these two groups, for wild-born fish, fry-stocked fish, and smolt-stocked fish.
When considering spawning years separately, the difference was significant for 2003 (37.1% among wild-born fish, 5.3% among hatchery-reared ones, $\chi^2 = 32.2, P < 0.001$) and 2004 (51.8% among wild-born fish, 33.6% among hatchery-reared ones, $\chi^2 = 11.8, P < 0.001$). The percentage of MSW was similar for both groups in 2002 (19% of wild born, 13% of hatchery, $\chi^2 = 0.4, P = 0.51$), that is the year when the representation of hatchery fish was likely the most underestimated. Among SSW fish, those stocked as fry had a higher RRS than fish stocked as smolt (respectively, 1.11 and 0.54), while we observed the inverse pattern for MSW fish (respectively, 0.58 and 0.81).

**Discussion**

In this study, we used molecular parental assignment to infer the reproductive success of hatchery-born anadromous Atlantic salmon released in the Malbaie River in Québec after a single generation in captivity and returning to spawn after their journey at sea. Over three consecutive spawning years, these fish had a significantly lower RS than wild-born salmon, a reduction in a large part attributable (38.5%). When considering spawning years separately, the difference was significant for 2003 (37.1% among wild-born fish, 5.3% among hatchery-reared ones, $\chi^2 = 32.2, P < 0.001$) and 2004 (51.8% among wild-born fish, 33.6% among hatchery-reared ones, $\chi^2 = 11.8, P < 0.001$). The percentage of MSW was similar for both groups in 2002 (19% of wild born, 13% of hatchery, $\chi^2 = 0.4, P = 0.51$), that is the year when the representation of hatchery fish was likely the most underestimated. Among SSW fish, those stocked as fry had a higher RRS than fish stocked as smolt (respectively, 1.11 and 0.54), while we observed the inverse pattern for MSW fish (respectively, 0.58 and 0.81).
to the modification of their life history. Specifically captive-bred salmon returned in a greater proportion than wild-born salmon after a single winter at sea and single-sea-winter had a lower RS than multi-sea-winter fish. However, the drop in RS was lower for fry-stocked than for smolt-stocked fish, suggesting a greater negative impact of the early life in hatchery on the later.

Reduced reproductive success of hatchery-reared Atlantic salmon in the wild

The lower reproductive success of captive-bred Atlantic salmon in natura relative to that of their wild-born conspecifics corroborates the results obtained for steelhead (*Oncorhynchus mykiss*) (Araki et al. 2007b), chinook salmon (Williamson et al. 2010), and coho salmon (*O. kisutch*) (Thériault et al. 2011). Therefore, for these four salmonids species, a single generation of hatchery rearing of local fish was sufficient to decrease the RS of individuals released in the wild. Other studies also showed that domestic Atlantic salmon escaped from commercial farms had a reduced RS in the wild (Fleming et al. 2000; McGinnity et al. 2003). Here, we uncovered RRS for stocked fish (0.55) similar to values reported by Araki et al. (2007b) for steelhead (0.55) and Thériault et al. (2011) for coho salmon (RRS ranging from 0.56 to 1.11). This level of RRS is, however, higher than that for escaped domestic Atlantic salmon (0.24 for females and 0.32 for males; Fleming et al. 2000), which are likely more exposed to selection and environmental carryover effects of captive life than stocks from local genetic origin used in supportive breeding programs, especially when the latter involve a single generation in captivity (Araki et al. 2008).

Sex ratio and reproductive success

Our results showed a higher RS for females than for males, but a similar decrease in RRS for hatchery-reared males and females. It is consistent with the fact that the sex ratio of spawning Atlantic salmon is usually male biased, with several males competing for the fertilization of the eggs from each female (Fleming 1996, 1998; Fleming and Reynolds 2004). Accordingly, we found a male-biased sex ratio among anadromous returning adults, with males representing on average from 55% to 86% of the individuals (the uncertainty originating from the fact that the sex of 31% of fish was not confidently determined). Moreover, several studies reported that variable proportions of eggs could be fertilized by early maturing freshwater male parr (Bohlin et al. 1986; Martinez et al. 2000; Garant et al. 2003; Weir et al. 2005; Saura et al. 2008), which could increase the bias in sex ratio among breeders and the male–male competition and further decrease the reproductive success of anadromous males. The fact that we did not find a noticeable difference between the RRS of hatchery-reared males and females suggests that captive breeding may affect males and females to a similar degree, as found by Araki et al. (2007b) but in contrast with Fleming et al. (2000), Williamson et al. (2010), and Thériault et al. (2011).

