CONTRIBUTED PAPER

Supportive breeders of Atlantic salmon *Salmo salar* have reduced fitness in nature

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Abstract

Wild Atlantic salmon (*Salmo salar*) are in decline over the entire distribution area, and populations are enhanced by supportive breeding. Parental fish are sampled in rivers, crossed and the offspring reared in hatcheries until smolting when released, ready for ocean migration. Naturally reproducing salmon entering the River Imsa from the ocean were monitored from 1976 through 2013, and since 1982, supportive breeders spawning in the river were also monitored. The supportive breeders were first-generation salmon, reared for 1—2 years in a hatchery before being released at the mouth of the river so they could migrate to sea (i.e., sea-ranching). Wild and sea-ranched salmon live in the ocean for 1—2 years before they return to the river for spawning. In years when only wild adults were present, mean number of smolts produced per 100 m^2 river area and female breeder was 0.47. When there were 5% wild females, the mean production was only 0.088 (19%). The gradual decrease in offspring production with decreasing proportion of wild females ($r^2 = .41$) indicates that the reduced offspring production was caused by inferior spawning behavior of hatchery females or reduced survival of their offspring in nature. Previous experimental evidence suggests that wild males fertilize the eggs of wild but also hatchery females. It is discussed how epigenetic effects caused by hatchery environments influence the developing juveniles, lead to phenotypic changes that may reduce their fitness in nature even after free ranging for a year or more in the ocean before they return and spawn.

KEYWORDS
Atlantic salmon, fitness, River Imsa, *Salmo salar*, sea-ranching, smolt emigration, stock-recruitment, supportive breeding

1 | INTRODUCTION

Supportive breeding (Ryman & Laikre, 1991) is extensively used to enhance terrestrial (Carrete & Tella, 2015; Brichieri-Colombi, Lloyd, McPherson, & Moehrenschlager, 2019) and aquatic (Horreo et al., 2018; McLean, Seamons, Dauer, Bentzen, & Quinn, 2008) populations. It involves gathering

and crossing of gametes to produce offspring in captivity and release the progeny at a stage where the probability of survival is high. Populations of endangered species, such as Mexican wolf *Canis lupus baileyi*, red wolf *C. rufus* (Hedrick & Fredrickson, 2008), and Fennoscandian Arctic fox *Vulpes lagopus* (Landa et al., 2017), were reestablished by releases of captively bred individuals. Supportive

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breeding is used to compensate for degraded habitats, over-exploitation, and to increase population abundances above natural levels. However, the efficiency of released organisms enhancing natural populations is seldom quantified.

Especially salmonid populations are enhanced by supportive breeding. Hatcheries have propagated salmon and trout since the 1850s and viewed this an important tool in improving small and declining populations in rivers where habitats or the connectivity between habitats are degraded or destroyed (Johnson et al., 2012; B. Jonsson & Jonsson, 2011). Dannewitz et al. (2004) reported that the reproductive successes of hatchery and wild brown trout *Salmo trutta* were similar when tested in an experimental stream. Similarly, Araki, Ardren, Olsen, Cooper, and Blouin (2007) found that steelhead trout *Oncorhynchus mykiss* from a supplementation hatchery had similar reproductive success in nature as their wild parents. However, domestication over two generations reduced reproductive capabilities of steelhead trout by approximately 40% per generation (Araki, Cooper, & Blouin, 2007). There are also other examples showing that wild steelhead trout are more effective spawners than hatchery produced fish (Kostow, Marchall, & Phelps, 2003; Leider, Hulett, Loch, & Chilcote, 1990). In line with this, Hansen, Hynes, Loeschcke, and Rasmussen (1995) reported that the genetic contribution of released hatchery brown trout in a Danish river was much lower than expected from the number of stocked fish. However, no one appears to have tested the efficiency of long-term, recurrent releases of a hatchery-produced salmonid into a wild population.

Several ecological traits appearing at a later life stage may be influenced by early experiences in nature or in hatcheries (B. Jonsson & Jonsson, 2014a). For instance, developmental, phenotypic effects caused by early rearing environment are manifested in life-history traits from studies of various fish species, with examples of impacts on growth, behavior, sex determination, and resource allocation to eggs and sperm (reviewed in B. Jonsson & Jonsson, 2014a). For instance, temperature during embryogenesis is one factor that influences later life history decisions and behavior of salmon (B. Jonsson & Jonsson, 2019), and the tank environment of hatcheries is another (Le Luyer et al., 2017). Thus, type of environment may influence the fitness of supportive breeders in nature.

