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A two-generation experiment comparing the fitness and life history traits of native, ranched, non-native, farmed, and 'hybrid' Atlantic salmon under natural conditions

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INTRODUCTION

In recent years there has been widespread stocking of Atlantic salmon rivers using juvenile salmon derived from non-native broodstock. Stocking has also been undertaken using surplus juveniles from the Atlantic salmon farming industry. In addition, farmed salmon enter rivers due to escapes from smolt rearing units and from sea cages. The increase of Atlantic salmon *Salmo salar* culture has meant that large-scale escapes are now inevitable and frequent occurrences. For example, farmed salmon escapes in Scotland in 2000 totalled 491,980 fish (Intrafish 2000), five times the total wild catch, with escapees potentially outnumbering wild adult salmon returning to many Scottish rivers. In Norway, where escapes generally exceed one million fish per year, which is more than four times the natural spawning runs, overall about one-third of salmon entering rivers are escaped fish with over 80% in some rivers (NASCO 2000).

Since Atlantic salmon from different rivers are genetically different (Youngson *et al.* 2002), these non-native introductions have the potential to change the genetic make-up and juvenile production (fitness) of the recipient wild populations. In addition to genetic differences as a result of their different geographical origins, farmed fish are often genetically distinct from those of the native populations in the rivers which they enter as a result of directional and inadvertent selection, hybridisation, and genetic drift (Skaala *et al.* 1990). Introductions may also have ecological effects due to competition, density dependent mortality, etc. While there has been much theoretical discussion on the genetic and ecological impacts on native populations of the deliberate and inadvertent introductions of Atlantic salmon, there have only been a few empirical studies (e.g., McGinnity *et al.* 1997, Fleming *et al.* 2000). Such studies of an anadromous fish with a 4+ years life cycle are expensive to carry out and require a river with total juvenile and adult trapping capabilities. In addition it is necessary to undertake studies for two generations since, in many organisms, first and second generation hybrids often survive and perform quite differently. Thus F₁ hybrids often show intermediate or even

enhanced performance compared with their parents (hybrid vigour) with F₂ hybrids showing reduced performance relative to parents (hybrid breakdown or outbreeding depression).

The only currently available way to determine if adaptive genetic differences are present between different groups of fish is to carry out 'common garden' experiments. That is, fish are reared from egg to adult in a common environmental situation. With the exception of any maternal physiological effects mediated through the egg, any differences found in performance in this common environment are thus a reflection of genetic differences. Up until about 10 years, with a few exceptions where suitable allozyme markers were available, it was not possible to do this as it was not possible to identify different groups established at the egg stage. Separate rearing of each group was required to a size where the fish were large enough to be physically tagged. This separate rearing potentially confounds environmental and genetically mediated differences and makes a comparison at the early, high mortality stage impossible. The development of DNA profiling, involving first minisatellites and later microsatellites, allowed accurate parentage identification and opened the way to direct comparison of stocks from egg stage onwards under realistic common natural conditions (Ferguson *et al.* 1995).

MATERIALS & METHODS

The experiment, comprising three cohorts (1993, 1994, 1998) of Atlantic salmon, was undertaken in the Burrishoole system in western Ireland. This system consists of a freshwater lake, connected to the sea by two channels with permanent smolt and adult trapping facilities, and a number of afferent rivers. One of these latter rivers was equipped with a juvenile and adult trap and was used for the experiment, which involved multiple families of the following nine groups: native wild (WILD - all cohorts); native ranched (RANCH - 98 only); non-native from the adjacent Owenmore river (OWEN - 98 only); farmed (FARM - all cohorts); F₁ wild x farmed (male and female reciprocal groups) (F₁HyW♀, F₁HyF♀, - 93 & 94 cohorts); F₂ wild x farmed (F₂Hy - 98 cohort); backcross to wild (BC₁W - 98 cohort); and backcross to farmed (BC₁F - 98 cohort). As the aim of the experiment was to look at genetic differences, without the confusion of behavioural differences, which have been shown between wild and farmed salmon (Fleming *et al.* 2000), eggs and milt were stripped from mature adults and artificially fertilised. Fertilised eggs were incubated to the eyed stage in the hatchery with cumulative mortalities being recorded. At the eyed stage, eggs were counted accurately, families and groups mixed, and planted out in incubators (Donaghy & Verspoor, 2001) in a river from which natural spawning had been excluded. Samples of parr were electrofished from the river and all emigrant parr and smolts were captured in the downstream traps. Aliquots of each group were maintained communally in the hatchery. Smolts from this communal rearing, together with additional smolts from individual tanks for the 98 cohort, were tagged with coded wire tags and released to sea (except F₂ hybrids). Subsequent returning adults sampled from the Irish coastal drift nets, as part of the National microtagging programme, and in the Burrishoole system by angling and at the permanent upstream traps. Offspring were assigned to family and group parentage by minisatellite or microsatellite DNA profiling. Survival, growth, migration and maturity characteristics were examined at each stage and overall lifetime success was estimated. Overall 7033 parr and 1502 smolts from the experimental river, 1300 parr from hatchery controls, and 1385 returning adults were examined.

RESULTS & DISCUSSION

The highest mortality in the fertilisation to eyed stage occurred in the F₂ hybrid group (65%) and this was significantly higher than all other groups. The backcrosses, which involved the same eggs as the F₂ hybrids, show significantly lower mortality (20%) demonstrating that the high mortality in the F₂ hybrids is not due to maternal or egg quality effects. There was also no difference in mortality between the two male groups of families produced by crossing 15 females with two males, indicating that it is not a paternal effect either. This high mortality of the F₂ hybrids most likely reflects outbreeding depression.