Proportion of single- and multi-sea-winter fish and reproductive success in smolt-stocked fish

Our study underscores that the differences in reproductive success between wild-born and captive-bred salmon were mostly driven by the larger proportion of smolt-stocked returning as SSW and, to a lesser extent, by the poorer performance of captive-bred fish within each migratory class. Given that MSW are typically larger than SSW, this is in line with studies showing that salmon breeding success is positively correlated with body size and thus the number of winters at sea (Fleming 1996). The higher proportion of SSW among smolt-stocked fish than among fry-stocked or wild-born fish may originate from a higher growth rate of juveniles in hatchery than in the wild and be responsible for plastic modification of migration tactics (Naevdal et al. 1978; Kallio-Nyberg and Koljonen 1997; Jonsson and Jonsson 2006; Ford et al. 2012). On the other hand, an increasing number of studies have reported a reduced survival of stocked fish (Ford and Myers 2008 and Araki and Schmid 2010) that could result in a decrease in the proportion of MSW fish. In the Malbaie River, estimates of the abundance and origin of smolt migrating to sea in 2002 and the abundance and origin of adult salmon entering the River 1 year later revealed that the return rate of salmon stocked as smolt (0.36%) was 6–7 times lower than that of naturally produced smolt (2.4%) (Auclair et al., unpublished data). Furthermore, the marine growth of SSW salmon derived from stocked smolt was significantly less than that of SSW salmon derived from naturally produced smolt (Auclair et al., unpublished data). Other studies have shown that stocked salmon tend to spend fewer winters at sea than wild-born salmon as a potential result of either carryover effects of the hatchery environment or selection (Kostow 2004; Jonsson and Jonsson 2006; Kallio-Nyberg et al. 2011; but see McGinnity et al. 2003). As time spent at sea correlates with body size, which in turn correlates with reproductive success, the reduction in time at sea appears to play an important role in reducing the fitness of the fish stocked in the Malbaie River.

Life-history trade-offs and relative reproductive success (RRS) in hatchery-born fish

Trade-offs between the time spent growing at sea, survival, and fecundity could be involved in the RRS pattern...
observed in particular for smolt-stocked fish. Growth rate and body size are heritable traits in salmon (e.g., Riddell et al. 1981), and a genetic correlation was uncovered between sexual maturation and anadromous migration in Atlantic salmon (Paez et al. 2011). Consequently, a lower survival of smolt-stocked fish may favor a SSW strategy at the cost of a lower fecundity.

Alternatively, a greater growth rate of juveniles in hatchery than in the wild could result in a plastic response in migration tactics (Naevdal et al. 1978; Kallio-Nyberg and Koljonen 1997; Jonsson and Jonsson 2006). This also agrees with life-history theory predicting a negative correlation between growth rate and age at maturity (Stearns and Koella 1986). A study by Jokikokko et al. (2006) suggest a reduced survival of smolt-stocked Atlantic salmon, which likely affects the optimal age of maturation and migration in view of life-history trade-offs discussed previously. The survival of smolt could be reduced by a poor timing of release (Chittenden et al. 2010). Carryover effects of an environmentally impoverished hatchery environment may modify phenotypes and consequently the fitness of wild populations by affecting risk-taking behavior (Roberts et al. 2011), feeding capability (Rodewald et al. 2011), or through negative interactions among wild-born and stocked fish (e.g., competitive or aggressive behavior) (Fleming et al. 2000; Jonsson and Jonsson 2006, 2009). Importantly, Blanchet et al. (2008) found that juvenile born in hatchery and stocked in the Malbaie River were more aggressive and responded differently from their wild counterparts to competition.

Reproductive success in fry-stocked salmon

The lower reproductive success of fry-stocked fish in spite of proportions of SSW/MSW similar to those in wild-born fish could originate from a modified selective regime in captivity. Viability selection can occur during early life feeding (Elliott 1989). If early mortality is lower in the hatchery, then this might also relax selection on genes involved in fecundity. Moreover, limited sexual selection in hatchery may have a similar effect on fry-stocked fish (Wedekind 2002; Neff et al. 2008).

Limitations of the study

While only 10.4% of the parental anadromous genotypes were incomplete and thus not used in PASOS parental assignments, between 25% and 30% of parent-fry dyads involved uncollected parents, in other words offspring assigned either to one collected + one uncollected parent (37–42% depending of the year) or to two uncollected parents (3–11%). This result may be consistent with a non-negligible participation of precocious parr to reproduction. Indeed, these males can represent a large proportion (up to 60%) of the male breeders in Atlantic salmon populations (Hutchings and Jones 1998). Here, the number of missing parents might have been slightly over-estimated in our simulations. In PASOS cumulative allocation procedure, the estimation of the number of missing parents decreases as loci are added to the analysis, until it levels off to a lower bound that should be the correct estimation. Thus, we cannot exclude that adding one or two loci would have lead to slightly lower estimations of missing parents. In addition, PASOS does not allow genotyping error models with more than two offsets. Such errors (e.g., larger allele dropout) will typically cause allocations to an uncollected parent, and there is no reason why they should be more frequent in one group of spawners (wild or stocked) than the other. Consequently, these errors will mostly result in a loss of power (increased allocations to uncollected parents).

