

Lifetime success and interactions of farm salmon invading a native population

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Farm Atlantic salmon escape and invade rivers throughout the North Atlantic annually, which has generated growing concern about their impacts on native salmon populations. A large-scale experiment was therefore undertaken in order to quantify the lifetime success and interactions of farm salmon invading a Norwegian river. Sexually mature farm and native salmon were genetically screened, radio tagged and released into the River Imsa where no other salmon had been allowed to ascend. The farm fishes were competitively and reproductively inferior, achieving less than one-third the breeding success of the native fishes. Moreover, this inferiority was sex biased, being more pronounced in farm males than females, resulting in the principal route of gene flow involving native males mating with farm females. There were also indications of selection against farm genotypes during early survival but not thereafter. However, evidence of resource competition and competitive displacement existed as the productivity of the native population was depressed by more than 30%. Ultimately, the lifetime reproductive success (adult to adult) of the farm fishes was 16% that of the native salmon. Our results indicate that such annual invasions have the potential for impacting on population productivity, disrupting local adaptations and reducing the genetic diversity of wild salmon populations.

Keywords: biological invasion; gene flow; lifetime reproductive success; hybridization; aquaculture; farm salmon

1. INTRODUCTION

The farming of Atlantic salmon (*Salmo salar*) has expanded exponentially from its beginnings in the 1960s to its production today, which dwarfs wild salmon fishery by two orders of magnitude (Anonymous 1999). One consequence is that large numbers of farm fishes escape and enter the rivers of native salmon throughout the North Atlantic (Hansen *et al.* 1991, and references therein; Carr *et al.* 1997; Youngson *et al.* 1997; Fiske & Lund 1999). The impact of such invasions has been the subject of mounting concern (Hansen *et al.* 1991; Hindar *et al.* 1991; Hutchinson 1997; Naylor *et al.* 1998), particularly given a global decline in native salmon populations (Parrish *et al.* 1998; Kellogg 1999).

This concern arises from the potentially deleterious effects of ecological and genetic interactions between farm and native salmon. Farm salmon may compete directly with native salmon for resources such as space, food or mates, alter predation regimes and transfer diseases and parasites (reviewed in Jonsson 1997). Moreover, farm salmon are commonly derived from non-indigenous sources and their genetic make-up has been altered through selective breeding and domestication (Hansen *et al.* 1991, and references therein; Hutchinson 1997, and references therein; Mjølnerød *et al.* 1997; Clifford *et al.* 1998; Norris *et al.* 1999). Interbreeding thus represents an additional threat to native populations (i.e. disruption of local adaptations and genetic homogenization). However, no study to date has quantified the life-

time success (adult to adult) and interactions resulting from farm salmon invading a native population. We therefore undertook a large-scale experiment in order to simulate such an invasion of farm salmon into a Norwegian river and quantify their lifetime success and interactions with native salmon.

2. MATERIAL AND METHODS

(a) *Anadromous adults and breeding success*

The experimental release of farm Atlantic salmon was conducted in the River Imsa, south-western Norway (58°59' N, 5°58' E), a small, 1 km long river supporting a small native population of Atlantic salmon (described in Jonsson *et al.* 1998). Adult farm salmon (fifth generation) derived from Norway's national breeding programme (Gjedrem *et al.* 1991) and reared locally were transported to the Norwegian Institute for Nature Research (NINA) station at Ims in September–October 1993 where they were maintained in 4000-l holding tanks. Over 50% of the world's farm Atlantic salmon derive from this programme or its predecessor with the fishes having been used in Australia, Canada, Chile, Ireland, Norway, Scotland and the USA. Native salmon returning to the Imsa were collected during July–October in a fish trap (100 m upstream of the river mouth) that controls the ascent and descent of fishes (Jonsson *et al.* 1998), and held in similar 4000-l tanks.

The fishes were biopsied and screened genetically for the muscle enzyme *MEP-2*^{*} during the second half of October (Cross & Ward 1980). Twenty-two farm salmon homozygous for *MEP-2*^{*} (*125/*125) and 17 native salmon homozygous for *MEP-2*^{*} (*100/*100) were selected for release. The selection reflected the background gene frequencies of the farm (0.399 *100 allele and 0.601 *125 allele) (*n* = 207) and native populations (0.595 *100 allele and 0.405 *125 allele) (*n* = 63). Natural

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selection acting on *MEP-2** or a linked locus has been suggested (Jordan *et al.* 1997), but does not appear to influence cohorts of the Imsa population significantly (genotype proportions in 18 groups of half-sibs sampled as age 0+ on two occasions following hatching, Fisher's combined probability $p > 0.20$, and genotype proportions of five-year classes sampled as age 1+, 2+ or 3+ smolts, combined $p > 0.90$; age 0+ refers to fishes in the first year of life, age 1+ refers to fishes in the second year, subsequent to winter annulus formation, etc.) (K. Hindar, unpublished data). Moreover, parallel experiments using non-genetically marked fishes have produced similar results to those found in the present release experiment (Fleming *et al.* 1996; Einum & Fleming 1997; Fleming & Einum 1997; present experimental arena study). The selected farm salmon were larger (mean length \pm s.d. = 575 ± 34 mm) than the native salmon (545 ± 39 mm) ($F_{1,35} = 6.75$ and $p = 0.014$ and no sex or interaction effects $p > 0.30$) reflecting the natural size difference.

