

**Possible genetic interactions between reared strains and wild populations of cod (*Gadus morhua*): lessons from salmon (*Salmo salar*) common garden field experiments**

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**Abstract**

With the increase in production from cod (*Gadus morhua*) farming and ranching around the North Atlantic, concern has been raised about detrimental effects of accidental or deliberate introductions of reared strains into the wild. Here we concentrate on the possible genetic effects of interactions of captive bred fish with wild conspecifics by extrapolating from the major findings of Irish field experiments with reared and wild Atlantic salmon *Salmo salar*. We then discuss the likelihood of similar effects being observed in cod. In the case of *S. salar* in a “common garden” scenario in a natural freshwater stream, native wild populations were found in many situations, simulating both farm escapes and stocking, to have significantly higher lifetime reproductive success (LRS) than their reared counterparts. Where wild X reared hybrids were produced LRS was lower depending on the extent of reared involvement (e.g. wild backcrosses more fit than F<sub>2</sub> hybrids). The role of MHC in determining the fitness of introduced individuals was also demonstrated and suggested a high degree of local adaptation in salmon populations. There is also evidence that ranched reared salmon can affect fitness of wild populations when they breed in the wild. Cod differ from salmon in many aspects of their biology (e.g. there

is considerably less observed genetic population structure), so the applicability of salmon results to cod is debateable, although genes associated with adaptation have been identified. However, some extrapolation should be possible and should be attempted using a combination of inference and modelling, because field experiments are time-consuming and expensive to conduct. Though field experiments are likely to be more difficult in cod than salmon, they none-the-less provide the most robust findings so suggestions are made as to how these might be designed for cod.

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## **1 Introduction:**

The general question addressed herein is “How detrimental might cod *Gadus morhua* culture be to the reproductive fitness of wild conspecifics, should either accidental (as in farm escapes) or deliberate (as in stocking/ranching) introductions occur?” Most previous studies on the genetic aspects of interactions have been on Atlantic salmon *Salmo salar*, where aquaculture production exceeds 1 million tonnes, and have demonstrated substantial detrimental effects for wild populations (McGinnity et al., 2003). However, the biology of the species are very different (salmon are largely anadromous, and have relatively low fecundity with strong population structure, whereas cod are a high fecundity marine species with much weaker population structure) and thus extrapolation from findings with salmon to cod may not always be possible. Many reasons for inadvertent introductions of reared fish into the wild (“escapes”) are identical in both species, e.g. human error, failure of cages due to adverse weather and predator damage, etc. In the case of cod there are two additional causes; spawning in cages and chewing holes in cages but the results are similar-reared fish escaping to the wild. Cross et al. (2008) suggested that cod culture/wild interactions might be less detrimental than those for salmon, but there are now reasons to be cautious about these suggestions as outlined below (original ideas in quote fields):

1. “Current cod production is much lower than salmon so the scale of the problem is likely to be less.” We note however that the aspiration is to greatly increase cod production in many countries surrounding the North Atlantic.

2. “Breeding programmes for cod are at a much earlier stage than those for salmon.” This situation is likely to change rapidly, since the most crucial changes in the genetic composition of reared strains occur during the first few generations in captivity, due to strong domestication selection (Verspoor, 1988).
3. “Wild cod have a census population size many orders of magnitude greater than current culture strains, producing a “buffer” effect to introductions. The situation in salmon is quite different since reared production exceeds wild biomass by at least two orders of magnitude.” However, wild cod populations are substantially declining in many areas within the native range due to overfishing.
4. “There appears to be far less quantifiable genetic population structure in cod than salmon.” The smaller differences between cod populations are usually interpreted as indicative of high contemporary gene flow. However, this finding may instead relate to population size, with the far greater size of cod populations resulting in exponentially reduced genetic drift and thus substantially less observed contemporary population structure. Furthermore, as more sensitive molecular methods are applied to cod (Hutchinson et al., 2001; Neilsen et al., 2001; O’Leary et al., 2006) greater population structure is becoming apparent.