A source of uncertainty that could affect our conclusions is the proportion of fry-stocked spawners estimated for each year. As explained previously, this proportion is likely less underestimated from 2002 to 2004. Nevertheless, the performance of the captive-bred fish is lower than that of wild-born parents for the 3 years. Another source of uncertainty is around the assumption that wild-born spawners had themselves wild parents. Actually, some of their parents (hence grandparents of the fry that we sampled) could have been stocked in the Malbaie River in the 1990s. Consequently, the baseline comparison may not be purely with wild fish, thus leading to an overestimation of the RRS of stocked fish. However, we do not consider this as a major issue in the current context because our main objective was to specifically focus on the effect of captive breeding over one generation and because any additional effect owing to the captivity of some ancestors of wild-born spawners will likely introduce noise and thus reducing the apparent difference between wild and captive-bred fish.

Evolutionary and practical consequences of supporting breeding on wild populations

The use of supportive breeding programs is widespread but nonetheless controversial (Aprahamian et al. 2003; Araki and Schmid 2010). For instance, a recent study on steelhead demonstrates that only one generation in captivity can result in a substantial response to selection on traits that are beneficial in captivity but maladaptive in the wild (Christie et al. 2012). Our results raise several issues regarding the conservation of wild salmonid populations.

First, as a large part of the performance reduction in stocked salmon appears to originate either from carryover effects or from selection during hatchery life on smolt-stocked fish, this study supports previous recommendations to limit the time spent by individuals in captivity.
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(Frankham 2008; Fraser 2008; Williams and Hoffman 2009; Araki and Schmid 2010). To this end, it is noteworthy that the provincial authority in charge of managing Atlantic salmon in Québec (Ministère des Ressources Naturelles et de la Faune) has recently abandoned stocking salmon at the smolt stage and continue to release salmon at fry stage. However, selection and carryover effects could still occur at younger life stage, affecting fry-stocked fish performances in the wild. In that matter, our study also supports propositions in favor of more natural rearing conditions for captive juveniles (Blanchet et al. 2008; Kallio-Nyberg et al. 2011; Rodewald et al. 2011) or for their release at a younger age, such as unfed fry (Metcalfe et al. 2003; Thériault et al. 2011). Shortening the life in hatchery may furthermore increase the survival of stocked fish (Rideout and Stolte 1988; but see Thériault et al. 2010) but may also limit the cost of such operations.

Second, it is recognized that maintaining a relatively small number of native captive breeders may on the long term result in a decrease in the effective population size and genetic diversity of the stocked population (Wang and Ryman 2001; Hansen et al. 2000; Blanchet et al. 2008; but see Gow et al. 2011). Although heterozygosity in hatchery-born spawners was not lower than that in wild-born Atlantic salmon population from the Malbaie River, without examining older samples (prior to 1990), we cannot totally exclude that long-term stocking has reduced the genetic diversity in the river, as shown in coho salmon Eldridge et al. (2009). Besides, the relatively low returns of smolt-stocked fish in the Malbaie River may not only reflect a high mortality but also dispersal in other wild populations (Jonsson et al. 2003), which would modify the local genetic makeup elsewhere (Perrier et al. 2011).

Third, supportive breeding can have a cumulative negative effect on the reproductive success of spawners via introgressive hybridization of hatchery and wild stocks (Fleming et al. 2000; McGinnity et al. 2003; Araki et al. 2007a, 2009; Roberge et al. 2008). As already mentioned, this may have led to an overestimation of the RRS of stocked fish. Such introgressive hybridization could moreover explain why the population has still not recovered to its suitable conservation size (estimated to approximately 1400 adult spawners). Since the beginning of supportive breeding program in the Malbaie River, the increase in the total number of breeders has been modest in previous years (on average 279 spawning adults between 1997 and 2007; data available at http://www.mrn.gouv.qc.ca/publications/faune/bilan-saumon-2011.pdf), although it has increased in more recent years (on average 818 individuals between 2008 and 2011). Overall, this study suggests that the potential negative evolutionary consequences of repetitive supportive breeding on the managed population should be carefully considered before applying this management strategy as a long-term viable option.

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Data archiving statement

Raw data for this study are available in Dryad: doi:10.5061/dryad.4k739.

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**Supporting Information**

Additional Supporting Information may be found in the online version of this article:

**Figure S1.** Histogram of the number of wild-born progeny assigned per adult individual caught at the dam.

**Table S1.** Number of fish annually stocked within the Malbaie R. (at the egg, fry and smolt stages); spawning run and conservation threshold reached (estimated by the Minister of Natural Resources and Wildlife, Québec) = non available.

**Appendix S1.** We conducted additional simulations in PASOS to assess whether i) it is easier to assign an offspring born to wild-born parents than an offspring born to stocked parents; ii) different patterns of assignment errors for the two groups could bias our conclusions about the RRS of captive-bred adults returning to the Malbaie River.