Fitness reduction and potential extinction of wild populations of Atlantic salmon, *Salmo salar*, as a result of interactions with escaped farm salmon

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The high level of escapes from Atlantic salmon farms, up to two million fishes per year in the North Atlantic, has raised concern about the potential impact on wild populations. We report on a two-generation experiment examining the estimated lifetime successes, relative to wild natives, of farm, F_1 and F_2 hybrids and BC_1 backcrosses to wild and farm salmon. Offspring of farm and 'hybrids' (i.e. all F_1, F_2 and BC_1 groups) showed reduced survival compared with wild salmon but grew faster as juveniles and displaced wild parr, which as a group were significantly smaller. Where suitable habitat for these emigrant parr is absent, this competition would result in reduced wild smolt production. In the experimental conditions, where emigrants survived downstream, the relative estimated lifetime success ranged from 2% (farm) to 89% (BC_1 wild) of that of wild salmon, indicating additive genetic variation for survival. Wild salmon primarily returned to fresh water after one sea winter (1SW) but farm and 'hybrids' produced proportionately more 2SW salmon. However, lower overall survival means that this would result in reduced recruitment despite increased 2SW fecundity. We thus demonstrate that interaction of farm with wild salmon results in lowered fitness, with repeated escapes causing cumulative fitness depression and potentially an extinction vortex in vulnerable populations.

Keywords: escaped farm salmon; common garden experiment; DNA profiling; outbreeding depression; lifetime success; extinction vortex

1. INTRODUCTION

The increase of Atlantic salmon culture in the North Atlantic to a current level of *ca.* 700 000 tonnes, together with the vulnerability to damage of marine net cages, has meant that large-scale escapes are now frequent occurrences. Escapes occur both during routine handling and as a result of large-scale accidents, with, for example, 600 000 salmon escaping in a single storm incident in the Faroes in 2002 (Atlantic Salmon Federation 2002). It is estimated that some two million salmon escape each year in the North Atlantic region, which is *ca.* 50% of the total prefishery abundance of wild salmon in the area (based on data in Atlantic Salmon Federation 2002). In Norway, on average, about one-third of adult salmon entering rivers are escaped fishes, rising to over 80% in some rivers (Fiske & Lund 1999). On the east coast of North America, escaped farm salmon outnumber wild fishes by as much as 10 to one in some rivers (Atlantic Salmon Federation 2002). Fears have been expressed (Hansen *et al.* 1991; Hindar *et al.* 1991; Youngson *et al.* 1998; McDowell 2002) about the potential detrimental genetic and other changes that may occur in wild populations as a result of escaped farm salmon entering rivers and interacting with

wild populations. Because natural populations of Atlantic salmon are a major resource for angling, tourism and commercial exploitation, as well as being an important component of biodiversity with cultural and aesthetic significance, these intrusions are of increasing concern, especially as the species is now extinct, or in critical condition, in over 27% of rivers, and endangered or vulnerable in a further 30% (WWF 2001).

Farm Atlantic salmon are genetically different from wild populations as a result of geographical origin (e.g. Norwegian farm strains are widely used in all salmon-farming countries) and founder effects, as well as directional selection, inadvertent selection and genetic drift during domestication (Skaala *et al.* 1990; Gjedrem *et al.* 1991; Fleming & Einum 1997; Gjøen & Bentsen 1997; Johnsson *et al.* 2001; Fleming *et al.* 2002). Although their breeding performance has been shown to be inferior to that of wild salmon (Fleming *et al.* 1996, 2000), escaped farm salmon do breed successfully and hybridize with wild fishes (Lura & Sægrov 1991; Crozier 1993, 2000; Clifford *et al.* 1998), thereby potentially changing the genetic make-up, fitness (i.e. juvenile recruitment in subsequent generations) and life-history characteristics (e.g. age and timing of life-history events) of wild populations. Thus far, discussions on the topic have been largely theoretical or inferential (Hutchings 1991; Youngson *et al.* 1998). The few empirical studies undertaken (McGinnity *et al.* 1997;

Fleming *et al.* 2000) have involved only F_1 hybrids between wild and farm salmon. However, it is necessary to undertake studies for at least two generations, because F_1 hybrids often show intermediate or even enhanced performance compared with their parents (hybrid vigour), but F_2 hybrids can show reduced performance (outbreeding depression) (Templeton 1986). Because Atlantic salmon have both freshwater juvenile and marine life-history phases, it is necessary to study both these phases as well as migrations.