The selected fishes were radio tagged (Økland *et al.* 1996) and released into the Imsa above the fish trap on 4 November 1993. They were subsequently tracked daily until 22 December (excluding 21, 25 and 28 November and 10 December) and then again on 28 December and 2, 6 and 10 January. The locations of all individuals were recorded during each tracking and visual focal observations (2 min) were made of individuals stationed in spawning areas in order to record activity.

An experiment, which involved the release of 12 farm and nine native salmon (randomly selected) into an arena designed to mimic a natural spawning environment (47 m^2) (described in Fleming *et al.* 1996), was initiated on 5 November in parallel with the river release. The experiment was a smaller-scale version of that carried out earlier by Fleming *et al.* (1996) and was designed to supplement the river release by providing more detailed data about breeding behaviour and success. The arena was monitored 24 h day^{-1} by video until 23 December and spawning activity and nest locations were recorded. This was supplemented with daily manual observations, which included a 20 min scan sample of behaviour. The arena was excavated during 14 and 15 March 1994 and all nests present were recovered and the number of live and dead eggs recorded. The nests were assigned to females using spawning records and cross-checked using egg-size data. The breeding success for females was measured as the total number of live embryos recovered from their nests. Male breeding success was calculated as the number of live embryos recovered from nests that they fertilized and, in cases of multiple-male paternity (9% of spawnings involved both farm and native males), it was calculated following the method of Fleming *et al.* (1996). This method incorporates the order of male precedence at spawning, which is an important determinant of fertilization success in Atlantic salmon (Mjølnerød *et al.* 1998).

All fishes from the experimental arena and those recovered from the river were examined at the end of the spawning season for gamete retention, which was expressed as a percentage of their estimated pre-spawning gamete investment. Females' initial fecundity was estimated from their weight using relations established for Imsa females (Jonsson *et al.* 1996) and for 18 unspawned farm females sampled during the study (fecundity = $0.0091 \times (\text{weight})^{1.814}$) ($r^2 = 0.644$ and $p < 0.001$). These relationships were also used to estimate the potential egg deposition in the river by the farm and native females. Ten fresh eggs from each of the 18 farm females were also weighed individually in order to compare them with those of Imsa females (Jonsson *et al.* 1996). Males' initial testes weight was estimated from

gonadal-somatic indices for Imsa males (Jonsson *et al.* 1991) and for 17 unspawned farm males sampled during the study (mean \pm s.d. = $6.08 \pm 1.51\%$).

(b) *Offspring and lifetime reproductive success*

Offspring (age 0+ parr) from the spawnings in the river were sampled by electrofishing the length of the Imsa on 6 and 7 September ($n = 55$) and 18 and 19 October 1994 ($n = 67$). The location of capture was recorded and the fishes were sacrificed, weighed, their lengths measured and stomachs dissected and a sample of muscle was placed in ethanol and another was frozen. Their stomach contents were analysed following the methods of Hindar *et al.* (1988) and Breistein & Nøst (1997) and a similarity index was calculated following Schoener (1968).

The origin of the offspring was accurately identified by genetic typing (*MEP-2**) since all spawners had been genetically screened and no spawning had occurred during the previous two years (i.e. few if any mature male parr present) (Jonsson *et al.* 1998). In addition, DNA was extracted from the ethanol-preserved tissue by phenol-chloroform extraction. The mitochondrial ND-1 gene (NADH dehydrogenase 1) was polymerase chain reaction amplified (Cronin *et al.* 1993) and digested with restriction enzymes showing fragment length polymorphism in *HaeIII* and *RsaI* digests (no additional mtDNA heterogeneity was found at two other ND genes).

Juveniles descending the Imsa to the ocean in 1995–1996 were captured in the fish trap, anaesthetized, measured, muscle biopsied, tagged with a unique Carlin tag and released after 24 h recovery. The biopsy of every other fish was analysed for *MEP-2** expression (i.e. 50% of all migrants); no significant differences existed between typed and untyped fish (descent date, length, weight and condition factor) ($p > 0.50$). The production of downstream migrants relative to the estimated total potential egg deposition (described in §2(a)) was compared to the population's stock-recruitment relationship (Jonsson *et al.* 1998).

Returns of adult offspring were recorded from the coastal and river fisheries (Carlin tag recoveries) and the Imsa fish trap. Fishes recovered at the fish trap were weighed and their lengths measured and tissues sampled. The data for fishes captured in the fishery were less complete, but all individuals could be genetically typed by cross-referencing their Carlin tag identification to the tissue samples taken at the Imsa fish trap during juvenile seaward migration.