A general overview of the relevance of genetic aspects of salmon wild/reared findings for similar cod interactions was provided by Bekkevold et al. (2006). In the case of salmon, field experiments have provided the greatest amount of information on the genetic aspects of interactions (see Cross et al., 2008). Here, we concentrate on the Irish “common-garden” experiments (McGinnity et al. 1997, 2003, 2004, 2009; deEyto et al. 2007) and explore how the results might be extrapolated to cod and also how they may be used to help design future experiments with reared and wild cod.

## **2 Inadvertent introductions**

### **2.1 Irish field experiments simulating farm escapes in salmon.**

In the early 1990s a tributary (2 to 5m wide) of the Burrishoole catchment in the west of Ireland, with a wild native salmon breeding population, was chosen and an upstream and downstream trap constructed 1.7 km downstream of an impassable waterfall. During the next and subsequent spawning seasons all upstream migrating

native salmon were caught in the trap and held in tanks. In the majority of experiments (McGinnity et al. 1997, 2003) farm escapes were simulated by acquiring broodstock from the most popular farm strain in Ireland (of Norwegian Mowi origin) and establishing experimental populations. In the first and second years, similar numbers of wild X wild (WW), farm x farm (FF) and F<sub>1</sub> hybrids in both directions (WF and FW) families were created, using manual stripping.

This design gave all potential parents an equal chance of contributing progeny and ignored behavioural differences in reproductive success. The latter have been extensively investigated by Fleming et al. (2000) in the river Imms in Norway. Fleming et al. (2000) showed that such differences occur, with natives being considerably more reproductively capable than farmed salmon, particularly farmed males. Incorporating such variations in reproductive success in the Irish experiments would have made interpretation of results unduly complicated, so it was decided to incorporate the design described above, which concentrated on post-hatch fitness differences. However, such differences should possibly be incorporated into models of cod wild/reared interactions, as discussed below.

In the Irish salmon “common garden” experiments all parents were tissue sampled for subsequent VNTR typing (initially with minisatellites and then microsatellites, to enable parental assignment). Fertilised eggs from each family were held separately until the eyed egg stage, when the majority of ova from each family were placed in the experimental stream in specially designed egg boxes (investigating relative performance in freshwater). The remainder of eggs were held until hatching, to check for survival and subsequently reared to the one year-old smolt (S1) stage for ocean ranching (investigating relative performance at sea). Fry were sampled by electrofishing at the end of the first summer, and as parr and smolts in the downstream trap. After measuring, they were tissue sampled and typed for the same VNTRs as the adults, and subsequently identified back to parents using parental assignment software. In this way, the different groups of parents (WW, FF or hybrid) could be identified. The results from the first two years of experimentation were similar; significantly higher survival than expected for WW progeny, lower than expected for FF, and with both types of hybrid offspring being intermediate in terms of survival (McGinnity et al. 1997). Interestingly, FF progeny were significantly larger at age and had a significantly lower level of precocious maturity, presumably as a result of several generations of artificial selection for fast growth and late maturity. The

various hatchery groups of smolts were ranched and survival results combined to estimate lifetime reproductive success (LRS) of each group. Again, significant life history differences were observed with most WW progeny returning as grilse (1SW), whereas many FF and hybrid offspring migrated back into freshwater as multi sea winter fish (MSW). The latter were considerably larger than grilse and had higher fecundity, but their numbers and thus potential egg deposition were lower.

In subsequent years,  $F_1$  hybrid and parental ranched returns (identified by a combination of freeze branding, coded wire tags (CWT) and genetic tagging) were used as parents to produce  $F_2$  and  $F_1$  x parental backcross progeny in both directions (W or F), and similar experiments repeated both in the freshwater experimental stream and with ocean ranching of reared smolts. Results, accumulated in terms of LRS, were reported in McGinnity et al. (2003) and showed that survival was negatively related to the degree of farm influence in a progeny group (Survival:  $WW > F_1W \text{ BC} > F_1 > F_2 > F_1F \text{ BC} > FF$ ). There was also evidence of outbreeding depression in the  $F_2$  hybrids.