Here, we estimated effects on the smolt abundance of whether the spawners were wild or reared as juveniles in a hatchery and released in nature at the smolt stage. The results support the hypothesis that the river production of Atlantic salmon smolts per female decreased with decreasing proportions of wild females in the study river.

2 | MATERIALS AND METHODS

In the River Imsa, south-western Norway (58°50′N, 6°E), we released first-generation, sea-ranched Atlantic salmon *Salmo salar* that have spawned with natural conspecifics since 1982 (B. Jonsson, Jonsson, & Jonsson, 2017). The sea-ranched fish were released in the main smolt migration period in the beginning of May (B. Jonsson & Jonsson, 2014b). The population consists of approximately 50 natural spawners of which more than 80% are similar-sized one-sea-winter salmon, and the rest are two-sea-winter salmon with some variation in proportion among years (B. Jonsson, Jonsson, & Albretsen, 2016). For more than 40 years, all salmon have been tagged before leaving the river and monitored on the return. Brood stocks were sampled in the river, the offspring reared to smolts in the local hatchery and released as smolts at the river outlet. When mature, they returned to the river for spawning.

The River Imsa is approximately 1 km long. The river area was ca. 10,000 m^2 until 1993 when an upstream impassable waterfall was built, reducing the river area by 9%. An inclined plane trap (Wolf, 1951; apertures 10 mm, inclination 1:10) situated 150 m above the river outlet, caught downstream migrating smolts. All upstream migrating salmon were captured in a fixed box trap located alongside the Wolf trap on top of a three-step fish ladder (B. Jonsson & Jonsson, 2011). The traps were emptied twice a day all year round, and natural tip lengths (sensu Ricker, 1975), mass (g), and sex were recorded. Before leaving the river, all smolts were individually tagged with numbered Carlin tags. From 1983 onward, every tenth smolt descending into the trap was sampled for age determination by use of scales and otoliths (B. Jonsson, 1976). The smolt age distribution was used to calculate the number of smolts originating from different brood years. For years before 1983, we assumed that the age distribution was the average of that between 1983 and 2012. We estimated number of smolts produced from egg cohort of year i as number of smolts in year $i + 2$ times the proportion of 1-year-olds that year, plus number of smolts in year $i + 3$ times the proportion of 2-year-old smolts that year, plus number of smolts in year $i + 4$ times the proportion of 3-year-old smolts that year. There was no smolt younger than 1 year or older than 3 years. This means that 3-year-old smolts in 2017 were offspring of adults spawning in 2013, the last year of brood stock sampling. All adult Atlantic salmon that returned to the trap were recorded and divided in two groups. One group was taken into the hatchery for stripping, the other group was released upstream of the trap for natural reproduction. These latter fish were used for estimating the within river stock–recruitment relationship (B. Jonsson et al., 2017).

We regressed number of smolts per unit river area (100 m^2) and female spawner over proportion of wild females to all females for each year. The data, which were 35 annual counts of outmigrating smolts (Appendix S1), were statistically validated (M. Jonsson, 2018), log-transformed into a homoscedastic (Zuur, Ieno, Walker, Saveliev, & Smith, 2008), normally distributed, time series, and fitted using the simple linear model (Agresti, 2015). There was no significant autocorrelation in the data series (Durbin-Watson test, $D = 1.6172$, $p = .1079$) (Durbin & Watson, 1950). The linear predictor was:

$\text{Log}_{10}(Y_{\text{counts}}) = \beta_0 + \beta_1 \log_{10}(X_{\text{wild}})$ if and only if $Y_{\text{counts}} = 10^{\beta 0}(X_{\text{wild}})^{\beta 1}$.

There were five missing observations. That is 1991–1993 when no Atlantic salmon was allowed access to the river due to construction of the waterfall, and 1995 and 1997 when there were only sea-ranched fish present making the estimated proportions zero. These are unusable as the logarithm is undefined at zero. There is no significant difference between number of outmigrating smolt as a function of eggs counts and spawning area before and after 1993 (B. Jonsson et al., 2017; analysis of variance: $F_{1,28} = 2.62$, $p > .05$).

Relationships between fecundity (F) and total body mass (M [g]) of the River Imsa Atlantic salmon were (N. Jonsson, Jonsson, & Fleming, 1996):

$$F = 1.22 M + 741.90, df = 16, r^2$$
$$= .79, p < .001 \text{ for naturally produced females, and}$$

$$F = 1.79 M + 238.18, df = 41, r^2$$
$$= .85, p < .001 \text{ for sea-ranched females.}$$

From these, we calculated number of eggs deposited in the river each year. Fecundity of sea- ranched females was higher than that of naturally produced females of corresponding size. We also estimated number of smolts per female over estimated number of eggs of wild female spawners divided by all eggs spawned each year. In addition, we estimated number of smolts per kilogram adult females over number of wild-female spawners divided by all female spawners in the river each year.

