



Maternal inheritance influences homing and growth of hybrid offspring between wild and farmed Atlantic salmon

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ABSTRACT: The occurrence of domesticated organisms in nature is a major biological issue. Many can survive and reproduce with wild conspecifics, but little is known about the ecology of the hybrid offspring. Here, we investigated recapture, homing and growth of the released offspring of farmed (domesticated) and wild Atlantic salmon *Salmo salar* as well as their crosses. The fish were hatchery-reared for 1 yr and released as smolts in the River Imsa, Norway, the home river of the wild fish. The released fish migrated to the ocean. Many disappeared, but between 0.6 and 2% were sampled on their return as adults 1 or 2 yr later. Homing to the river of release was low for farmed salmon (88% strays). Among hybrids, having a wild mother provided increased homing accuracy (36% strays) relative to having a wild father (64% strays). Offspring of the local River Imsa salmon exhibited the best homing (28% strays). The growth capacity of the farmed salmon appeared to be not fully utilized in nature, as there was little difference in maximum size between wild and farmed salmon. However, minimum size at maturity was larger for farmed than wild conspecifics. Inheritance from a farmed mother increased minimum size of the hybrids versus that of the pure farmed salmon. Thus, maternal inheritance from domesticated, farmed salmon decreased homing and increased minimum size at adulthood of the offspring, making domesticated salmon a risk for locally adapted salmon in nature.

KEY WORDS: *Salmo salar* · Straying · Domesticated · Growth · Recapture · Survival

INTRODUCTION

Domesticated organisms occur in nature where they can breed and introgress natural gene pools. This holds for fish (Araki et al. 2008), birds (Fleming et al. 2011) and mammals (Kidd et al. 2009). This interbreeding may lead to altered ecological and behavioural characters of native populations with negative effects on their viability (Fleming et al. 2000, Debes & Hutchings 2014). Thus, domesticated organisms in nature have become a major biological issue.

Salmonid fishes, and Atlantic salmon *Salmo salar* in particular, are a centre of much research on the effects of captive-bred organisms because their high numbers in nature (Blanchet et al. 2008). The sur-

vival of their offspring may be lower than that of wild conspecifics, although this may not always be the case (McGinnity et al. 2003). Captive-bred salmonids are deliberately released to counteract the depletion of wild populations (Jonsson & Jonsson 2011). In addition, farmed salmon escape from captivity and enter rivers for spawning. It is known that farmed offspring survive in rivers, migrate to sea for feeding and return to fresh water for spawning (Fleming et al. 2000). However, the offspring of farmed salmon appear to stray more during the return migration and many end up in foreign rivers (Jonsson et al. 2003). In rivers, farmed salmon may also interbreed with wild conspecifics, but little is known about the homing ability of the hybrid offspring.

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Artificial rearing changes the morphology, physiology and ecology of the fish, partly because of phenotypically plastic responses to the rearing environment, but also because of genetic changes (Jonsson & Jonsson 2011). Farmed Atlantic salmon in Norway have been genetically changed in a large-scale breeding programme that began in the early 1970s, based on wild fish from several rivers. In the programme, the fish are selectively bred to increase growth, avoid early sexual maturation, increase disease resistance and improve flesh colour and fat content (Gjedrem 2010). Such changes, and those caused by adaptation to the artificial hatchery environment, may alter the natural performance of the fish and influence their survival in the wild (Fleming et al. 2000, Thorstad et al. 2008, Bolstad et al. 2017, Glover et al. 2017).

Here, we tested growth, recapture rate and homing of the offspring of farmed and wild Atlantic salmon, and crosses between the two, when released into nature at the smolt stage. We tested whether returning adults differed in size, survival and degree of dispersal and homing to the river of release depending on their genetic origin.

