Council

CNL(06)41

Scientific Advice from ICES – Assessing Genetic Effects

In the Request for Scientific Advice from ICES, adopted by the Council of NASCO at its Twenty-Second Annual Meeting in Vichy, France, CNL(05)12, ICES was requested *inter alia* to assess the genetic effects of the introgression of farmed Atlantic salmon on wild salmon populations. This paper contains the advice from ICES in response to this one question, and was presented at NASCO's Twenty-Third Annual Meeting.

CNL(06)41

Scientific Advice from ICES – Assessing Genetic Effects

2.4 To assess the genetic effects of the introgression of farmed Atlantic salmon on wild salmon populations (ToR e)

This text was based on a working paper prepared by P. McGinnity and Eric Verspoor; adopted by WGAGFM at Newport, Ireland in 2006.

2.4.1 Introduction

Since its origin in 1969, salmon farming in the North Atlantic has increased production to c. 800,000 million tonnes in 2004, with Norway and Scotland being the major producers in Europe. NASCO (2005) reports that during the same period the international catch of Atlantic salmon has declined from the 10,000 tonnes reported in the 1960s to 2,100 tonnes in 2005. Currently in the order of 2 million salmon escape from salmon farms each year in the North Atlantic, which is equivalent to about 50% of the wild pre-fishery abundance of salmon in this ocean. Escaped farm salmon comprise some 20–40% of the salmon in some North Atlantic areas and rivers with over 80% in some Norwegian rivers (Ferguson *et al.,* 2006). Farm salmon parr also escape from juvenile rearing units but the extent of this has been poorly studied.

Two decades of intensive research into the genetic impacts of farm escape salmon on natural populations has provided a substantial body of useful quantitative data. It is worth noting that this has been one of the best and most successful examples of the application of genetics in answering a difficult fisheries management question. For comprehensive reviews of this research, see Youngson and Verspoor (1998), Naylor *et al.*, (2005), Ferguson *et al.*, (2006), and most recently Hindar *et al.* (2006).

The objective of this paper is to briefly summarise the principal findings of twenty years of research into the genetic effects of the introgression of farmed Atlantic salmon on wild salmon populations, to report on attempts to incorporate the data arising from these studies into realistic life history impact models, to review some of the most recent research in the area, to summarise some of the implications of this research for the management of wild fisheries and to recommend useful avenues for future research.

2.4.2 Genetic impacts (taken directly from the summary presented in Ferguson *et al.*, 2006 with permission of authors)

Farm salmon are genetically different from wild stocks due to geographical origin, founding effects, and as a result of deliberate and accidental selection, and genetic drift, during domestication. Many farm salmon differences can be related to selection for faster growth and later maturity together with inadvertent changes affecting survival, deformity, feed conversion rate, spawning time, morphology, aggression, egg viability, egg production, and risk-taking behaviour.

Escaped salmon enter rivers generally adjacent to the site of escape but sometimes at considerable distances. These fish have been shown to breed, and interbreed with wild fish,

although the greater reproductive success of farm females relative to males, and differences in behaviour, mean that more hybrids are produced than pure farm offspring.

Farm salmon have both indirect and direct genetic effects on wild populations. Indirect genetic effects occur due to behavioural, ecological, and disease interaction thereby reducing the effective population size of the wild population and increasing genetic drift. In particular competition with farm fish and hybrids, which are larger, can reduce wild smolt production. Direct genetic effects occur due to interbreeding with wild fish and backcrossing in subsequent generations.

Farm salmon offspring and hybrids show substantially reduced lifetime success with poorer survival in the early juvenile stages and again in the sea. This results in a loss of fitness (reduced recruitment) in individual wild populations. Since farm escapes are regular occurrences, such reductions in fitness are cumulative and potentially lead to an extinction vortex in 'weak' populations (i.e. on the verge of self-sustainability).