The only current direct method of examining quantitative genetic differences among wild, farm and 'hybrid' salmon is to carry out 'common garden' experiments, where fishes are reared from egg to adult in a communal environment. As environmental variability is eliminated, any differences found in performance will reflect genetic differences (with the exception of maternal physiological effects). The development of DNA profiling has enabled accurate parentage identification and allows direct comparison of groups from the egg stage onwards under natural conditions (Ferguson *et al.* 1995). McGinnity *et al.* (1997) reported the freshwater performance of F_1 hybrids between wild and farm salmon (in 1993 and 1994 cohorts). Here, we extend this previous study by examining the freshwater performance of second-generation F_2 hybrids and BC_1 backcrosses to wild and farm salmon (a 1998 cohort), as well as adult return from the sea for all cohorts. The results from all cohorts are combined to allow estimation of two-generation lifetime success.

2. MATERIAL AND METHODS

The experiment was undertaken in the Burrishoole system in western Ireland (McGinnity *et al.* 1997). This system consists of a freshwater lake (Lough Feeagh), connected to Lough Furnace, a tidal brackish lough, by two outlet channels with permanent smolt and adult trapping facilities ('sea entry traps'), and a number of afferent rivers (figure 1). One of these rivers (Srahrevagh: *ca.* 7250 m² of juvenile salmonid habitat) was used for the freshwater stages of the experiment and was equipped with a further trap capable of capturing all downstream juvenile migrants and upstream adults (hereafter referred to as the 'experiment river' and 'experiment trap'). Experimental details for the 1998 cohort freshwater stage were as for the 1993 and 1994 cohorts (McGinnity *et al.* 1997), with the following changes and additions for the 1998 cohort groups. Native wild Burrishoole salmon of one sea winter maturity (1SW) and 2SW farm salmon (Norwegian Mowi origin) were used, whereas 3SW and 4SW farm fishes were used for the earlier cohorts. Returning F_1 hybrid Atlantic salmon (2SW), which had been ranched from the 1994 cohort, were captured at the Burrishoole traps from August to November 1997 and used to produce the F_2 hybrids and BC_1 backcrosses (table 1). Family tie or full reciprocal mating designs were used (Winkelman & Peterson 1994), giving some 500 to 800 eggs per family, with all families being established on the same day. A muscle-tissue specimen from each parent was retained for DNA profiling. Fertilized eggs were incubated in the hatchery on the Burrishoole system until the developmental stage when eyes were visible ('eyed eggs'), with cumulative mortality being recorded daily. At this stage, live eggs were counted accurately (table 1) and families were mixed and planted out in the experiment river in artificial redds constructed according to Donaghy & Verspoor (2000). Ten eggs
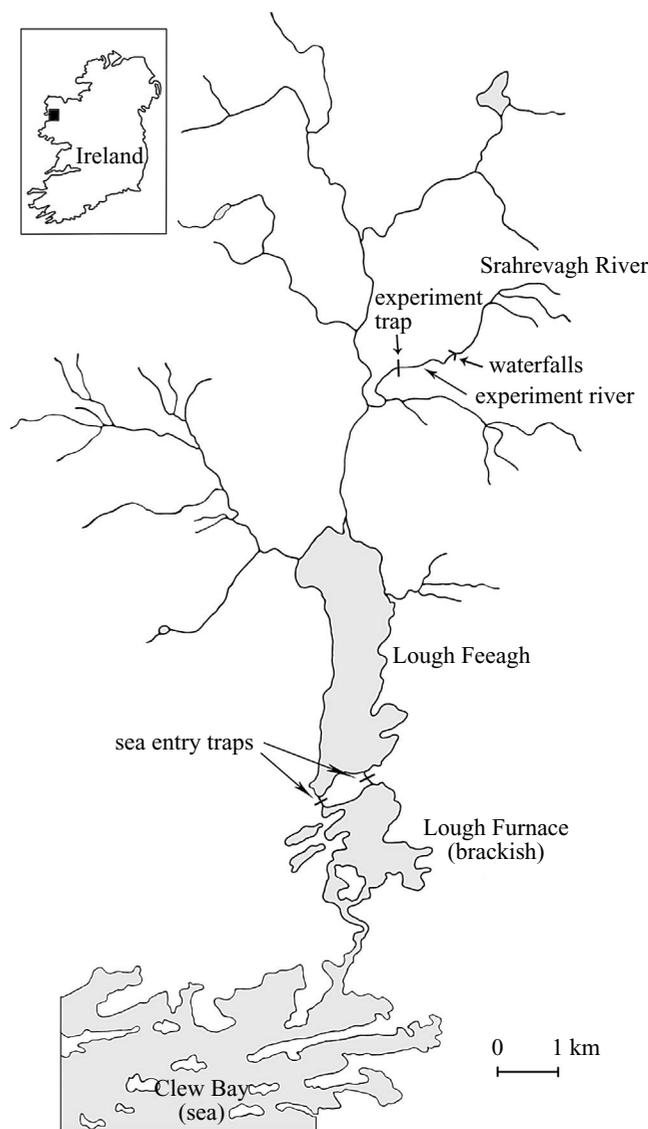

Figure 1. Sketch map of the Burrishoole river system showing the location of the experiment river and traps.

from each family were retained in the hatchery in a communal tank, with additional eggs (*ca.* 300 per family) (but not F_2 hybrids) being reared in separate group tanks. The communally reared hatchery parr were sampled ($n = 523$) in March 1999, i.e. at *ca.* 11 months of age. Juveniles were sampled ($n = 295$) from the experiment river by electrofishing in August 1998, and the experiment trap was inspected daily from 24 April 1998 to 30 June 2001 (parr, $n = 169$; smolts, $n = 177$). All 1998 cohort parr and smolts from the experiment trap were sacrificed.