From the electrofished samples of 0+ parr taken from each of the three cohorts in August it was found that offspring of farmed Atlantic salmon showed the fastest growth rate. Ranking of both length and weight was as follows: Farm, BC₁F, F₂Hy, F₁HyF♀, F₁HyW♀, BC₁W, Wild. This ranking clearly indicates the genetic basis of growth rate. All groups, other than ranched, showed a lower relative representation compared to wild in these August 0+ samples. However, prior to the August sampling parr emigration had occurred from the experimental stream. These emigrant parr captured in the downstream trap showed a greater representation of wild parr relative to farmed and hybrid parr. This downstream migration was inversely proportional to parr size and proportional to cohort density indicating competitive displacement of wild parr by the larger farm and hybrid fish. The Owenmore also showed a substantial early parr migration but, as these fish were not significantly different in size from other parr in the same section of river, this appears to have been an active migration. This active downstream migration may represent an adaptation to the Owenmore where there is good nursery habitat in the main river but which is unsuitable for spawning, this taking place in the small tributaries.

Smolt output (including autumn presmolts, which were largely mature males) was determined at two places. First, a direct count of smolts was possible at the experimental trap. Second, the number of smolts at sea entry, produced by parr emigrating from the experimental river, was estimated assuming that these emigrating parr had a similar survival to those remaining in the experimental river. For the 93 cohort, where emigrating parr were fin-clipped for parentage identification and tagged prior to release, such tagged fish were found to result in smolts at the sea entry traps. Clearly survival of displaced parr would only occur in a river system below its parr carrying capacity, i.e. with unoccupied downstream juvenile habitat such as freshwater Lough Feeagh in the Burrishoole system which is known to provide such habitat. Due to the displacement of wild parr from the experimental stream, the lower representation of groups relative to wild seen at the 0+ parr stage was no longer present in the experimental trap smolts, with the F₂ hybrid group showing a significantly greater number of smolts than the wild. However, taking the estimated smolt output at sea-entry, all groups except ranched, F₂ hybrid and backcross to wild had significantly lower smolt output than wild. Farm salmon, which were present in all three cohorts, consistently showed a significantly lower smolt output relative to wild (34%, 34%, 55%). Thus in a river at carrying capacity, introduction of farm and hybrid juveniles will lower the wild smolt production due to displacement of wild parr by these large fish. In a river with spare juvenile habitat, overall smolt production could be increased under these conditions.

No significant differences in survival among groups were found in the hatchery communally-reared controls. However, overall survival was greater than 90%. Growth differences, similar to those in the experimental river were found. The control groups serve to show that all

groups were potentially equally viable that the differences found in the experimental river were the result of genetic differences among groups.

Adult fish returned from sea after one and two sea winters (1SW, 2SW). In the 1SW group, all groups except the ranched and backcross to wild group showed a significantly lower return. Out of 16178 farm smolts released, only 47 returning adults were obtained (0.3%) compared with 4.5% return for wild smolts. The F1 hybrid groups showed significantly more 2SW returns than other groups. As egg deposition is the likely to be the limiting factor in salmon recruitment, taking account of the differential egg production of 1SW and 2SW females shows that total egg production was significantly lower than wild for all groups except ranched. That is, although 2SW salmon produce some 2.4 times the number of eggs of 1SW fish, this increase is not sufficient to make up for the greater mortality that occurs for the 2SW returning groups.

The product of survival at the different life history stages can be used as a quantitative measure of overall life-time survival which, by taking account of differential egg production, can be equated to fitness. In a situation where a river is not at its parr carrying capacity, farmed salmon have a lifetime fitness equivalent to 1% of wild fish. In a river at carrying capacity this relative fitness increases to 2% due to displacement of wild fish. The 'hybrids' showed intermediate fitness decreasing in the rank order of: BC1 wild; F1 wild x farm; BC1 farm; F2 hybrid (but marine stage not measured for this group); F1 farm x wild. The Owenmore group showed an overall fitness of 17% and 20% in the two scenarios. Only the ranched did not show a reduction in fitness relative to the wild group.

The impact of deliberate and inadvertent introductions of non-native Atlantic salmon into a river will be highly dependent on the density of wild parr in the river. Thus where the river is below carrying capacity the introduced fish may survive alongside the natives resulting in an overall increase in smolt and adult production. The production of hybrids will lower the wild production but, in the case of farm hybrids, may increase the return of 2SW salmon and overall the fitness of the population may increase slightly in the first generation. Depending on the extent of hybridisation in the second generation, fitness however may be reduced to below that prior to the introduction. The poor lifetime survival of farmed salmon means that introduction of such fish will have no beneficial effect.

Where a river is already at carrying capacity, introductions can reduce wild smolt production and reduce fitness in the first generation even if there is an increase in the number of 2SW fish. Deliberate introduction of farm salmon in such situations is particularly damaging due to displacement of wild fish by farm parr with subsequent poor marine survival of farm fish resulting in an overall reduction in adults. Farm escapes entering a river generally result in hybrids rather than pure farm offspring due to differential spawning behaviour of males and females (Fleming *et al.* 2000). Again such hybrids will result in displacement of wild fish but the reduction in fitness of these hybrids will lower the population fitness. Since reduction in fitness is cumulative, repeated introductions in a population on the verge of self-sustainability could result in an extinction vortex. The low fitness of non-native wild fish means that deliberate introductions of such fish are just as damaging as farm escapes. Indeed such introductions may be more damaging since relatively greater numbers may be involved with annual introductions rather than periodical ones as typical of farm escapes.

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