Hybridisation and introgression can change the performance characteristics in wild populations with, for example, an increase in multi-sea-winter salmon in otherwise predominantly grilse populations, which may be desirable from an angling perspective in such rivers. However, given their reduced lifetime success, 'hybrids' do not compensate for the loss of wild recruitment resulting in a decrease in fitness in the population.

Hybridisation and introgression due to backcrossing will result in gene flow from farm to wild. As only a few farm strains are used throughout the industry, this gene flow will reduce the natural interpopulation heterogeneity found in Atlantic salmon, thereby reducing the adaptive potential of the species.

Genetically modified (transgenic) salmon would be expected to result in the same genetic effects as non-modified ones, both with respect to changes in genetic structure and with respect to fitness. However, the negative impact on fitness is likely to be even greater.

2.4.3 Incorporating data into life history models

Experimental studies confirm that in at least some situations escaped farm salmon can have major negative impacts on wild populations. However, the experimental work is confined to only a few of the potential escape interaction scenarios which are likely to exist. As such existing information is still inadequate for providing robust scientific information on the management of farm escapes in many situations. In light of the length of time and cost of undertaking experimental studies of a range of escape scenarios, the only realistic way forward is to develop predicative models which allow for risk assessment across the range if escape scenarios which could be expected to be encountered. This could range from a few farm escapes interbreeding with a large healthy population, in which case it would be unlikely that there would be a large negative impact, to a situation where you have a large continuous input into a small depressed population. Furthermore, in light of the fact that we know that farm escapes have this negative impact, the political will to support studies where we are deliberately releasing farm fish into control situations on a wide-scale is unlikely to be there and justifiably so. This means that the only realistic way forward to progress understanding and assess risk is through computer-based modelling of the data that has already been collected or that will collected in the future from a few dedicated facilities. In the case of Atlantic salmon this is a very real option because of the detailed understanding that already exists regarding the population dynamics of wild populations and the good understanding of the genetic implications of the interbreeding of farm and wild fish. Furthermore, in recent years theoretical geneticists have begun to develop realistic multilocus models of genetic structuring in populations (hybrid zone scenarios, etc.).

A recent example of the potential of modelling is Hindar *et al.*, (in press) where they provide a quantitative picture of the rapid change likely to occur in many wild populations as a consequence of farm escapes. Based on data from spawning and whole-river experiments, they model the future of wild salmon populations experiencing invasions of escaped farm salmon. Simulations with a fixed intrusion rate of 20% farm escapes at spawning suggest that substantial changes take place in wild populations within ten salmon generations. Lowinvasion scenarios suggest that farm offspring are unlikely to establish in the population, whereas high-invasion scenarios suggest that populations are eventually composed of hybrid and farm descendants. Recovery of the wild population is not likely under all circumstances, even after many decades of no further escapes. They also observe that managers of wild fish will have problems finding broodstock of the original wild population after a few generations of high intrusion rates.

A recent initiative to examine the scope for modeling and the ways forward has been put in place as part of the recently funded EU GENIMPACT community action where a workshop will review this issue. The workshop will bring together researchers working on farm wild interactions in a range of European aquaculture species with modelers attempting to identify the key research questions and the most optimum approach to answering questions and also to develop research initiatives for future EU funding. For example, from the work of Hindar *et al.* (2006), as well as others (Gilbey *et al.*, in prep; Bacon *et al.*, unpublished) have identified density-dependent factors as being critical in providing realistic outputs from these models. Furthermore, it is clear that the genetic model used also is critically important in determining the predictive power of these models.