Because insufficient adult returns would have been obtained from the smolts produced in the experiment river, the marine phase of the life cycle of all cohorts (with the exception of F_2 hybrids) was examined by ranching, i.e. smolts were reared in the hatchery and released to the sea to complete their life cycle. Prior to release, smolts were tagged with coded wire microtags (Wilkins *et al.* 2001). Communally reared smolts from the 1993 and 1994 cohorts were each given a single code, whereas each group of the 1998 cohort was reared in a separate tank and could be assigned a unique group code. Smolts (table 1) of the 1993, 1994 and 1998 cohorts were released to Lough Furnace on 3 May 1994, 3 May 1995 and 29 April 1999, respectively. Microtags and tissue specimens were recovered from returning

Table 1. Experimental groups of Atlantic salmon in the 1993, 1994 and 1998 cohorts.

group	cohort	code	number of females	number of males	number of families	eyed eggs to river[a]	smolts to sea[b]
Burrishoole wild	1993	Wild93	6	6	6	5273	1842
farm	1993	Farm93	15	15	15	14997	1722
F_1 hybrid: wild females × farm males	1993	F_1HyW93	6	6	6	5886	1962
F_1 hybrid: farm females × wild males	1993	F_1HyF93	8	8	8	8659	1914
Burrishoole wild	1994	Wild94	11	11	11	10537	954
farm	1994	Farm94	11	11	11	10537	1138
F_1 hybrid: wild females × farm males	1994	F_1HyW94	11	11	11	10537	1211
F_1 hybrid: farm females × wild males	1994	F_1HyF94	11	11	11	10537	1028
Burrishoole wild	1998	Wild98	8	5	12 (24 sea)	8787	2544
farm	1998	Farm98	6	9	33	9832	9131
F_2 hybrid: F_1 hybrid × F_1 hybrid	1998	F_2Hy	15	2	26	8337	0
BC_1 wild backcross: F_1 hybrid × wild	1998	BC_1W	15	5	45	9549	5661
BC_1 farm backcross: F_1 hybrid × farm	1998	BC_1F	15	5	45	9928	7297

[a] The number of eggs planted out in the experiment river.
[b] The number of microtagged smolts released to sea.

adult salmon (1993 cohort: $n = 49$; 1994 cohort: $n = 67$; 1998 cohort: $n = 535$) caught by angling in Lough Furnace and at the sea entry upstream traps on the Burrishoole system. For the 1998 cohort, additional returning fishes ($n = 357$) were also obtained from the commercial net fisheries around the Irish coast through the National Microtag Recovery Programme (Wilkins *et al.* 2001). Fecundity (F) was estimated from the weight (W) (in grams) of returning females using the formula given by Mangel (1996): $F = cW^k$, where $c = 4.832$ and $k = 0.8697$.

Sampled individuals, except returning adults of the 1998 cohort (identifiable from microtags), were identified by microsatellite profiling involving six microsatellite loci as three sets of two multiplexed primers: *Ssa* 407 (Cairney *et al.* 2000) and *Ssa* 202 (O'Reilly *et al.* 1996); SSSP2201 and SSSP2210; and SSSP1605 and SSSP2215 (Verspoor *et al.* 2002). PCR amplification protocols varied for each of the three sets of primers. Common components in all three assays (12 μl final volume) were: 100 ng template DNA, 20 mM Tris–HCl (pH of 8.4), 50 mM KCl, 1.5 mM MgCl$_2$, 100 μM dNTP and 0.5 units *Taq* DNA polymerase (Invitrogen). The forward primer of each primer set was fluorescently labelled (IRD 700 Li-Cor for *Ssa* 202, SSSP2201, SSSP2210 and SSSP1605; IRD 800 Li-Cor for *Ssa* 407 and SSSP2215). The varying amounts of each primer used in the multiplex PCR reactions were as follows: *Ssa* 407 (4 pmol) and *Ssa* 202 (1.5 pmol); SSSP2201 (3.5 pmol) and SSSP2210 (0.5 pmol); and SSSP1605 (0.3 pmol) and SSSP2215 (3 pmol). Following an initial cycle at 94 °C for 4 min, PCR cycling parameters were specific to each of the three primer sets: *Ssa* 407 and *Ssa* 202, 24 cycles of 94 °C for 50 s, 57 °C for 50 s and 72 °C for 50 s; SSSP2201 and SSSP2210, 29 cycles of 94 °C for 40 s, 55 °C for 40 s and 72 °C for 40 s; SSSP1605 and SSSP2215, 28 cycles of 94 °C for 1 min, 62 °C for 1 min and 72 °C for 1 min. Following PCR, 4 μl of stop solution (95% formamide, 10 mM NaOH, 10 mM EDTA and 0.01% pararosaniline) was added to each 12 μl reaction. The resulting amplified products were denatured at 80 °C for 3–4 min, and 1 μl of the reaction was loaded onto 96-well, 25 cm long, 6% polyacrylamide gels (1 × TBE buffer containing 5.6 M urea) mounted in an automated Li-Cor double-dye system. A commercially available size ladder for the Li-Cor system (MicroStep-20a from Microzone, UK) was run every 15 speci-