3 | RESULTS

Body sizes of wild and sea-ranched salmon spawning in the river were similar. Mean total mass of sea-ranched and wild females were $2,336 \pm 974$ g and $2,475 \pm 1,046$ g, respectively ($t = 0.546$, $p > .05$). Thus, based on body size one can reliably compare the offspring production of wild and sea-ranched females.

Number of smolts per female per 100 m^2 river area (Y_{counts}) increased with proportion of wild females to all females (X_{wild}) in the river between 1976 and 2013 (Figure 1a). When there were only wild adults in the river, mean number of emigrating smolts per 100 m^2 river area per female breeder was on average 0.47 ($\log_{10}[-0.326]$). When there were 5% wild females, the corresponding smolt production was on average 0.088 ($\log_{10}[-1.3]$). The regression model explained 41% of the variation in smolt production. There was no tendency toward increased production per female when the proportion of wild females approached 0, indicating that the sea-ranched fish were inferior breeders, or that the survival of their offspring was lower than that of naturally produced Atlantic salmon.

A similar positive regression was found for number of smolts per 100 m^2 river area and per female spawner over estimated proportion of eggs spawned by wild females each year (Figure 1b). The higher the proportion of eggs spawned by wild females, the higher was the production of smolts per female and unit river area. Also, the regression of number of smolts per 100 m^2 river area and total mass of female spawners over proportion of wild females spawning each year increased similarly (Figure 1c). The latter two models, however, explained less of the variance did number of smolts per female and unit area (Figure 1a). Apparently, female mass and number of eggs were more variable relative to the smolt production than number of female spawners present each year.

4 | DISCUSSION

Supportively bred first-generation, sea-ranched Atlantic salmon gave fewer offspring per female than wild conspecifics did. This was revealed by the positive association between number of smolts and proportion of wild females. Similar relationships were obtained when we regressed number of smolts per female on estimated proportion of eggs produced by wild females, or we used number of smolts per unit mass of females at the time of river entry as dependent variable. Thus, hatchery-rearing to smolts reduces the fitness of Atlantic salmon in nature.