Hindar et al. (2007) used the relative survival values from this experiment to model the reproductive fitness of a wild population subjected to interactions with farm fish and demonstrated a long term persistence, particularly of  $F_1W \text{ BC}$  and  $F_1$  hybrids (the forms with the highest survival relative to WW), leading to an overall decrease in productivity, particularly if large escapes happen on a recurrent basis.

It should be noted that Cross et al. (2008) define such effects as “direct genetic effects” resulting from interbreeding and fitness differences between progeny, whether WW, FF or some type of hybrid. They also describe “indirect genetic effects” where reared animals either compete successfully or transfer disease to wild conspecifics (without or in addition to interbreeding) leading to a decline in the size of the wild population to the extent that inbreeding effects reduce productivity. Many Atlantic salmon populations are small in number, so this is a realistic concern but whether it is a consideration with cod remains to be determined. Indirect effects will be discussed below in relation to immune response genes, but initial concentration will be on direct genetic effects.

## **2.2 Extrapolation of salmon results to cod farm escapes.**

Might we expect similar issues for wild cod populations with farm escapes? It is well known with Atlantic salmon that interbreeding occurs between farm escapes

and wild conspecifics, but the extent of mating between farm and wild cod needs to be established. Undoubtedly, some natural interbreeding occurs, as demonstrated by the appearance of heterozygotes in the early Norwegian genetic marking experiments on cod ranching (Jorstad et al., 1994). On the other hand, a high degree of assortative mating must be postulated to keep Arctic and coastal cod from interbreeding around the Lofoten Islands (Wennevik et al., 2008), so case-specific quantification is necessary. In an ongoing field experiment in Norway, on tracking progeny of cage spawning of farm strains, genetic marking is again being used (Jorstad et al., 2006). If it is possible to sample fry for the next few years, it may be feasible to assess the degree of interbreeding (provided that wild population size in the area is known and it is presumed that initial spawning by farm fish in the cages did not involve the production of hybrids with wild cod around the cages (by intermingling of drifting gametes)).

The other major question in relation to cod, and a very relevant one in the context of interactions, is the degree of philopatry. Atlantic salmon show a high degree of natal homing so the effects of incursions of reared fish on a single population can be studied. However, in the case of cod, local population structure and the degree of gene flow between neighbouring regions have not been established, except in particular transitional areas like the North Sea and Baltic (Neilsen et al. 2005). Thus, more research, perhaps with the potentially highly discriminatory single nucleotide polymorphisms (SNPs) is urgently needed. This is crucial for consideration of interactions because the nature and size of wild cod population/s is not currently clear. If contemporary gene flow is high and a single wild population, with an effective population size of millions of individuals, occupies a huge geographic area, then the effect of reared incursions will be minimal even if reared individuals have very low fitness in the wild. On the other hand, the magnitude of the effect will depend on the location of the farm contributing escapes. If the farm is in a semi-isolated fjordic situation with a small non-migratory population of wild cod, the effect on fitness of the latter could be considerable. While the actual fitness differences (if any) between different wild populations and reared strains are being established empirically (see below), it should be possible to model the potential effects presuming fitness differences as observed in salmon (Hindar et al., 2007) and considering a range of wild population sizes, differing over several orders of magnitude.

In the case of reared strains it is presumed (as has been observed with farmed salmon) that these will differ in genetic composition from wild populations and thus have reduced fitness in the wild, for several reasons:

- Different population origin for the reared strain from local wild cod
- Use of small numbers of broodstock to found a strain. Mesocosm spawning has been common in cod propagation but can result in far fewer parents than expected contributing offspring (see Cross et al., 2008) so individual stripping is now favoured in breeding programmes. Even with individual stripping, the tendency may be to use low numbers of parents because of the high fecundity of the species. These issues can lead to loss of genetic variability due to genetic drift, thus changing genetic composition. In addition, genetic composition can vary between year classes. Such temporal instability means that performance and fitness in the wild of different year classes of reared strains can vary.
- Inadvertent selection to hatchery conditions termed “domestication selection” can occur very rapidly and compromise the performance of reared strains in the wild.
- Breeding programmes will apply artificial directional selection for traits such as fast growth and late maturity, further altering genetic composition.