MATERIALS AND METHODS

The experiment was conducted at the NINA (Norwegian Institute for Nature Research) Research Station, Imsa, near Stavanger, in southwestern Norway (59° N, 6° E). The Research Station is situated at the mouth of the River Imsa, a small salmon river with annual mean water flow of $5.1 \text{ m}^3 \text{ s}^{-1}$. The hatchery is supplied with River Imsa water at slightly elevated temperature, ranging from 2 to 8°C in winter to summer maxima of about 20°C. Thus, all hatchery fish are exposed to identical water sources and the same potential set of odorants. Two strains of Atlantic salmon and 10 individuals of each sex and strain were used as brood stock. We used 10th generation artificially selected farmed salmon derived from Norway's national breeding programme, AquaGen (Gjedrem 2010). Over 50% of the world's farmed Atlantic salmon are derived from this programme (Fleming et al. 2000). Mean (\pm SD) lengths of female and male spawners were 104.6 ± 3.1 and 101.9 ± 2.7 cm, respectively. As a wild control, we used offspring of Atlantic salmon of the River Imsa. The brood stock, sampled in autumn 2012, were captured in a fish trap placed 100 m above the river outlet (see illustration in Jonsson & Jonsson 2011). Mean lengths of the female and male spawners were 64.9 ± 5.6 and 63.4 ± 6.2 cm, respectively.

In November 2012, we stripped the parental fish and divided the eggs of each female into 2 parts: one half was fertilized with sperm of a male of its own strain, and the second half fertilized with a male from the other strain. This gave the following 4 crosses: AquaGen female \times AquaGen male, AquaGen female \times Imsa male, Imsa female \times AquaGen male, and Imsa female \times Imsa male. Eggs and sperm of the fish were reared in Heath vertical stack incubators with a water flow of 4 l min^{-1} at the NINA Research Station. The half-sib groups were maintained separately until the onset of exogenous feeding (10×4 groups), after which fish from the same parental groups were combined (4 groups).

From the onset of exogenous feeding (April/May 2013), the 0+ fish were reared in 1 m^2 pools with a water depth of 20 cm and a flow of 5.5 l min^{-1} . In early June 2013, the 0+ fish were transferred to 4 m^2 pools with a water depth of 50 cm and a flow of about 40 l min^{-1} to grow until smolting commenced in April 2014. The fish were fed EWOS® food pellets every 10 min during daylight until they reached about 10 cm in total length, after which they were fed every 20 min during daylight. The 1 yr old smolts were anaesthetized with benzocaine, measured (length; mm) and tagged with individually numbered Carlin-tags (Carlin 1955). The fish were tagged more than 2 wk before being released in the River Imsa, 100 m above the river estuary. The smolts were released in the first days of May, early in the migration period of the natural River Imsa smolts. The fish were released from a rearing tank through a pipeline into the backwater just downstream of the traps near the bank of the river (cf. by the arrow in Fig. 6.5b of Jonsson & Jonsson 2011). This allowed them to migrate to sea whenever they liked.

Atlantic salmon of the River Imsa attained maturity after 1 or 2 yr in the ocean (1-sea-winter and 2-sea-winter salmon), when they returned to Norway for spawning. Upon return, the fish were captured in sea water along the coast and in fjords by local fishermen, in other rivers by anglers and in the trap in the River Imsa. At recapture, the length of adult fish was measured. The proportion of adult fish recaptured was used as an index of survival at sea. This was estimated as total number of recaptured adults divided by the number of smolts forming the cohort at release. The values were not adjusted for any possible mortality effect of tags or tagging, because there was no intention of estimating the absolute survival rate of the fish. The straying rate was estimated as number of adult salmon caught in rivers other than the River Imsa, divided by the total number of recaptures

in fresh water. Growth at sea was estimated as length at recapture minus smolt length. Differences among groups in numbers recaptured were tested by χ^2 -tests, and differences in size by t -tests.

RESULTS

Recaptures varied among the 4 crosses (Fig. 1). Recapture rate was highest for River Imsa salmon and hybrids with River Imsa mothers, and higher for hybrids with River Imsa mothers than those with AquaGen mothers ($\chi^2 = 5.88$, $df = 1$, $p = 0.015$). However, there was no significant difference in the proportion recaptured between the offspring of the AquaGen fish and hybrids with AquaGen mothers (mean recapture: 0.79, $\chi^2 = 1.81$, $df = 1$, $p = 0.18$), or between the River Imsa fish and hybrids with the River Imsa mothers (mean recapture: 1.73, $\chi^2 = 1.02$, $df = 1$, $p = 0.31$).