2.4.4 Update of most recent research

Evolutionary change in farmed populations

Roberge *et al.* (2006) compared the transcription profiles of 3,557 genes in the progeny of farmed and wild salmon from Norway and Canada grown in control conditions and showed that five to seven generations of artificial selection led to heritable changes in gene transcription profiles (see Box 1), the average magnitude of the differences being 25% and 18% for at least 1.4% and 1.7% of the expressed genes in juvenile salmon from Norway and Canada, respectively. Remarkably, genes showing significant transcription profile differences in both farmed strains all exhibited parallel changes. The authors of this paper suggest that these findings, along with the identification of several genes whose expression profiles were modified through artificial selection, suggest how gene flow from farm escapes may affect the genetic integrity of wild populations. It also suggests that we are closer to understanding the specific genetic differences between farmed and wild stocks that are responsible for the fitness differences seen in the wild that arise due to selective breeding and domestication. Once these are understood this information can be used to provide more realistic genetic models of interactions, which can be used in modelling exercises.

Potential for indirect genetic effects of farm escapes on natural salmon populations

While direct genetic effects of introgression between wild and hatchery-reared salmon have been demonstrated (McGinnity et al., 2003), the impact of diseases originating from aquaculture (Håstein and Lindstad, 1991; Johnsen and Jensen, 1994; McVicar, 1997) on the genetic integrity of wild fish has not been addressed (E. deEyto, Marine Institute, Ireland, unpublished) compared genotype frequencies of Atlantic salmon (Salmo salar) surviving in a natural river six months after their introduction as eggs with frequencies expected from parental crosses. In order to distinguish between natural selection and other forces that might impact on genetic variation, they included eight putatively neutral microsatellite loci in the analysis as controls as well as immunogenetic loci (see Box 2) from both MHC class I and class II. They found that Atlantic salmon MHC class II alpha genes were under selection in the wild, while the MHC class I-linked microsatellite or at eight non-MHC-linked microsatellite loci were not. They concluded that selection at the MHC class II locus was a result of an immune response, rather than any demographic event. They also showed that survival was associated with additive allelic effects rather than heterozygote advantage at the MHC class II locus. These results have implications for both the conservation of wild salmon stocks, and also the susceptibility of hatchery fish to disease. The authors concluded that natural or hatchery populations have the best chance of dealing with episodic and variable disease challenges if MHC genetic variation is preserved both among and within populations.

Indirect genetic effects on co-occurring wild sea trout

Several studies have documented the genetic effects of intra-specific hybridisation of reared and wild Atlantic salmon, most notably Youngson *et al.*, 1993. However, the effects of salmon aquaculture on wild congeners are less well understood. It is possible that diseases, introduced or increased in incidence by salmon aquaculture activities, have the potential to impact co-occurring wild sea trout (*Salmo trutta* L.). Coughlan *et al.*, (in press) have recently presented data that suggests that salmon farming and ocean ranching can have an indirect genetic effect (most likely mediated by disease) on cohabiting sea trout by reducing variability at major histocompatibility class I genes. Samples of DNA extracted from scales taken from sea trout in the Burrishoole River, in the west of Ireland, before and at intervals during aquaculture activities, were investigated. In these samples allelic variation at a microsatellite marker tightly linked to a locus critical to immune response (*Satr-UBA*) was compared with variation at six neutral microsatellite loci. A significant decline in allelic richness and gene diversity at the *Satr-UBA* marker locus, that was observed since aquaculture started (and which may be an indication of a selective response), was not reflected by similar reductions at neutral loci.

2.4.5 Management considerations (taken directly from Ferguson et al., 2006)

- 1 The Guidelines on Containment of Farm Salmon, developed by the North Atlantic Farming Industry and the North Atlantic Salmon Conservation Organization (NASCO) should be the minimum standard for the construction and operation of fish farms. Research into further improving both technological and operation standards should be undertaken.
- 2 Smolt rearing units should not outflow into salmon rivers (as already required in Norway).
- 3 Marine cages should not be situated within 30km of salmon rivers.

- 4 Where escapes occur, appropriate recovery plans and resources should be available for immediate deployment.
- 5 Further investigations in the use of triploids and other bioconfinement methods should be undertaken.
- 6 If it is intended to introduce sterile transgenic salmon in the industry in the future, research should be undertaken, prior to permission being granted, to determine the ecological impact that such fish may have on wild populations.