Why is the success of sea-ranched salmon lower than that of wild conspecifics? Both groups left the river as smolts and spent at least 1-year free ranging in the north Atlantic Ocean before they returned to the trap in the River Imsa. Their body sizes at maturity were similar. However, B. Jonsson, Jonsson, and Hansen (1990) reported that sea-ranched salmon returned to the river later in the autumn and left sooner after spawning than wild conspecifics do. While almost all wild females spawned their eggs when being in the river, on average 13.5% of the sea-ranched females returned to sea in late autumn without having spawned.
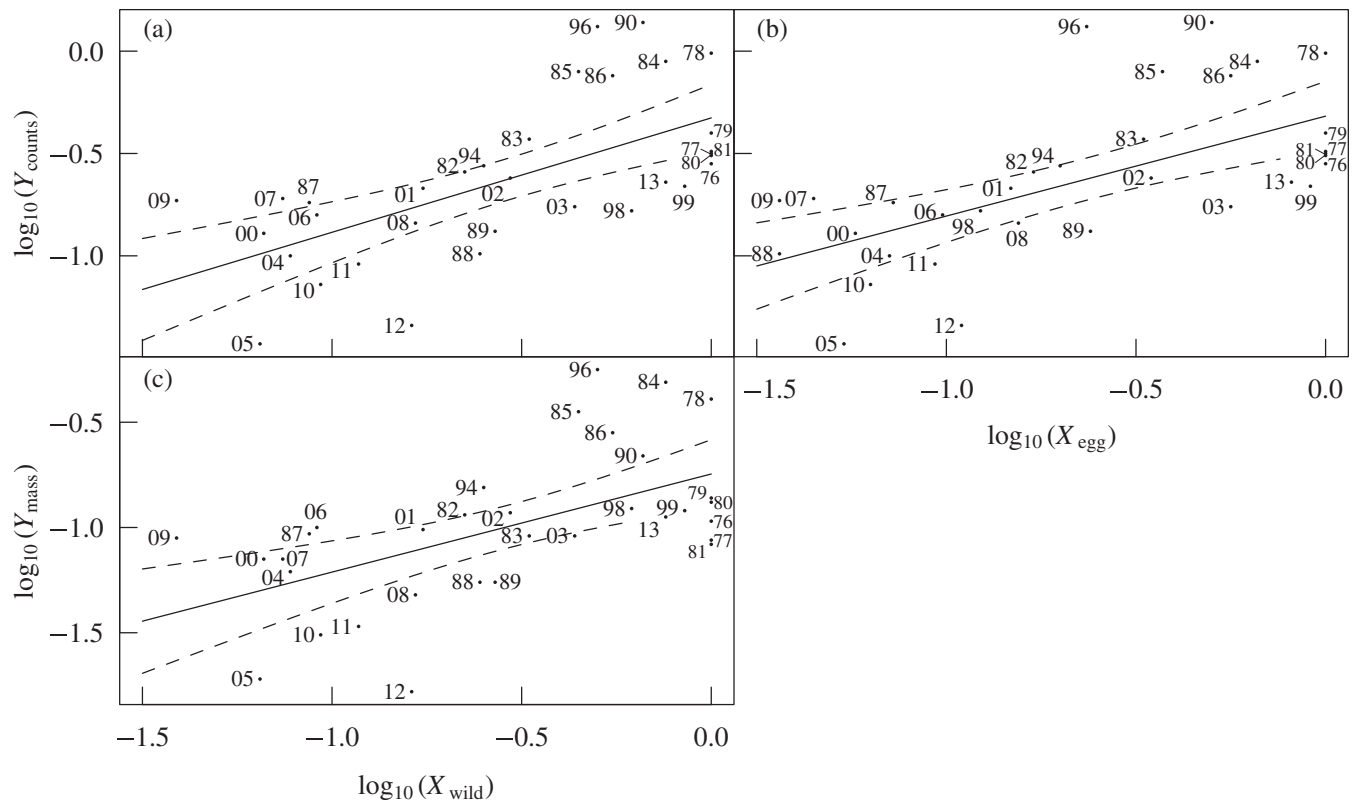
FIGURE 1 Number of Atlantic salmon *Salmo salar* smolts per 100 m^2 river area and female spawner (log$_{10}Y_{counts}$) on (a) number of wild females divided by all female spawners (log$_{10}X_{wild}$) ($\pm SE$): log$_{10}Y_{counts}$ = 0.559($\pm$0.120)log$_{10}X_{wild}$ − 0.326($\pm$0.083); r^2 = .411, $F_{1,31}$ = 21.6, t_{const} = −3.92, t_x = 4.65, and (b) estimated number of eggs spawned by wild females divided by all eggs spawned each year (log$_{10}X_{egg}$): log$_{10}Y_{counts}$ = 0.488($\pm$0.108)log$_{10}X_{egg}$ - 0.316($\pm$0.087); r^2 = .397, $F_{1,31}$ = 20.4, t_{const} = −3.66, t_x = 4.50. (c) Number of smolts per 100 m^2 river area and mass of females (Y_{mass}, kg) on number of wild females divided by all females each year (log$_{10}X_{wild}$): log$_{10}Y_{counts}$ = 0.465($\pm$0.120)log$_{10}X_{mass}$ − 0.746($\pm$0.083); r^2 = .327, $F_{1,31}$ = 15.1, t_{const} = −8.98, t_x = 3.88. All p < .001. Broken lines give 95% confidence limits, numbers at data points give year-class of spawners, and arrows in (a) and (b) show double data points

Moreover, sea-ranched salmon were more often seriously injured during spawning than were wild conspecifics. In addition, the sea-ranched salmon moved more about in the river, possibly because they were competitively inferior or lacked experience from early life in the river (B. Jonsson, Hansen, & Jonsson, 1994).

In supportive breeding, one manipulates natural breeding systems and interferes with partner selection. There are examples of that captivity can influence mating preferences from house mice *Mus musculus* (Slade et al., 2014). However, skewed partner selection may not be important in the present system with one restricted spawning area and no apparent subpopulations. Moreover, experiments in large-scale spawning arenas suggest that wild males fertilize most of the eggs of both hatchery-reared and wild females (Fleming, Lamberg, & Jonsson, 1997).

Genetic selection in the hatchery should be small (Finstad & Jonsson, 2012). We used 10–20% of the returning wild fish each year as brood stock, randomly picked on their return to the river, and the mortality of eggs and juveniles was low. The released fish were first-generation hatchery fish and therefore not genetically adapted to hatchery conditions that could otherwise have compromised their fitness in the wild (Araki, Berejikian, Ford, & Blouin, 2008; Hagen et al., 2019). But still, only a short period of hatchery rearing was enough to change the behavior of captively bred salmon (B. Jonsson & Jonsson, 2018). On the other hand, in nature early mortality is high, and this strong selection in each generation may contribute to their reproductive success of wild salmon.