(c) *Statistical analysis*

The fishes' growth rate from emergence was adjusted to a common body mass and calculated following Elliott & Hurley (1997). Emergence was estimated based on the mean spawning dates for the farm and native females, daily river temperatures and equations relating temperature to hatching (Crisp 1981) and emergence (Jensen *et al.* 1991).

The predicted effect of t generations of one-way gene flow from farm salmon on the allele frequency q_t of the recipient (native) population was calculated as

$$q_t = (1 - m)^t q_0 + [1 - (1 - m)^t] q_m, \quad (1)$$

where q_0 is the allele frequency of the recipient population before migration and q_m is the allele frequency of the migrants (Hedrick 1983). The equation applies not only to allele frequencies but also approximately to weakly selected quantitative genetic traits having an additive genetic basis (Bulmer 1980).

Table 1. Comparisons of the native and farm spawners in the River Imsa and the experimental arena (control)

(Nesting by one farm and one native female and courting by two farm and one native male was never observed for the river data for initiation of nesting/courting (Julian day) and nesting location. Intact carcasses were recovered from six female and five male native salmon and seven female and seven male farm salmon for the river data for gamete retention. One farm female did not spawn for the experimental arena data for egg survival in nests. The breeding success data were adjusted for unequal variances. The data are means \pm standard deviations or medians with quartiles in parentheses. The statistics are *t*-tests, ANCOVAs with body weight as a covariate ($p < 0.05$) or Mann–Whitney *U*-tests (ζ). * $p < 0.05$, ** $p < 0.01$.)

location trait	females			males		
	native	farm	statistic	native	farm	statistic
river						
daily migration (m)	59 \pm 24	59 \pm 29	$t_{17} = 0.328$	111 \pm 44	121 \pm 27	$t_{18} = 0.63$
initiation of nesting/courting (Julian day)	331 \pm 12	315 \pm 6	$t_{15} = 3.87^{**}$	311 \pm 2	311 \pm 3	$t_{15} = 0.01$
nesting location (metres upstream of fish trap)	316 \pm 155	312 \pm 219	$t_{15} = 0.42$	—	—	—
females courted/male courting (number of observations)	4.0 (1.0–8.0)	6.0 (2.3–8.3)	$\zeta = 0.66$	6.0 (3.0–9.0)	2.0 (1.0–2.0)	$\zeta = 2.15^*$
gamete retention (% of initial gametes)	0.8 (0.3–2.5)	1.1 (0.2–2.5)	$\zeta = 0.08$	30.6 (13.3–75.8)	104.8 (81.2–120.3)	$\zeta = 2.03^*$
experimental arena						
initiation of nesting/courting (Julian day)	324 (311–361)	311 (310–315)	$\zeta = 1.10$	311 \pm 1	311 \pm 1	$t_9 = 0.09$
females courted/males courting (number of observations)	30.0 \pm 18.9	15.0 \pm 16.3	$t_8 = 1.36$	29.8 \pm 17.9	11.7 \pm 7.8	$F_{1,8} = 5.67^*$
gamete retention (% of initial gametes)	0.3 (0.1–0.6)	7.7 (0.1–28.5)	$\zeta = 1.28$	82.4 (54.3–85.1)	104.3 (86.9–107.1)	$\zeta = 2.01^*$
female nests/male spawnings	6.3 \pm 1.3	3.8 \pm 1.9	$t_8 = 2.85^*$	7.0 \pm 5.2	2.2 \pm 2.4	$F_{1,8} = 9.88^*$
egg survival in nests (%)	82.8 \pm 1.9	56.5 \pm 15.6	$t_7 = 2.97^*$	—	—	—
breeding success (embryos parented)	1912 \pm 182	611 \pm 539	$t_{6,5} = 5.46^{**}$	1516 \pm 1303	360 \pm 554	$F_{1,8} = 7.43^*$

Half of the genetic difference between the donor and recipient remains after $t_{0,5} = \ln(0.5)/\ln(1-m)$ generations. The calculations assume that the effects of genetic drift and selection in the recipients are small relative to migration and that the allele frequencies of the migrants remain stable.

All of the proportion/percentage data were arcsine, square-root transformed and the courting and breeding success data were log transformed prior to analysis in order to meet the assumptions of analysis of variance. Data that did not meet the requirements for parametric analysis were analysed using non-parametric tests.

3. RESULTS

(a) Reproduction

The farm and native adults had similar migration patterns and nesting locations in the river, though the farm females spawned before the native females (table 1). Courting by both the farm and native males began shortly after release. However, the native males courted females more often than the farm males and retained less of their initial testes unspawned (table 1). Evidence from the experimental arena indicates that the latter correlates inversely with the number of spawnings (Spearman $r = -0.695$ and $p = 0.018$).

The findings from the experimental arena paralleled those from the river. The farm females began spawning before the native females while both male types began courting females almost immediately after release. Moreover, the farm males appeared competitively disadvantaged, courting females less frequently than native

males (table 1) and at times showing inappropriate mating behaviour. As a result, they participated in fewer spawnings and retained a larger proportion of their testes unspawned. Ultimately, the farm males attained just 24% of the breeding success of the native males. The farm females also incurred a breeding disadvantage, constructing fewer nests, having lower egg survival and achieving only 32% of the success of the native females. The eggs of the farm females (mean \pm s.d. = 804 \pm 128 mg) ($n = 18$) were also significantly smaller than those of the native females (896 \pm 144 mg) ($n = 104$) ($t_{120} = 2.53$ and $p < 0.05$) (Jonsson *et al.* 1996).