Offspring of wild River Imsa salmon strayed less (27.8%) than those of AquaGen origin (87.5%), while hybrids with River Imsa and AquaGen mothers strayed 35.7 and 64.0%, respectively (Table 1). This difference was significant among groups ($\chi^2 = 10.8$, $df = 3$, $p = 0.01$). The number of recaptures in coastal waters and estuaries, on the other hand, did not differ significantly among groups ($\chi^2 = 0.40$, $df = 3$, $p = 0.75$). The adults were chiefly caught in southwestern Norway, in the River Imsa, and south and north of the river. The origin of the recaptures spread from the River Otra, (58°N) in southernmost Norway, to the Ranafjord (66°N) in northern Norway. The distribution of recaptures in rivers between in the River Imsa, <100 km and ≥ 100 km away from the river differed significantly among the groups (Table 1; $\chi^2 = 18.8$, $df = 6$, $p = 0.005$). Relatively more offspring of AquaGen mothers were recaptured in rivers >100 km from the River Imsa.

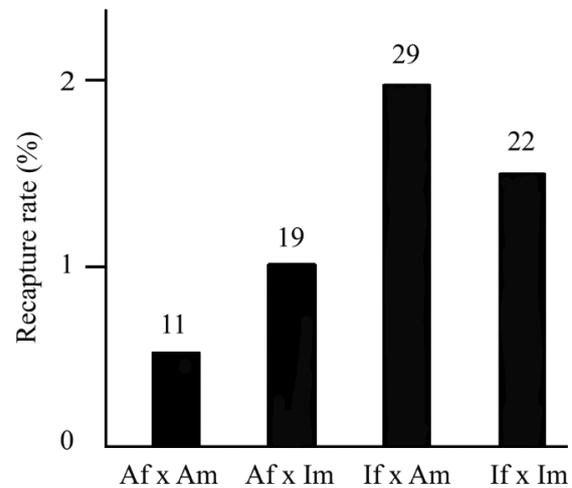


Fig. 1. Recapture rate of all maturing Atlantic salmon *Salmo salar* from offspring groups of AquaGen (A) and the River Imsa (I) salmon and crosses between the 2 strains released as smolts in the River Imsa varied significantly ($\chi^2 = 15.0$, $df = 3$, $p = 0.002$). Number of recaptures are given above the columns; f = females; m = males

AquaGen fish and those with AquaGen mothers were on average larger than the other groups at smolting (Table 2; $t = 2.45$, $df = 77$, $p < 0.02$). In contrast, there was no significant difference in mean smolt length between the pure strains and the hybrids from the same mother group (both $p > 0.05$). The difference in mean adult length is mainly because the minimum size of the AquaGen fish and those with AquaGen mothers was larger than the minimum size of the River Imsa salmon and fish with River Imsa mothers. Mean sea growth of 1-sea-winter AquaGen salmon was higher than that of the pure River Imsa salmon of corresponding age ($t = 2.22$, $df = 26$, $p = 0.04$). There was no significant difference in mean sea growth between 1-sea-winter fish of the pure strains and the hybrids from the cor-

Table 1. Numbers of recaptured Atlantic salmon *Salmo salar* <100 km or ≥ 100 km (percentages in rivers in parentheses) and mean (\pm SD) distance to place of recaptures of AquaGen and River Imsa salmon and crosses between the two from the outlet of the River Imsa, in rivers and at sea. F = female; M = male

Group	In rivers				At sea		
	Imsa	<100 km	≥ 100 km	Mean distance (km)	<100 km	≥ 100 km	Mean distance (km)
AquaGen F \times AquaGen M	1 (12.5)	2 (25.0)	5 (62.5)	178 \pm 104	0	3	187 \pm 55
AquaGen F \times Imsa M	5 (35.7)	6 (42.9)	3 (21.4)	163 \pm 176	2	3	427 \pm 445
Imsa F \times AquaGen M	16 (64.0)	7 (28.0)	2 (8.0)	132 \pm 135	0	4	248 \pm 131
Imsa F \times Imsa M	13 (72.2)	4 (22.2)	1 (5.6)	112 \pm 120	2	2	140 \pm 79
Total	35 (53.9)	19 (29.2)	11 (16.9)	149 \pm 136	4	12	265 \pm 269

Table 2. Mean (\pm SD) smolt length and length increment at sea (mm), and range of variation of AquaGen and the River Imsa salmon *Salmo salar* and crosses between the two. F = females; M = males