It is important to consider biological differences between the species when using results from salmon experiments to provide advice in designing field experiments to determine the fitness differences between wild populations and farmed strains of cod. The anadromous life history with its contained freshwater component and the strongly-defined natural population structure of Atlantic salmon meant a “common garden” experimental stream design could be adopted. The stream used for the Irish salmon experiments had natural feeding, a full complement of intra- and interspecific competitors, predators and disease organisms. In designing the Irish field experiments it was first considered essential to use a closed system. It might be possible to run analogous trials with cod in at least semi natural conditions using enclosed coastal inlets. In Norway, polls (where a coastal freshwater lake has been emptied and filled with seawater) have been used for semi-natural rearing and

production of genetically marked cod (Jorstad et al., 1994), and such an enclosed system might be adapted for use in interaction experiments. In a system like this, performance of wild and reared families and hybrids between them could be compared by typing all parents for high resolution genetic markers, sampling progeny randomly from the experimental area and then identifying back to parents using the same molecular markers (assuming that there are discernable genetic differences between wild and reared cod at the molecular markers chosen).

There were several other considerations in designing the Irish field experiments with salmon which may be difficult to achieve with cod or other fish species used in marine aquaculture, but these would need to be considered in an experiment that tests relative fitness is to be designed:

- By selecting salmon broodstock from a larger group it was possible to synchronise spawning of adequate numbers of females and males of wild and reared individuals. Synchronised spawning was considered essential for elucidating the genetic basis of traits such as growth, and should be duplicated in cod, enabled perhaps using hormonal treatment.
- With salmon stripping, single pair mating is easy to achieve and was considered essential for subsequently assessing the relative performance of different groups. This approach should also be adopted with cod.
- In order to minimise hatchery effects fish should be moved to the experimental area as early as is practical. In the case of the Irish experiments with salmon this transfer was made at the eyed egg stage. Note, that at this stage quantification, which was necessary for analysing subsequent survival, could be easily achieved. With cod, careful planning and perhaps experimentation should be used to establish the earliest practical stage for transfer, while enabling accurate counting of individuals.
- Numbers to be introduced to equal or slightly exceed carrying capacity were carefully estimated in the case of the salmon experiments. This issue should also be considered in the case of cod.
- Adequate sampling subsequently is also crucial. This was achieved in the case of the salmon experiments in the freshwater stream, by collecting fry by electrofishing at the end of the first summer (a key life stage where 90% of natural mortality has already occurred) and subsequently by taking parr from



the stream (by electrofishing) or out-migrating fry, parr or pre-smolts from the downstream trap. Early life history of cod would need to be considered when designing an adequate sampling regime to yield fish for parental assignment by genetic methods and for morphological assessment. It is considered essential to assess survival at all life stages (and to keep hatchery controls to check for catastrophic mortality in certain families) and if possible to include a multi-generational element. This was achieved with salmon by ocean ranching hatchery controls and using mature upstream migrating fish as parents for the subsequent generation. To achieve similar multi-generational assessment in cod will be difficult and will require detailed consideration.

- Inclusion of  $F_1$  hybrids in the first generation experiments with salmon and  $F_2$  hybrids and parental backcrosses in the second generation was considered essential to adequately detail fitness differences (see McGinnity et al., 2003, where it is demonstrated that relative survival appears to act as an additive trait being lower with greater reared influence). Thus the inclusion of hybrids in any cod interaction experiment is considered essential.
- Considerably more confidence in the salmon results was generated by observing the same trends in a number of years. Thus it is urged with cod that any field experiments be repeated.