mens to size allelic fragments. Gels were run at a constant power of 40 W and at a temperature of *ca.* 50 °C for 1–2 h. The GENE-PROFILER genotyper software (Scanalytics) was used to score genotypic data from the Li-Cor, with all data being subsequently checked manually. Progeny were identified to family and group parentage using the FAP program (J. B. Taggart, unpublished data) as previously described (McGinnity *et al.* 1997). Overall 96.7% of individuals were unambiguously assigned to a single group.

As relative sizes of groups in some samples is determined by both survival and migration, this is referred to as representation. Differences in survival and representation, relative to the wild group, were tested using *G*-tests incorporating Williams' correction (Sokal & Rohlf 1995; McGinnity *et al.* 1997), and were expressed relative to a wild value of 1.0. Length data did not meet the requirements for parametric analyses and were analysed using the Kruskal–Wallis non-parametric one-way ANOVA and, if this showed significant overall heterogeneity, unplanned pairwise comparisons were carried out using Dunn's multiple comparison test.

3. RESULTS

(a) *Fertilization to eyed-egg stage and hatchery controls*

The highest egg mortality occurred in the F_2 hybrid group (median 68%); this was significantly higher than in all other groups (e.g. wild 3%; figure 2). Because the backcrosses, which used aliquots of the same eggs as F_2 hybrids, showed significantly lower mortality (8%), this high F_2 hybrid mortality is not caused by maternal or egg-quality effects. There was also no significant difference in mortality between the two paternal groups of families, indicating that it is not a paternal effect. Thus, this high F_2 mortality most probably reflects outbreeding depression.

No significant differences in survival between groups were found in the hatchery control sampled at 11 months. However, given that total mortality was less than 10% under 'protected' hatchery conditions, there was little opportunity to detect differential survival. The lack of differences in the hatchery controls serves to demonstrate
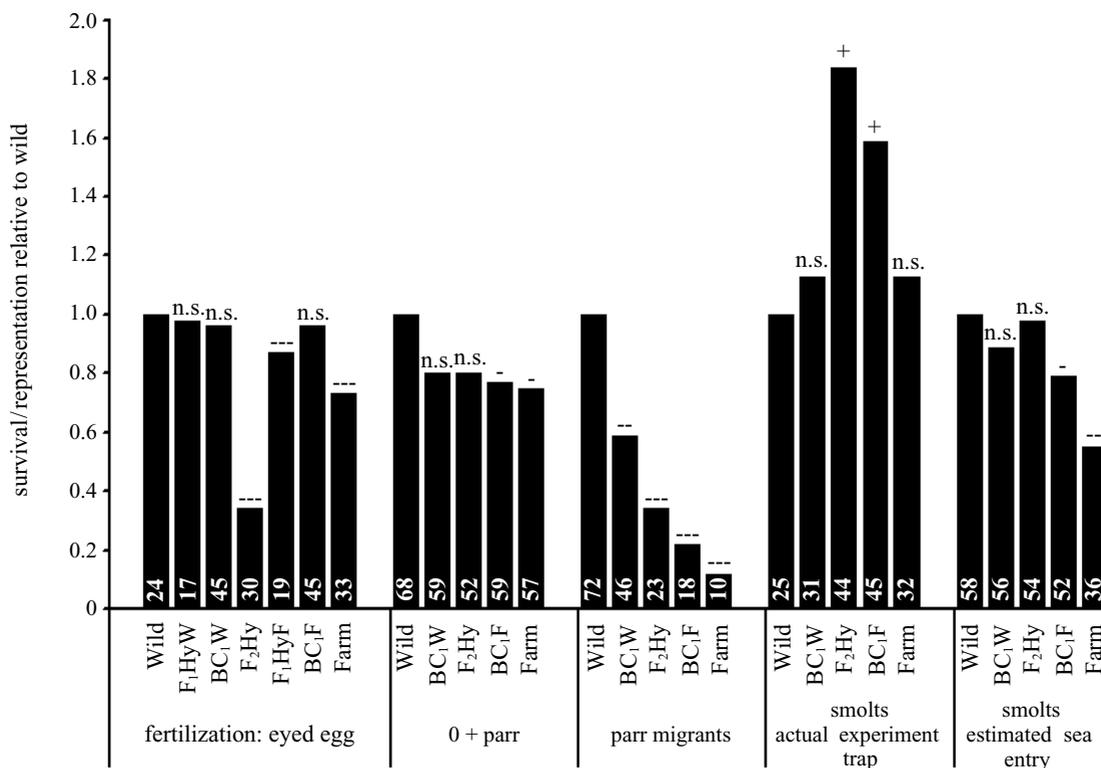
Figure 2. Survival/representation in samples of farm and 'hybrid' groups relative to a wild value of 1.0. Data for the fertilization to eyed-egg stage are shown for all cohorts and numbers indicate total number of families. Parr and smolt data are shown for the 1998 cohort only (earlier data in McGinnity *et al.* 1997) and numbers indicate individuals in sample. Significance of pairwise differences from the wild group (χ^2) are indicated above the bars: n.s., non-significant; $-$ indicates significantly less; $+$ indicates significantly more; $-/+$, $0.05 < p < 0.01$; $--/++$, $0.01 < p < 0.001$; $---/+++$, $p < 0.001$. Two measures of smolt output are given: smolts actual experiment trap is the actual count of smolts leaving the experiment river; smolts estimated sea entry is the estimated output of smolts to the sea based on the assumption that displaced parr have the same survival as parr of the same group remaining in the experiment river.