Crossing	Mean smolt length (range of variation)	Mean sea growth 1-sea-winter fish (range of variation)	Mean sea growth 2-sea-winter fish (range of variation)	Mean adult length (range of variation)	Smolts released
AquaGen F \times AquaGen M (range)	195 \pm 12 (177–214)	443 \pm 37 (371–513)	624	654 \pm 67 (557–830)	1860
AquaGen F \times Imsa M (range)	174 \pm 12 (155–194)	440 \pm 35 (375–491)	583 \pm 30 (542–610)	645 \pm 72 (560–790)	1943
Imsa F \times AquaGen M (range)	167 \pm 13 (138–186)	419 \pm 42 (341–541)	617 \pm 71 (568–698)	607 \pm 77 (527–860)	1478
Imsa F \times Imsa M (range)	163 \pm 11 (144–176)	416 \pm 47 (326–521)	572 \pm 56 (504–641)	607 \pm 79 (490–805)	1464
Total mean	171 \pm 16	426 \pm 42	590 \pm 52	623 \pm 76	1686

responding mother groups. The sample sizes of 2-sea-winter salmon were small and no significant difference was found.

Most fish attained maturity as 1-sea-winter fish with a variation between 79 and 91 % among groups. The proportion of 1-sea-winter fish did not differ significantly among groups ($\chi^2 = 1.53$, $df = 3$, $p = 0.7$).

DISCUSSION

Released hatchery Atlantic salmon migrate to sea for feeding, and some return as adults to spawn in rivers. Typically, the recaptures of Carlin-tagged, returning adults are in the range of 0.5 to 3 % (Juttila et al. 2003, Jonsson & Jonsson 2011), covering the range of variation in the present experiment. These low recapture rates decrease the power of the results, and may be partly influenced by the handling and tagging of the smolts (Hansen & Jonsson 1988). More importantly, however, Atlantic salmon mortality at sea is high and has increased since the mid- to late 1980s (Chaput 2012, Jonsson et al. 2016). Furthermore, hatchery smolts (used in the present experiment) have lower sea survival and stray more than wild conspecifics (Jonsson et al. 2003, Jonsson & Jonsson 2006, Araki et al. 2008, Westley et al. 2013). Possible tag loss (not included in the present study) may also have influenced the estimated return rate. Isaksson & Bergman (1978) estimated the tag loss of Icelandic Carlin-tagged smolts at 10 %. A similar tag loss may hold for the present salmon, but we have no reason to believe that tag loss differed among the experimental groups used.

The recaptures of Carlin-tagged River Imsa salmon and hybrids with River Imsa mothers were more than

twice as high as for those of AquaGen and hybrids with AquaGen mothers. For untagged fish in nature, this difference might have been even larger, because of differences in smolt size. Isaksson & Bergman (1978) estimated marine mortality of Carlin-tagged hatchery smolts, and found that the mortality at sea of 9.5 to 14.5 cm long Carlin-tagged smolts was 3 times higher than for corresponding, micro-tagged smolts. For longer smolts, but shorter than 19.5 cm, marine mortality was on average ca. 1.5 times higher for Carlin-tagged than micro-tagged smolts. For smolts of Arctic charr *Salvelinus alpinus* longer than 19 cm, Strand et al. (2002) found no effect of Carlin tagging on survival at sea, which may be similar for Atlantic salmon. Thus, mortality due to tagging may have been highest for the 2 groups with River Imsa mothers because of their smaller size.

The estimated straying rates were high, but still, they are minimum estimates. All adult salmon entering the spawning area of the River Imsa are registered at the river mouth, but only a portion of the fish entering other rivers were registered by the fishermen. The percent of returning Atlantic salmon caught in some Norwegian rivers has been estimated. For instance, in the large River Drammen, between 28 and 53 % of the total run are caught (Sandhaugen & Hansen 2001). In the River Lærdal, Rosseland (1979) estimated the fishing mortality at between 43 and 70 % (mean: 55 %) for the years 1960 to 1977, and Sættem (1995) gave even higher estimates for 10 small rivers in western Norwegian rivers in the 1990s. On average, 83 % of the fish less than 3 kg in weight were caught. In the River Tana, a border river between Norway and Finland, Karpinen et al. (2004) estimated that 72 % of the 1-sea-winter salmon were caught. Thus, because all adult

salmon were monitored in the River Imsa, the estimated straying rates are minimum estimates. We may add, however, that observed straying does not mean that the fish would spawn in a foreign river. If not caught, some of them might have left and returned to the River Imsa.