(b) Early life history

The proportion of native to farm genotypes among the offspring (age 0+ parr) from spawnings in the river shifted significantly from that of the spawners ($\chi^2 = 37.97$, d.f. = 1 and $p < 0.001$) (figure 1). Most of the fishes were now of pure native origin (65.1%) with farm genetic representation occurring mainly through hybridization with native fishes. The maternal origin, which was identified using the mitochondrial ND-1 gene, revealed that 25 out of the 31 hybrid offspring had a unique farm female haplotype (found in eight farm females), five a common haplotype (found in three farm and six native females) and none a unique native female haplotype (found in two native females; one offspring was not analysable). Thus, most if not all hybrids had farm mothers.

The farm adults had only 19% of the reproductive success of the native fishes up to this stage (i.e. breeding

and early survival). Furthermore, based on breeding success in the experimental arena (farm:native 28%), early survival of the farm genotypes was estimated at 70% that of the native genotypes. Thereafter, there was little evidence of differential freshwater survival (parr to smolt, $\chi^2 = 1.85$ and $p = 0.397$) (figure 1).

However, there were indications of resource competition as the diets of the farm, native and hybrid offspring were similar, having a mean diet overlap of $82 \pm 7\%$ (proportional composition of different food types, ANOVAs controlling for sampling date $p > 0.30$). In addition, the total production of smolts (i.e. oceanic migrants) from the spawnings was 28% below that expected based on the potential egg deposition (48 831) and the stock-recruitment relationship for the River Imsa (Jonsson *et al.* 1998). Moreover, the smolt production by the native females (494 pure native smolts plus 0–17% (based on mtDNA analyses of age 0+ fishes) of the farm \times native smolts) was 31–32% below that expected in the absence of farm females. This effect may reflect competitive asymmetries as the native juveniles were smaller at age 0+ (figure 2) (also weight $F_{2,116} = 4.67$ and $p = 0.011$, and controlling for sampling date $p < 0.001$) due to differences in the female spawning dates (table 1) and offspring growth rates ($F_{2,116} = 3.09$ and $p = 0.049$, and controlling for sampling date $p < 0.001$). Native offspring (age 0+ parr) were captured further upstream than their farm and farm \times native counterparts ($F_{2,115} = 12.55$ and $p < 0.001$, and independent of sampling date $p = 0.295$ and fish weight $p = 0.143$).

(c) Seaward migration and return

Most fishes descended as smolts in the spring with 13% (93 out of 718) descending as parr during the winter of 1995–1996. The proportional compositions of the farm, native and hybrid fishes did not differ between smolts and descending parr ($\chi^2 = 0.50$ and $p = 0.778$). There were distinct behavioural and life history differences among the smolts as the farm smolts descended earlier ($F_{2,303} = 70.50$ and $p < 0.001$) (year $F_{1,303} = 127.13$ and $p < 0.001$) and at a younger age ($\chi^2 = 41.91$ and $p < 0.001$) (figure 1) than the wild smolts, with the hybrids being intermediate (all pairwise comparisons $p < 0.05$ with Bonferroni adjustment). The hybrid smolts were also longer (figure 2) and heavier than the native smolts ($F_{1,289} = 18.21$ and $p < 0.001$, and controlling for smolt age $p < 0.001$), while the farm smolts weighed less for a given length than their counterparts (figure 2).

There was no significant difference between the offspring types in survival from seaward migration to maturity ($\chi^2 = 0.04$ and $p = 0.840$) (figure 1). As a result, the lifetime reproductive success (adult to adult) of the farm salmon was 16% that of the native salmon. All adult recaptures occurred in either the coastal fishery or the River Imsa and no fishes were reported straying into other rivers. There were no significant differences between the offspring types in body size and condition at recapture (figure 2) or in sea age at maturity (22 out of 26 matured after one year at sea) (Mann–Whitney U -test, $Z = 0.14$ and $p = 0.929$, with single farm fish excluded). However, the mean age at maturity of the hybrid fishes (mean \pm s.d. = 3.4 ± 0.5 years) was less than that of the native fishes (4.2 ± 0.4 years) (Mann–Whitney