that all groups were potentially equally viable and that the differential survival apparent in the wild was the result of genetic and/or maternal differences.

(b) *Juveniles in fresh water*

As found for the 1993 and 1994 cohorts (McGinnity *et al.* 1997), in the samples of 0+ parr (i.e. first-year juveniles) of the 1998 cohort from the experiment river at the end of the first summer, farm salmon showed significantly lower representation than wild salmon. The BC_1 backcross to farm salmon also showed significantly lower representation but the F_2 hybrid and BC_1 backcross-to-wild groups were not significantly different from wild salmon (figure 2). As previously (McGinnity *et al.* 1997), the relative numbers of parr in the river underestimate the differences in survival, as downstream movement occurred prior to the sample being taken. During the period from May 0+ to September 1+ (i.e. the second year), the highest proportion of emigrant parr, caught in the experiment trap, was from the wild group and the lowest from the farm group, with 'hybrids' intermediate in representation. There was significant heterogeneity in length (Kruskal–Wallis χ^2_4, $p < 0.001$) among the groups in the 0+ parr with the decreasing order of size being: farm; BC_1 backcross to farm; F_2 hybrid; BC_1 backcross to wild; and wild. The inverse relationship between emigration and size indicates competitive displacement of the wild salmon by

the larger farm and 'hybrid' fishes, in agreement with earlier findings for the 1993 and 1994 cohorts (McGinnity *et al.* 1997).