So such a study with cod or other marine fish species might be excessively difficult or would involve so many variables that no clearcut results would be forthcoming. None-the-less the issue of whether such experiment/s could be designed should be given detailed consideration, since, as demonstrated with salmon, many useful empirical results would be forthcoming which cannot otherwise be achieved.

While it might be argued that cage experiments (with artificial feeding), like those carried out commercially to compare strain performance, would give adequate information, our experience with salmon suggest that survival is very high under such conditions and not discriminatory amongst groups. In contrast, significant differences are evident in the much harsher natural conditions (with no artificial feeding and in the presence of competitors, predators and disease organisms).

If experiments in closed systems are deemed impractical then using semi-enclosed or open systems are a less favourable option. (Some of the latter are already being pursued-see Jorstad et al., 2006). Use of SNP technology could assist here (in

addition all reared parents being typed for highly discriminatory markers such as microsatellites to enable parental assignment) and would enable investigations in completely open systems (though the problem of the “limits” of the wild population, alluded to above, could complicate the issue). The suggested design would mean typing a sample of the wild population and reared strain for several hundred SNPs and choosing, if possible, several fully discriminatory unlinked nuclear markers (fixed for alternative homozygotes in the two groups). Another option, which might be advantageous in studying introgression, would be to choose discriminatory microsatellite loci.

If absolute SNP markers were not detectable, a much more expensive and time consuming alternative would be to use selective breeding to produce a large batch of cod fixed for alternative SNP alleles (so-called “genetic marking”). In either case having several absolute markers would allow determination of genetic composition of F<sub>2</sub> hybrids (whether WW, FF or hybrid at each locus) or backcrosses (hybrid or parental type at each locus), to further investigate the genetic architecture of interactions.

### **3 Deliberate releases**

#### **3.1 Salmon field experiments and other investigations of stocking and ranching**

Using the experimental stream and ocean ranching “common garden” approach described above, McGinnity et al. (2004) compared the relative fitness of native Burrishoole salmon with progeny of wild salmon from the neighbouring Owenmore river (which has its source in the same mountain range but enters the sea more than 50 km distant). The aim was to simulate stocking from a non-native source while minimizing the extent of domestication selection by reducing hatchery intervention to initial holding of eggs. (Note that there was very little mortality in the hatchery.) Interestingly, while there were significant fitness differences in the first summer in freshwater, with survival of natives being substantially higher, the differences in sea survival were even greater (again favouring the native population). This led the authors to suggest that there may be major adaptational differences between the populations and was cited as evidence of local adaptation in the native population. Unfortunately, that experiment did not include hybrid families between the populations. Thus, the experiment is currently being repeated incorporating hybrid groups in both directions (native mother or father).

Also relevant in this context is a recent publication by McGinnity et al. (2009) which considers 37 years of egg to grilse survival of “wild” salmon from the Burrishoole system (derived from trap data) and shows *inter alia* that survival is significantly lower in years when the proportion of ranched fish escapement to upstream natural spawning areas is high. Ranched salmon on the Burrishoole system were derived from the native population more than 50 years ago. Small numbers of broodstock were used to found the original year classes and molecular differences are evident between ranched and wild salmon (and between cohorts of ranched strains) both at allozyme (Cross and King 1983) and microsatellite (McGinnity 1997) loci. While an effort was made each year to collect all ranched fish at upstream traps at the top of the tide, substantial numbers escaped upstream in certain years and presumably either spawned amongst themselves or with native salmon. Spawning success was probably variable in different groups (wild or ranched) as demonstrated by Fleming and colleagues in Norway (see above). It is notable that a similar finding has been made by Chilcote (2003) with steelhead trout *Oncorhynchus mykiss* in the western USA, suggesting, at least in salmonid fish, that stocking may be detrimental, rather than positive as usually presumed (see Ferguson, 2007).