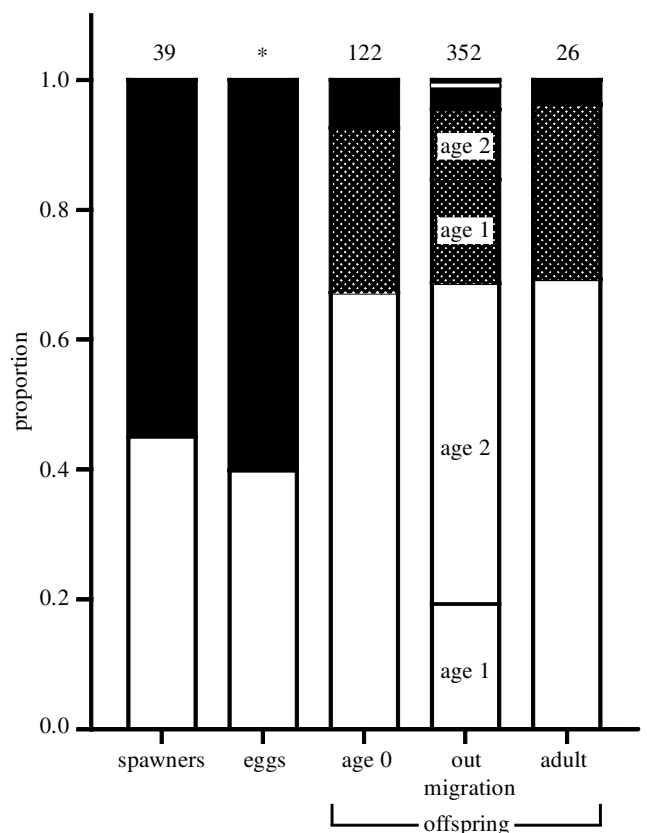


Figure 1. Changes in the proportional constitution of the Atlantic salmon population in the River Imsa following the release of native and farm spawners. The number above each bar represents either the total population size (spawners and adult offspring) or the sample size examined at each life stage (age 0+ and out migration). Two age groups of out migrants existed, age 1+ and 2+ and are stacked on top of each other for each offspring type. The asterisk denotes that the potential egg deposition was 19 443 for the native females and 29 388 for the farm females (see §2). Solid bars, farm offspring; open bars, native offspring; hatched bars, hybrid offspring.

U -test, $Z = 3.11$ and $p = 0.002$) because of differences in their age at smolting and poor survival of native age 1+ smolts (none were recaptured).

4. DISCUSSION AND CONCLUSIONS

We were able to document, for the first time to our knowledge, the lifetime success of farm salmon invading a natural river and found it to be 16% that of the native fish. Both the results from the river and the parallel experiment in the stream arena indicated that breeding was the major bottleneck impeding the invasion. The farm salmon reared to maturity were competitively and reproductively inferior, achieving less than one-third the breeding success of the native fishes. This may be a general pattern for farm salmon invading native populations (Fleming *et al.* 1996; Clifford *et al.* 1998). The present results also indicated that this inferiority was sex biased, being more pronounced among farm males than females. Few if any of the farm \times native offspring recovered from the river were fathered by farm males. Thus, gene flow occurred mainly through native males breeding with

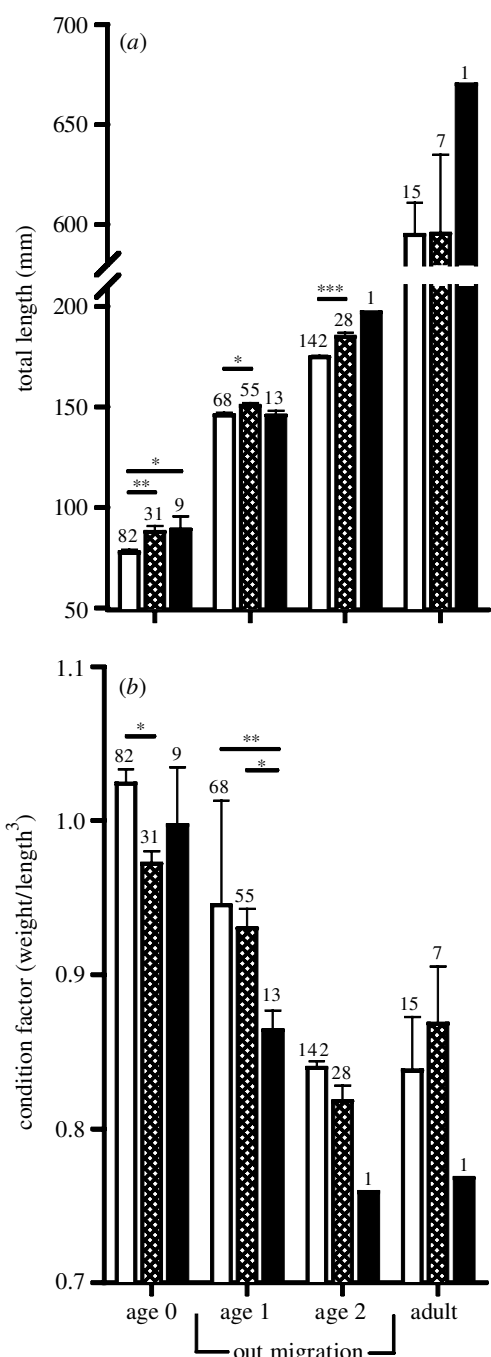


Figure 2. (a) Comparison of the mean (+1 standard error) body length at various life stages for the native (open bars), farm (solid bars) and hybrid (hatched bars) offspring. (b) Comparison of condition factor for the same groups. The sample size is given above each bar. Significant pairwise differences (Tukey test for multiple comparisons) are shown. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

farm females. This parallels the findings of Fleming *et al.* (1996) where farm males were found to be behaviourally deficient, infrequently attained access to spawning females and exhibited inappropriate mating behaviour.