Additional recommendations

- 7 Building of realistic working simulation models, which can be used to assess risks of direct genetic interactions, which can be used to identify research priorities.
- 8 Research into indirect genetic and ecological impacts associated with issues such as introduction disease and effects of density-dependent population dynamics.
- 9 Spatial and temporal studies.

Box 1

Transcription profiles are the direct intensity measurements of "gene expression" levels for individual genes using DNA "micro-array" technology. "Gene expression" is the term used to describe the transcription of the information contained within the DNA, the repository of genetic information, into messenger RNA (mRNA) molecules that are then translated into the proteins that perform most of the critical functions of cells. A DNA "micro-array" is a tool for analysing gene expression that consists of a small membrane or glass slide containing samples of many genes arranged in a regular pattern. It works by exploiting the ability of a given mRNA molecule to bind specifically to, or hybridise to, the DNA template from which it originated. By using an array containing many DNA samples the expression levels of hundreds or thousands of genes within a cell can be determined simultaneously in a single experiment by measuring the amount of mRNA bound to each site on the array. With the aid of a computer the amount of mRNA bound to the spots on the microarray is precisely measured, generating a profile of gene expression in the cell.

Box 2

The genes of the major histocompatibility complex (MHC) encode proteins that play a crucial role in the vertebrate immune response and several lines of evidence suggest that MHC variability is maintained by pathogen-driven balancing selection.

2.4.6 References

- Ferguson, A., Fleming, I., Hindar, K., Skaala, Ø., McGinnity, P., Cross, T., and Prodöhl, P. 2006. Farm escapes. *In* The Genetics of Atlantic Salmon: Implications for Conservation. Ed. by E. Verspoor, J. Nielsen and L. Stradmeyer. Blackwell, Oxford. (In press)
- Håstein T., and Lindstad, T. 1991. Diseases in wild and cultured salmon: possible interactions. Aquaculture, 98: 277–288.
- Hindar, K., Fleming, I. A., McGinnity, P., and Diserud, O. 2006. Genetic and ecological effects of salmon farming on wild salmon: modelling from experimental results. ICES Journal of Marine Science, 63: xx-xx.
- Johnsen, B.O., and Jensen, A.J. 1994. The spread of furunculosis in salmonids in Norwegian rivers. Journal of Fish Biology, 45: 47–55.
- McGinnity, P., Prodöhl, P., Ferguson, A., Hynes, R., Ó Maoiléidigh, N., Baker, N., Cotter, D., O'Hea, B., Cooke, D., Rogan, G., Taggart, J., and Cross, T. 2003. Fitness reduction and potential extinction of wild populations of Atlantic salmon *Salmo salar* as a result of interactions with escaped farm salmon. Proceedings of the Royal Society of London, Series B, 270: 2443–2450.
- McVicar A.H. 1997. Disease and parasite implications of the coexistence of wild and cultured Atlantic salmon populations. *ICES Journal of Marine Science*, 54: 1093–1103.
- NASCO, 2005. Report of the Twenty-Second Annual Meeting of the Council. CNL(05)50, North Atlantic Salmon Conservation Organization, Edinburgh. 591 pp.
- Naylor, R., Hindar, K., Fleming, I.A., Goldburg, R., Williams, S., Volpe, J., Whoriskey, F., Eagle, J., Kelso, D., and Mangel, M. 2005. Fugitive salmon: Assessing risks of escaped fish from aquaculture. BioScience, 55: 427–437.
- Roberge, C., Einum, S., Guderley, H., and Bernatchez, L. 2006. Rapid parallel evolutionary changes of gene transcription profiles in farmed Atlantic salmon. Molecular Ecology, 15: 9–20.
- Youngson, A.F. and Verspoor, E. (1998). Interactions between wild and introduced Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences, 55: (1): 153–160.