Straying of released hatchery salmon is known to be higher than that of wild conspecifics (Jonsson et al. 2003, Ford et al. 2015), but the straying of AquaGen salmon used for farming was extremely high—higher than found for earlier generations of this strain released between 1986 and 1997 in the River Imsa (on average 54%; Jonsson et al. 2003). The straying rates of the hybrids were intermediate, indicating that homing is a genetically influenced trait. Earlier experiments have demonstrated that homing of Atlantic salmon is a learned behaviour (B. Jonsson et al. 1990, Kieffer & Colgan 1992, Hansen et al. 1993). Similarly, local populations of Pacific salmon homed better than transplanted ones, and hybrids exhibited intermediate homing accuracy (Bams 1976, McIsaac & Quinn 1988, Candy & Beacham 2000). Furthermore, hybrids with mothers from the River Imsa exhibited more accurate navigational behaviour than those with AquaGen mothers. Although the sample size is small and the experiment not replicated, this indicates that local maternal inheritance is more important for the ability to learn the location of their home stream than is local paternal inheritance, and that homing ability may be gradually lost during the domestication process in hatcheries. For instance, released rainbow trout kept in hatcheries in Norway since 1902 appear to have lost their ability to orient back to the place of release (Jonsson et al. 1993).

The straying rate of the pure River Imsa salmon was high, almost twice as high as the mean of earlier releases of first generation hatchery salmon of the River Imsa (28% versus 15%; cf. Jonsson et al. 2003). There is, however, variation among groups of released salmon, and the present sample size is small. Thus, one should be cautious when interpreting this result.

Earlier studies have exhibited particularly high straying rates when the salmon were released outside the smolting period (Hansen & Jonsson 1991, Dittman & Quinn 1996). We have, however, no indication that any of the groups had desmolted when released; not even those with AquaGen mothers seemed to have desmolted. They were larger and may have smolted a few days earlier than the 2 other groups in spring (N. Jonsson et al. 1990). However, large smolts may survive well and return even when migrating late in the season. Jonsson et al. (2017)

found similar return to the River Imsa of Atlantic salmon smolts larger than 20 cm, regardless of whether they migrated to sea in spring or summer.

Homing, however, may be associated with the small size of the river and the low number of smolts leaving the Imsa and the few salmon that return, wild salmon of the River Imsa included (Jonsson & Jonsson 2017). Hindar (1992) tested straying rate in relation to physical and biological factors in Atlantic salmon and brown trout *Salmo trutta* in Norway and the United Kingdom. He found that water flow had a more than proportional effect on straying rate in the Norwegian Atlantic salmon and brown trout data sets. In contrast, in the Atlantic salmon data set from the United Kingdom, there was no effect of water flow. By combining data on Atlantic salmon from Norway and United Kingdom in a single analysis, he demonstrated that homing increases with population size as well as increasing water flow in the home river. For salmon, a large river may be easier to locate than a small stream when they return from the ocean. Furthermore, salmon may benefit from collective navigation on their homeward journey, i.e. individuals in larger groups can better sense and respond to environmental cues and thereby increase their ability to navigate (Quinn & Fresh 1984, Jonsson & Jonsson 2011, Berdahl et al. 2016). Bond et al. (2017) compiled data from multiple studies of Chinook salmon *Oncorhynchus tshawytscha*, and for this species they found strong evidence that rates of successful homing increase with population abundance, consistent with the collective navigation hypothesis.

Sex of the fish can influence rate of straying, as males have been found to stray more than females, lending support to the hypothesis that maternal inheritance is most important for the homing ability. This has been demonstrated for Chinook salmon (Hard & Heard 1999), brook trout *Salvelinus fontinalis* (Hutchings & Gerber 2002), brown trout (Bekkevold et al. 2004), and masu salmon *Oncorhynchus masou* (Kitanishi et al. 2012), but see Consuegra & García de Leániz (2007) for a different result. Kitanishi et al. (2012) maintained that there is stronger selection for homing in females because females must locate suitable spawning habitat, whereas males only seek females, and habitats are less important. If so, this may explain the influence of maternal inheritance observed in the present study. In contrast, we did not find any difference in straying rate between male and female Atlantic salmon of the River Imsa (Jonsson et al. 2003).