The lower early survival of the farm genotypes compared to the native genotypes in the river also appeared to constrain invasion, though to a lesser extent than breeding. McGinnity *et al.* (1997) reported a similar degree of differential survival between farm and native genotypes in age 0+ juveniles outplanted as eggs in an

Irish river. Both findings may reflect the smaller egg size of farm females, which can affect survival after emergence directly (Einum & Fleming 2000) and differences in their innate behaviour, including predator avoidance (Einum & Fleming 1997; Fleming & Einum 1997). However, the survival differences occurred principally during the earliest life-history stages (see also McGinnity *et al.* 1997), which may prove to be common following the intense natural selection of early life (Einum & Fleming 2000).

The potential for significant resource competition existed as there was considerable overlap in the diets of the native, farm and hybrid offspring (see also Einum & Fleming 1997). Furthermore, there were indications of competitive displacement as the offspring distributions differed despite the native and farm females having had similar nesting locations. This may reflect the faster growth rate and, thus, larger size of the farm and farm \times native offspring than the native offspring (see also Einum & Fleming 1997; McGinnity *et al.* 1997). Norwegian farm salmon have undergone selection for rapid growth (Gjedrem *et al.* 1991), which may also explain their greater allocation of resources to length than weight growth (body condition) (figure 2), a pattern consistent with increased growth hormone production (Johnsson *et al.* 1996). Similarly, McGinnity *et al.* (1997) reported competitive displacement; however, in contrast to the present study the native offspring were displaced downstream into a lake by faster-growing and larger farm and hybrid offspring.

Moreover, the present results indicate that the production of seaward migrants was depressed, particularly that by the native females, which was more than 30% below that expected. While stock-recruitment relationships are notoriously variable, this depression was the second largest in 16 years (Jonsson *et al.* 1998) and occurred despite the absence of competition from older salmon cohorts, which should have been favourable for smolt production (Kennedy & Strange 1980; Gibson 1993). Moreover, the environmental conditions did not appear unfavourable because the juvenile growth was good, age at smolting was young (cf. Jonsson *et al.* 1998) and indications from other North-East Atlantic salmon rivers suggested that the broadscale conditions were favourable for smolt production (Anonymous 1999). Alternatively, the depression in smolt production may have reflected fluctuating selection on offspring type, with competition from the farm and hybrid offspring depressing the wild offspring survival during one or more life-history episodes and maladaptation depressing the farm and hybrid offspring at other times (McGinnity *et al.* 1997). While the definitive cause of the depression is unknown, it appears likely that interactions with the farm and hybrid salmon played a role.

There were no indications that the differences in age, size and condition at smolting and timing of descent affected the relative survival to maturity of the different offspring types overall or at least that of the native and hybrid fishes. Thus, the bottlenecks to the invasion by farm salmon occurred principally during breeding and early life history. The poor marine survival of age 1+ wild smolts compared with that of hybrid and age 2+ wild smolts is likely explained by their small size and late migration (cf. Hansen & Quinn 1998).

During the 1990s, escaped farm fishes were estimated to have composed 20–40% of the salmon recorded over large areas of the North Atlantic (Hansen *et al.* 1999) and more than 80% of the salmon in some Norwegian spawning populations (Lund *et al.* 1991; Fiske & Lund 1999). This approaches and exceeds that of our experiment (55%). The gene flow from the farm to native salmon, which occurred during one generation in this experiment, was $m = 0.19$. One-way gene flow of this magnitude is a potent evolutionary force (Hedrick 1983; Barton 1992). The native population will eventually be composed of individuals that have all descended from the migrants and this situation is approached rapidly for selectively neutral loci and/or traits. For $m = 0.19$, the genetic difference between the donor (farm) and recipient (native) population is halved every 3.3 generations, though this will be partly dependent on the fitness of hybrids and backcrosses during subsequent generations. The shorter generation time of the hybrid than native fish observed in the present study would also tend to increase the rate of introgression (Hedrick 1983), though this may not be a general pattern (McGinnity *et al.* 1997). For rates of gene flow reflecting average proportions of escaped salmon in the North Atlantic, the half-life of the difference would be in the order of ten generations. As farm salmon have been shown to differ genetically from their wild origin in allele frequencies, allelic diversity and quantitative traits (Fleming & Einum 1997; Mjølnerød *et al.* 1997; Norris *et al.* 1999), it is clear that escaped farm salmon may have wide-ranging genetic effects on native salmon populations. Such effects are frequently negative (reviewed by Hindar *et al.* 1991) and purging by natural selection will be hindered by the annual, repeated invasions of escaped farm salmon. This genetic impact comes on top of the potential effects of intraspecific interactions on productivity (e.g. smolt production) and calls into question the long-term viability of many salmon populations.