Reduced reproductive success of the hatchery females is probably influenced by inferior reproductive behavior of the parental fish (Fleming et al., 1997; Fleming, Jonsson, Gross, & Lamberg, 1996; B. Jonsson et al., 1990) or reduced survival of their young (Christie, Ford, & Blouin, 2014). We cannot distinguish effects of the one from the other. Submissive versus bold behavioral patterns of salmonids appear established when the young compete during the first 2 months of external feeding (Andriaenssens & Johnsson, 2013). In hatchery tanks, fish density is high, they are all similar sized, and there is nowhere they can hide, and bold behaviors appear favorable. In nature, on the other hand,

young salmon may encounter larger competitors and predators, and they avoid confrontations and survive by hiding in a structured habitat. Thus, when testing aggressive behaviors of young Atlantic salmon parr, Fleming and Einum (1997) reported that hatchery salmon were more aggressive than wild conspecifics in tank environments, but still competitively inferior to wild juveniles in stream-like environments, possibly because of their differences in behavior. Similar differences in behavior between hatchery and wild Atlantic salmon are observed on the spawning grounds where hatchery fish are more involved in physical conflicts and less effective spawners (Fleming et al., 1996, 1997). Hatchery environments appear to reduce their ability to compete for territories and avoid exhausting conflicts in nature (Huntingford, Metcalfe, Thorpe, Graham, & Adams, 1990).

Thus, hatchery and wild salmon may learn different behavioral patterns that they exhibit on the spawning ground years later (Fleming et al., 1996, 1997). Furthermore, hatchery salmon may be also physiologically inferior. Body proportions, anatomy of brain, sense organs, heart sizes, and physiological traits are changed by hatchery rearing (review in B. Jonsson & Jonsson, 2006). Also, the fitness of the captive-bred fish may be reduced by their smaller eggs compared with natural-bred conspecifics (N. Jonsson et al., 1996). All these differences may contribute to their decreased fitness in nature. The decreased reproductive success of hatchery females appears associated with changed boldness relative to that of wild females caused by the early rearing in the hatchery (Fleming et al., 1996; B. Jonsson et al., 1990).

Milot, Perrier, Papillon, Dodson, and Bernatchez (2012) estimated the relative success of Atlantic salmon released following a single generation of captive breeding. They reported that the reproductive success relative to that of natural bred conspecifics was 0.71 when they were released as fry and 0.42 when released as smolts. Our results showed an even lower success for released hatchery-reared compared with wild female salmon in the River Imsa.

Thus, captivity, even for a short time at young age, may influence the fitness of salmon in the wild. Hatchery rearing may cause an epigenetic effect that influences their behavior (Baerwald et al., 2016; B. Jonsson & Jonsson, 2018, 2019). DNA methylation is the best studied and understood epigenetic mechanism (Metzger & Schulte, 2016). It inhibits genetic transcription and is stable at the time scale of an individual's lifespan. Changes in DNA methylation affect many developmental processes and occur in certain regions of the genome. Le Luyer et al. (2017) compared genome-wide patterns of DNA methylation in hatchery-reared coho salmon *Oncorhynchus kisutch* with those of their wild counterparts in two rivers. They reported that rearing environment explained a large part of the ecological and epigenetic variation. These authors found evidence of epigenetic

modifications induced by hatchery rearing of the fish from both study rivers. The differentially methylated regions exhibited enrichment for biological functions that may influence migratory and reproductive capacities of the fish and may affect the capacity of hatchery-born coho salmon to spawn successfully in nature. Also, in steelhead trout, hatcheries induce epigenetic changes as reported by Garvey, Nichols, Goetz, Middleton, and Swanson (2018). They found differences in several methylated regions in red blood cells and sperm cells between hatchery and wild conspecifics. The identification of changes in sperm cells reveals the potential for transgenerational changes caused by hatchery environments (B. Jonsson & Jonsson, 2016).

Thus, supportive breeding gives viable offspring in nature, but much fewer than do similar-sized, naturally produced conspecifics. Artificial hatchery environments appear not well suited for young salmon used for supportive breeding. If regular hatchery fish are used as brood stock, the success may be even lower than observed here where first generation hatchery fish were used, with effects on natural populations like those of captively bred organisms in nature (Bolstad et al., 2017).

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CONFLICT OF INTEREST

The authors declare no potential conflict of interest.

AUTHOR CONTRIBUTIONS

All authors contributed to the study design and involved in the critical review. M.J. was involved in statistical treatment. B.J. wrote the first draft.

DATA ACCESSIBILITY

The data on which the analysis was based, are given in the Appendix S1.

ETHICS STATEMENT

The monitoring and tagging of the fish were approved by the Norwegian Animal Research Experimentation Agency.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.