Final migration from the river occurred in two phases: an 'autumn' migration of presmolts in the period from November to January, and a typical 'spring' smolt migration from March to May (McGinnity *et al.* 1997). In the autumn presmolts of the 1998 cohort, 81% were mature male parr, with wild parr showing greatest representation, farm parr the least and hybrids intermediate. As there was no significant difference (figure 2) in presmolt + smolt output between wild and farm salmon, this difference in parr maturity cannot be explained by differential survival or previous parr emigration. Most migration (90%) occurred in the second autumn and the following spring, i.e. 2+ smolts, with 6% as 1+ smolts and 4% as 3+ smolts. There were no significant differences between groups in the age of smolting. As previously, smolt output was assessed in two ways (McGinnity *et al.* 1997; figure 2). The first approach was to consider only the actual number of migrants (presmolts + smolts) caught in the experiment trap, which assumes that earlier emigrant parr do not survive. As a result of displacement of the wild parr, the F_2 hybrid and BC_1 backcross-to-farm groups produced significantly more smolts than the wild group, but farm numbers were not significantly different, in spite of this group showing the lowest parr emigration.
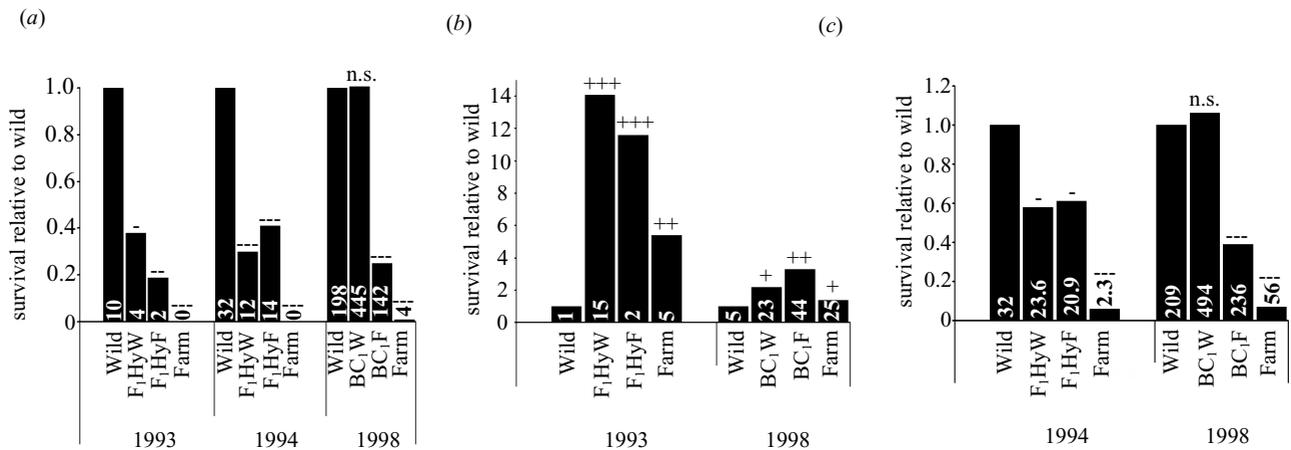
Figure 3. Return of adults relative to a wild value of 1.0: (*a*) 1SW adults; (*b*) 2SW adults; and (*c*) 1SW + 2SW adults with female 2SW fish numbers being multiplied by 2.3 to correct for increased fecundity; 1993, 1994 and 1998 refer to the three cohorts. Numbers within the bars for (*a*) and (*b*) indicate the numbers of individuals, and for (*c*) the corrected number of individuals. Sampling of the 1993 cohort 1SW was incomplete and the two age groups cannot be combined. No wild fishes returned as 2SW for the 1994 cohort and relative return cannot be calculated. Significances of pairwise differences from the wild group are indicated as for figure 2.

As suitable habitat is present in the river downstream of the experiment trap and in freshwater Lough Feeagh, emigrant parr were potentially able to survive and produce smolts, as was demonstrated for the 1993 cohort (McGinnity *et al.* 1997). The second measure of smolt output assumed that emigrant parr would have had the same survival downstream as parr of the equivalent group remaining in the experiment river, and combines the estimated number of smolts produced from these with the actual experiment-trap migrants to give an estimate of sea-entry smolts. The farm and BC_1 backcross-to-farm groups had significantly lower estimated sea-entry smolt production relative to wild salmon, with farm salmon producing 55% smolts relative to wild salmon (figure 2).

(c) *Marine survival and maturity: all cohorts*

Adult salmon returned from the sea after one or two winters (1SW and 2SW). In the 1SW returns, all groups, except the BC_1 backcross to wild, showed a significantly lower return relative to wild salmon (figure 3). In the 2SW returns, all groups showed a proportionately greater return than wild salmon. However, the Burrishoole wild population is primarily a 1SW stock, and the 2SW return was only 2.5% of the total return of 203 fishes. Farm salmon have been bred for late maturity, a trait with high heritability under such conditions (Jónasson *et al.* 1997). As egg deposition, rather than sperm, is likely to be a limiting factor in salmon recruitment, it is necessary to take account of the greater egg production of 2SW females compared with 1SW fishes. Based on the mean weights of returning females in the two groups, it was found that the 2SW fishes potentially produced 2.3 times more eggs. However, even taking account of this differential egg production of 1SW and 2SW females, the total potential egg deposition was significantly lower than for wild salmon in all groups except BC_1 backcross to wild (figure 3). If this correction for increased fecundity is not applied, the relative performances of farm and 'hybrid' groups (except BC_1 backcross to wild) were even lower. Thus, based on numbers of fishes alone, farm salmon had a return relative to

wild salmon of 4% but, when corrected for the greater return of 2SW salmon in the farm group, the value is 7% of potential egg deposition. Whether or not a correction factor is applied, and the exact value used, does not change the rank order of adult returns and has only a minor effect on the magnitude of the estimated overall lifetime success.

(d) *Overall lifetime success*

The product of the survivals at the different life-history stages can be used as a quantitative estimate of overall lifetime success, which, by taking account of differential egg production between 1SW and 2SW females, can be equated to potential fitness (table 2). It should be noted that the same fishes were not used for the freshwater and marine stages, and thus combined effects of selection in both stages are excluded. In the experimental conditions where parr emigrants survived, farm salmon had an estimated lifetime success of 2% relative to wild fishes. The 'hybrids' showed intermediate success and decreased in survival in the order: BC_1 backcross to wild; F_1 hybrid (wild mother); F_2 hybrid (but marine stage not measured for this group); BC_1 backcross to farm; and F_1 hybrid (farm mother). Under the scenario where only the actual smolts at the experiment trap are considered, all groups increased their relative survival, as a result of displacement of wild parr, but the rank order is similar.