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REFERENCES

- Anonymous 1999 *Report of the Working Group on North Atlantic Salmon*. Copenhagen, Denmark: International Council for Exploration of the Sea CM 1999/ACFM:14.
- Barton, N. H. 1992 On the spread of new gene combinations in the third phase of Wright's shifting balance theory. *Evolution* **46**, 551–557.
- Breistein, J. & Nøst, T. 1997 Standardization of methods: biomass of freshwater invertebrates. *NINA Oppdragsmelding* **480**, 1–19. (In Norwegian with an English abstract.)
- Bulmer, M. G. 1980 *The mathematical theory of quantitative genetics*. Oxford, UK: Clarendon Press.
- Carr, J. W., Anderson, J. M., Whoriskey, F. G. & Dilworth, T. 1997 The occurrence and spawning of cultured Atlantic salmon (*Salmo salar*) in a Canadian river. *ICES J. Mar. Sci.* **54**, 1064–1073.
- Clifford, S. L., McGinnity, P. & Ferguson, A. 1998 Genetic changes in Atlantic salmon (*Salmo salar*) populations of north-west Irish rivers resulting from escapes of adult farm salmon. *Can. J. Fish. Aquat. Sci.* **55**, 358–363.
- Crisp, D. T. 1981 A desk study of the relationship between temperature and hatching time for the eggs of five species of salmonid fishes. *Freshw. Biol.* **11**, 361–368.
- Cronin, M. A., Spearman, W. J., Wilmot, R., Patton, J. C. & Bickham, J. W. 1993 Mitochondrial-DNA variation in chinook (*Oncorhynchus tshawytscha*) and chum salmon (*O. keta*) detected by restriction enzyme analysis of polymerase chain-reaction (PCR) products. *Can. J. Fish. Aquat. Sci.* **50**, 708–715.
- Cross, T. F. & Ward, R. D. 1980 Protein variation and duplicate loci in the Atlantic salmon, *Salmo salar* L. *Genet. Res.* **36**, 147–165.
- Einum, S. & Fleming, I. A. 1997 Genetic divergence and interactions in the wild among native, farmed and hybrid Atlantic salmon. *J. Fish Biol.* **50**, 634–651.
- Einum, S. & Fleming, I. A. 2000 Highly fecund mothers sacrifice offspring survival to maximize fitness. *Nature* **405**, 565–567.
- Elliott, J. M. & Hurley, M. A. 1997 A functional model for maximum growth of Atlantic salmon parr, *Salmo salar*, from two populations in north-west England. *Funct. Ecol.* **11**, 592–603.
- Fiske, P. & Lund, R. A. 1999 Escapees of reared salmon in coastal and riverine fisheries in the period 1989–1998. *NINA Oppdragsmelding* **603**, 1–23 (in Norwegian with an English abstract).
- Fleming, I. A. & Einum, S. 1997 Experimental tests of genetic divergence of farmed from wild Atlantic salmon due to domestication. *ICES J. Mar. Sci.* **54**, 1051–1063.
- Fleming, I. A., Jonsson, B., Gross, M. R. & Lamberg, A. 1996 An experimental study of the reproductive behaviour and success of farmed and wild Atlantic salmon (*Salmo salar*). *J. Appl. Ecol.* **33**, 893–905.
- Gibson, R. J. 1993 The Atlantic salmon in fresh water: spawning, rearing and production. *Rev. Fish Biol. Fish.* **3**, 39–73.
- Gjedrem, T., Gjøen, H. M. & Gjerde, B. 1991 Genetic origin of Norwegian farmed Atlantic salmon. *Aquaculture* **98**, 41–50.
- Hansen, L. P. & Quinn, T. P. 1998 The marine phase of the Atlantic salmon (*Salmo salar*) life cycle, with comparisons to Pacific salmon. *Can. J. Fish. Aquat. Sci.* **55**(Suppl. 1), 104–118.
- Hansen, L. P., Håstein, T., Nævdal, G., Saunders, R. L. & Thorpe, J. E. (ed.) 1991 Interactions between cultured and wild Atlantic salmon. *Aquaculture* **98**, 1–324.
- Hansen, L. P., Jacobsen, J. A. & Lund, R. A. 1999 The incidence of escaped farmed Atlantic salmon, *Salmo salar* L., in the Faroese fishery and estimates of catches of wild salmon. *ICES J. Mar. Sci.* **56**, 200–206.
- Hedrick, P. W. 1983 *Genetics of populations*. Boston, MA: Science Books International.
- Hindar, K., Jonsson, B., Andrew, J. H. & Northcote, T. G. 1988 Resource utilization of sympatric and experimentally allopatric cutthroat trout and Dolly Varden charr. *Oecologia* **74**, 481–491.
- Hindar, K., Ryman, N. & Utter, F. 1991 Genetic effects of cultured fish on natural fish populations. *Can. J. Fish. Aquat. Sci.* **48**, 945–957.
- Hutchinson, P. (ed.) 1997 Interactions between salmon culture and wild stocks of Atlantic salmon: the scientific and management issues. *ICES J. Mar. Sci.* **54**, 963–1225.
- Jensen, A. J., Johnsen, B. O. & Saksgård, L. 1991 Temperature requirements in Atlantic salmon (*Salmo salar*), brown trout (*Salmo trutta*), and Arctic charr (*Salvelinus alpinus*) from hatching to initial feeding compared with geographic distribution. *Can. J. Fish. Aquat. Sci.* **46**, 786–789.
- Jonsson, J. I., Petersson, E., Jönsson, E., Björnsson, B. Th. & Järvi, T. 1996 Domestication and growth hormone alter anti-predator behaviour and growth patterns in juvenile brown trout, *Salmo trutta*. *Can. J. Fish. Aquat. Sci.* **53**, 1546–1554.