### **3.2 Applicability to investigations of interactions between wild cod populations and deliberately-released reared fish**

The results for simulated stocking with salmon outlined above suggest caution in embarking on major ranching/enhancement stocking programmes with cod. This of course assumes random breeding and similar fitness differences between wild cod and any deliberate introductions, to those observed in salmon. As stated by Cross et al. (2007), it is extremely important to establish the purpose and likely results of any stocking exercise. Extrapolating from salmon, the effort seems more likely to be successful if trying to restore an extirpated population, than when trying to enhance a wild population. However, the marine environment of cod is much more complex than the riverine environment where salmon spawn and spend the first part of their life. Furthermore, species replacement may take place with cod preventing restoration of that species.

As discussed above, there are two important variables to be considered when extrapolating from salmon to cod. One is the aforementioned assumption of fitness differences between natives and stocked cod. The other is the difficult problem of

delimitating of cod populations (see above). Both should be initially addressed in modelling exercises, while quantification of comparative fitness would require field experiments, as outlined above.

#### **4 Possible indirect genetic mechanisms causing reduced fitness of introductions and suggestions for future research in cod**

A “common garden” field experiment with introduced wild Owenmore salmon progeny and Burrishoole natives in the same experimental stream described above allowed deEyto et al. (2007) to demonstrate direct genetic effect of allelic composition at the major histocompatibility complex MHC-2 locus on fitness in the wild. Similar numbers of parents from each of the populations were typed for eight presumed-neutral microsatellite loci and for VNTRs tightly linked to the immune competence loci coding for MHC-1 and 2. The neutral microsatellites allowed identification of fry, electrofished at the end of the first summer, back to parent families and thus to population of origin. At these loci and at MHC-1 there was no significant change in allele frequency between parent and progeny, but MHC-2 in the introduced Owenmore salmon showed a significant change in allelic composition over the same time period. This was cited by deEyto et al. (2007) as evidence of natural selection against particular MHC-2 alleles operating in the wild (with the selective agent presumed to be aquaculture-related disease organisms such as the furunculosis bacterium *Aeromonas salmonicida*). As mentioned above, there has been a hatchery operating on the Burrishoole system for more than 50 years producing smolts for ranching and latterly for farming, and furunculosis has been a problem. In contrast there are no aquaculture activities on the Owenmore system. Added to this, earlier Norwegian tank experiments with furunculosis-challenged post smolts demonstrated differential survival of certain MHC-2 alleles (Grimholt et al. 2003).

Similar experiments would be more complicated in cod because more than one locus is expressed at the MHC-1 and 2 complexes meaning that consideration of allelic effects is difficult. (The situation is less complicated in salmonids because one MHC-1 and one MHC-2 codes for most prominent immune-competence protein in each case.) However, investigation of MHC and other immune-related genes in cod would be important both in interactions studies and in the farming industry, where disease can be a considerable economic impediment. Consideration of other transcribed genes, potentially affected by natural selection in cod, such as pantophysin

(PAN-1) would also be useful in these contexts. Cod genome sequencing programmes are in progress in both Canada and Norway, and will provide large amounts of genomic data which can be “mined” for genes and SNPs (Mode 2) involved in adaptive response. Manipulation of these data should allow for greatly increased understanding of the genetic basis of disease resistance in cod and for investigation of the phenomenon of local adaptation.

## 5 Conclusions

1. Knowing more about wild cod population structure is vital (if populations are huge there might be very little problem with introductions, but the opposite must also be considered)
2. Development of novel markers (mode 1 and 2 SNPs) for cod and their use in interaction studies is recommended
3. Modelling cod interactions for fitness using salmon figures is suggested.
4. Interactions could be investigated with short generation time laboratory species like zebrafish *Danio rerio*.
5. Transcribed genes should be studied in cod, especially those related to immune competence e.g. MHC
6. Cod genomic data should be “mined” to establish help extent of local adaptation and study other aspects of their biology.
7. Genetics of disease organisms of cod, like the intra-cellular bacterium *Francisella* sp., should be investigated.
8. If possible, field experiments should be designed and set-up to empirically assess the scale of the problem in cod and other marine species, and to provide data to further “tune” the models.

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