4. DISCUSSION AND CONCLUSIONS

Previous studies (Fleming *et al.* 1996, 2000) have shown that farm salmon differ in their breeding behaviour from wild fishes and have lower breeding success. Our experiment, starting with fertilized eggs, was designed to eliminate behavioural differences between spawning adults and to examine the effect of genetic differences on survival and performance. The concordance of the results in the three cohorts, where the same groups of fishes were compared, i.e. Burrishoole wild salmon and farm fishes, considerably increases confidence in the findings. Thus farm

Table 2. Lifetime successes of the wild, farm and 'hybrid' groups.

(Results averaged over several cohorts where available (this study and McGinnity *et al.* (1997)). Survival of the wild group is taken as 1.0. Where another group is not significantly different from the wild group, at a particular stage, it is also given a value of 1.0. Where a group is significantly different from the wild group, then the actual survival relative to the wild group is used. Note that data for marine survival of the F_2 hybrid group are not available and a value of 1.0 is used, hence lifetime success values are maximum estimates.)

group	fertilization–eyed egg	eyed egg–smolt[a]	eyed egg–smolt[b]	smolt–adult	lifetime success[a]	lifetime success[b]
wild	1.0	1.0	1.0	1.0	1.0	1.0
BC_1W	1.0	0.89	1.0	1.0	0.89	1.0
F_1HyW	1.0	0.73	1.0	0.58	0.42	0.58
F_1HyF	0.87	0.50	0.63	0.61	0.27	0.33
F_2Hy	0.34	1.0	1.84	n.a.	(0.34)	(0.63)
BC_1F	1.0	0.79	1.59	0.39	0.31	0.62
farm	0.79	0.41	0.76	0.07	0.02	0.04

[a] This assumes that displaced parr have the same survival as parr of the same group remaining in the experiment river, i.e. that the river is not at its parr carrying capacity and spare habitat is available for displaced parr.
[b] This assumes that displaced parr emigrating from the experimental river do not survive, i.e. that the river is at its parr carrying capacity.

salmon consistently show the lowest freshwater and marine survival in all cohorts. There is no evidence for hybrid vigour, with F_1 and BC_1 hybrids being intermediate between wild and farm salmon in survival, growth and parr maturity. There is clear evidence of outbreeding depression in the F_2 hybrids, as might be expected from a breakdown of coadapted sets of alleles following recombination of parental chromosomes. However, this outbreeding depression appears to be limited to the early developmental stage, with allelic combinations that survive this stage causing no further reduction in survival.

The order of lifetime success among the experimental groups is indicative of additive genetic variation for survival, with genetic changes having occurred in the farm strain that reduce its survival under natural conditions. Intentional and unintentional selection and genetic drift during domestication have resulted in many genetically based behavioural and physiological changes that could reduce survival under natural conditions. At least some of these differences appear to be the result of selection for faster growth in farm strains (Gjøen & Bentsen 1997). Recent evidence (Fleming *et al.* 2002) suggests that this selection has indirectly targeted individuals with higher growth-hormone production and that increased aggression and decreased response to predation risk (Fleming & Einum 1997; Johnsson *et al.* 2001) are consequences of this increased endocrine activity (Jönsson *et al.* 1996). The difference in overall survival between the wild-mother and farm-mother F_1 hybrids indicates that there is also a maternal component to survival. As expected, this component primarily influences early survival in both the fertilization-to-eyed-egg and freshwater juvenile stages.

Our results for marine survival and maturity differ from those of Fleming *et al.* (2000) in that they did not find any difference in survival between farm and wild salmon. They also found that F_1 hybrids had a lower mean age at maturity as a result of earlier smolting. In part, at least, the differences are probably caused by the fact that Fleming *et al.* (2000) used farm salmon from the largest Norwegian breeding programme whereas we used farm fishes derived from the Norwegian Mowi strain. The life-history characteristics of the wild populations used, and the different natural conditions under which the experiments were undertaken in Norway and Ireland, are also likely to have contributed to the differences observed.

In many cases, where escaped farm salmon enter a river, production of F_1 hybrids rather than pure farm offspring is the outcome (Clifford *et al.* 1998; Fleming *et al.* 2000). Thus part of the potential wild juvenile recruitment is converted to hybrids in the first generation and to backcrosses in the second and later generations. Inevitably the lower lifetime success of such 'hybrids' will reduce the fitness of the wild population. However, these 'hybrids' can also result in an increase in 2SW salmon in rivers that are naturally primarily 1SW producers. While this may be desirable from an angling perspective because it increases the number of larger fishes, given their reduced lifetime success, these larger 'hybrids' would not compensate for the loss of wild recruitment, thereby resulting in a decrease in fitness in the population. Also, in this study, only the potential egg deposition was estimated, and these larger fishes may, in addition, have reduced survival in fresh water (Fleming 1996) and possibly reduced mating success, further decreasing fitness. Thus our results provide long-awaited empirical support for many of Hutchings' (1991) predictions on fitness reduction and extinction in wild salmon populations, which were based on modelling the influence of spawning intrusions of farm fishes and assuming fitness reduction.