- Jonsson, B. 1997 A review of ecological and behavioural interactions between cultured and wild Atlantic salmon. *ICES J. Mar. Sci.* **54**, 1031–1039.
- Jonsson, N., Jonsson, B. & Hansen, L. P. 1991 Energetic cost of spawning in male and female Atlantic salmon (*Salmo salar* L.). *J. Fish Biol.* **39**, 739–744.
- Jonsson, N., Jonsson, B. & Fleming, I. A. 1996 Does early growth cause a phenotypically plastic response in egg production of Atlantic salmon? *Funct. Ecol.* **10**, 89–96.
- Jonsson, N., Jonsson, B. & Hansen, L. P. 1998 The relative role of density-dependent and density-independent survival in the life cycle of Atlantic salmon *Salmo salar*. *J. Anim. Ecol.* **67**, 751–762.
- Jordan, W. C., Verspoor, E. & Youngson, A. F. 1997 The effect of natural selection on estimates of genetic divergence among populations of Atlantic salmon. *J. Fish Biol.* **51**, 546–560.
- Kellogg, K. A. 1999 Salmon on the edge. *Trends Ecol. Evol.* **14**, 45–46.
- Kennedy, G. J. A. & Strange, C. D. 1980 Population changes after two years of salmon (*Salmo salar* L.) stocking in upland trout (*Salmo trutta* L.) streams. *J. Fish Biol.* **17**, 577–586.
- Lund, R. A., Økland, F. & Hansen, L. P. 1991 Farmed Atlantic salmon (*Salmo salar*) in fisheries and rivers in Norway. *Aquaculture* **98**, 143–150.
- McGinnity, P., Stone, C., Taggart, J. B., Cooke, D., Cotter, D., Hynes, R., McCamley, C., Cross, T. & Ferguson, A. 1997 Genetic impact of escaped farmed Atlantic salmon (*Salmo salar* L.) on native populations: use of DNA profiling to assess freshwater performance of wild, farmed, and hybrid progeny in a natural river environment. *ICES J. Mar. Sci.* **54**, 998–1008.
- Mjølnerød, I. B., Refseth, U. H., Karlsen, E., Balstad, T., Jakobsen, K. S. & Hindar, K. 1997 Genetic differences between two wild and one farmed population of Atlantic salmon (*Salmo salar*) revealed by three classes of genetic markers. *Hereditas* **127**, 239–248.
- Mjølnerød, I. B., Fleming, I. A., Refseth, U. H. & Hindar, K. 1998 Mate and sperm competition during multiple-male spawnings of Atlantic salmon. *Can. J. Zool.* **76**, 70–75.
- Naylor, R. L., Goldburg, R. J., Mooney, H., Beveridge, M., Clay, J., Folke, C., Kautsky, N., Lubchenco, J., Primavera, J. & Williams, M. 1998 Nature's subsidies to shrimp and salmon farming. *Science* **282**, 883–884.
- Norris, A. T., Bradley, D. G. & Cunningham, E. P. 1999 Microsatellite genetic variation between and within farmed and wild Atlantic salmon (*Salmo salar*) populations. *Aquaculture* **180**, 247–264.
- Økland, F., Lamberg, A., Heggberget, T. G., Fleming, I. A. & McKinley, R. S. 1996 Identification of spawning behaviour in Atlantic salmon (*Salmo salar* L.) by radiotelemetry. In *Underwater biotelemetry: Proceedings of the First Conference and Workshop on Fish Telemetry in Europe* (ed. E. Baras & J. C. Philippart), pp. 35–46. Liège, Belgium: University of Liège.
- Parrish, D. L., Behnke, R. J., Gephart, S. R., McCormick, S. D. & Reeves, G. H. 1998 Why aren't there more Atlantic salmon (*Salmo salar*)? *Can. J. Fish. Aquat. Sci.* **55** (Suppl. 1), 281–287.
- Schoener, T. W. 1968 The *Anolis* lizards of Bimini: resource partitioning in a complex fauna. *Ecology* **49**, 704–726.
- Youngson, A. F., Webb, J. H., MacLean, J. C. & Whyte, B. M. 1997 Frequency of occurrence of reared Atlantic salmon in Scottish salmon fisheries. *ICES J. Mar. Sci.* **54**, 1216–1220.

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