The size of the adults influences their tendency to stray, as large salmon tend to stray more than smaller

ones from the same population (Jonsson et al. 2003), and large salmon also avoid entering rivers when the water level is low (N. Jonsson et al. 1990, B. Jonsson et al. 2007, Tetzlaff et al. 2008). The latter may explain why Atlantic salmon size increases in rivers with a mean water flow of $\leq 30 \text{ m}^3 \text{ s}^{-1}$ (Schaffer & Elson 1975, Jonsson et al. 1991). Size differences between adults of the present test groups were, however, small, and well within the size of salmon regularly entering the River Imsa (Jonsson et al. 2016). However, one may speculate that AquaGen salmon, originating from populations of multi-sea-winter salmon, may be genetically adapted to spawn in rivers larger than the River Imsa, and thus actively avoid entering this small river on their return. Peterson et al. (2016) reported that dispersers of sockeye salmon *Oncorhynchus nerka* were sometimes observed in or at the mouths of their natal streams before spawning elsewhere, whereas philopatric individuals were rarely observed in or at the mouths of a non-natal stream. This result suggests that the strays were exposed to multiple spawning habitats, potentially allowing local environmental or demographic conditions to influence the dispersal pattern within the metapopulation. We have no knowledge about whether the strays returned to the River Imsa before entering another river. However, salmon density in the River Imsa is low (Jonsson & Jonsson 2017), and the straying fish were similar in size to those that entered the River Imsa. Thus, if the AquaGen fish do avoid the River Imsa, this may not be associated with their size, but rather an inherited tendency to avoid small streams.

Because of genetic selection, the mean mass of AquaGen salmon in fish farms has increased several fold compared with similar-aged, wild conspecifics (Gjedrem 2010, Solberg et al. 2013). Increased growth is also observed when farmed salmon are released into the wild (Fleming et al. 2002, McGinnity et al. 2003). However, the surviving AquaGen fish in the present experiment were not much larger than offspring of wild River Imsa salmon. The main difference was that the minimum adult size was larger for the AquaGen and hybrids with AquaGen mothers than the 2 other groups. If untagged, the size difference might have been even smaller. Carlin tagging probably decreased growth at sea of smaller more than larger smolts, and may have had little, if any, effect of the growth of smolts larger than 19 or 20 cm (Eames & Hino 1983, Berg & Berg 1990, Strand et al. 2002). Although the growth capacity of AquaGen salmon is large, the growth in nature is not exceptionally fast. Salmon have flexible growth rates that are strongly influenced by their energy con-

sumption. In a competitive, wild environment, the full growth potential of this farmed salmon may not have been realized. The smallest minimum sizes may be associated with paternal inheritance. Variable growth in River Imsa salmon could possibly be associated with an alternative male mating strategy (Wirtz-Ocaña et al. 2013), where small, anadromous males can mimic females on the spawning ground and are thereby able to approach spawning pairs and fertilize some of the eggs (Esteve 2005). Domestication of salmon involves artificial selection against low growth and adaptation to a captive environment with surplus feeding, which may not be expressed when the fish are released into the wild (Harvey et al. 2016). Thus, in the present experiment there were only minor differences in growth and adult size between surviving offspring of farmed and wild Atlantic salmon.

When farmed salmon enter natural spawning grounds, the reproductive success of males appears low, whereas farmed females often reproduce with wild males (Fleming et al. 1996, 1997, Weir et al. 2004). This should result in hybrids that exhibit increased growth potential and reduced homing, similar to farmed salmon. This may explain why salmon production has decreased in rivers where farmed salmon spawn with wild conspecifics (Fleming et al. 2000, McGinnity et al. 2003). Hybrids produced by interbreeding between domesticated and wild animals occurs in several species. In salmon, such interbreeding can induce changed homing, relevant for other species, such as trout and charr, when they escape from captivity. Hybridization with gene flow from farmed to wild salmon changes behaviour, survival and age at maturity in wild Atlantic salmon and threatens their viability (Fleming et al. 2000, Jonsson & Jonsson 2006, O'Toole et al. 2015, Bolstad et al. 2017).

Overall, the present results show that the offspring of farmed salmon and hybrids between farmed and wild salmon enter rivers for spawning, but the homing of farmed salmon is low. Inheritance from wild mothers increased the homing of the hybrids more than that from wild fathers. The growth capacity of the farmed salmon appeared not to be fully realized in nature, but minimum size at maturity was larger than that of wild conspecifics. Inheritance from a farmed mother increased minimum size of the hybrids versus that of wild salmon. Thus, hybrids between farmed and wild Atlantic salmon in nature exhibit homing and growth intermediate between their parents, and maternal inheritance determines whether the fish will be most similar to the wild or farmed salmon in these traits.

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