Backcrossing of F_1 hybrids to wild fishes in the second and subsequent generations will result in introgression of alleles from farm salmon to wild salmon. As only a few farm strains are in general use, this gene flow will result in a reduction in the genetic heterogeneity that is present among Atlantic salmon populations (Youngson *et al.* 2003). Given the evidence (Taylor 1991; Youngson & Verspoor 1998) for local adaptation of Atlantic salmon populations, loss of genetic heterogeneity will reduce the adaptive potential of the species. Because, typically, farm strains show reduced variability (Mjølnerød *et al.* 1997; Clifford *et al.* 1998), introgression will produce a reduction in genetic variability in wild populations

(Tufto & Hindar 2003) potentially resulting in inbreeding depression (Wang *et al.* 2001, 2002).

In addition to direct genetic effects, offspring of escaped farm fishes may also reduce the size of the wild population due to competition. Although overall survival of farm and 'hybrid' fish was lower in the experiment, due to their larger size, surviving fish resulted in competitive displacement of wild parr. Given the selection for increased growth in the farm strain, this larger size is not surprising. Fleming *et al.* (2002) have shown that farm salmon show increased aggression, which may further favour such fishes in competitive encounters. The impact of this displacement on wild smolt production will depend on whether or not these displaced parr can survive downstream. In the experimental conditions of the present study, these parr could survive as there was unoccupied juvenile habitat downstream and in Lough Feeagh. Such survival would not occur if suitable unoccupied habitat is absent, for example, when a river is at its parr carrying capacity or where the spawning area debouches directly to the sea, as may be typical for escaped farm salmon spawning in some rivers (Webb *et al.* 1991) but not others (Webb *et al.* 1993; Fleming *et al.* 2002). Fleming *et al.* (2000) noted a more than 30% reduction of smolt output in their simulated farm-escape experiment. As our experiment indicates, because farm salmon especially and 'hybrids' show lower marine survival than wild salmon, they do not make up for this loss of wild smolt production. Thus the competitive effect on its own serves to reduce the fitness of the wild population irrespective of any genetic changes to the population. Reduction of the effective population size of a wild population will result in lowered genetic variability. Mature male parr have been shown to fertilize a substantial proportion of eggs (Thomaz *et al.* 1997; Martínez *et al.* 2000; Taggart *et al.* 2001) and thus parr maturity may be an extremely important factor in increasing effective population size. The reduced level of parr maturity, as found in our experiment for farm and hybrid parr, may further reduce effective population size.

The overall extent of reduction in fitness in the wild population, as a result of both interbreeding and competition, will depend on many factors, including availability of unoccupied juvenile habitat, relative numbers of wild, farm and hybrid salmon, and mating success. However, the quantitative data available for the first time, to our knowledge, from this study of both F_1 and F_2 generations, and from the study of an F_1 generation by Fleming *et al.* (2000), will enable much more accurate modelling of the impact of farm escapes under a range of scenarios. Irrespective of the exact extent of fitness reduction, the fact that farm escapes are repetitive, often resulting in annual intrusions in some rivers, means that such reductions in fitness are cumulative, which could potentially lead to an extinction vortex in endangered populations, i.e. where recruitment is close to the replacement level. Thus only a small reduction in fitness is required to change populations with a marginally positive growth into populations with negative growth.

There have been recent calls in the angling press for surplus (often 2+) smolts from the salmon-farming industry to be used for deliberate stocking in an attempt to enhance population levels in depressed wild populations. Our results indicate that such a practice would be highly detrimental and would have the reverse effect to that intended. Indeed the effects would be even greater than those produced by accidental escapes owing to the large number of farm fishes introduced, relative to wild fishes, and to the regular nature of such deliberate stocking. Similar effects would also be expected from deliberate stocking with other domesticated strains of salmon and trout, the impact depending on the extent of domestication. Indeed this study provides a general model for the likely implications of the deliberate or accidental introduction of farm fishes and other aquatic animals into areas where natural populations exist. A reduction in fitness does not require that the wild populations are locally adapted, but only that domestication results in genetic changes that reduce the fitness of farm and hybrid offspring in the wild. As domestication inevitably occurs in captivity, this study may also have implications for the release of zoo-bred animals into areas where wild conspecifics still exist (Rodriguez-Clark 1999).

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