International Council for the
Exploration of the Sea

C.M.1991/M:3
Ref.: Mariculture Committee

THÜNEN

REPORT OF THE STUDY GROUP ON
GENETIC RISKS TO ATLANTIC SALMON STOCKS

Copenhagen, 13-15 March 1991

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1 INTRODUCTION

1.1 Terms of Reference

The terms of reference were as follows (C.Res.1990/2:40):

The Study Group on the Genetic Risks to Atlantic Salmon Stocks (Chairman: Mr A.F. Youngson, UK) will meet at ICES Headquarters from 13-15 March 1991 to:

a) review, consolidate and report on the current status of techniques to detect changes in Atlantic salmon stocks due to interbreeding of wild and cultured populations;

b) provide the experimental design for a research programme to evaluate the possible effects (including genetic, ecological and behavioural interactions) of fish farm escapees of Atlantic salmon on wild stocks;

c) hold a joint session with the Working Group on North Atlantic Salmon to discuss the research programme in b) above;

d) report to the Anadromous and Catadromous Fish and Mariculture Committees at the 1991 statutory meeting.

1.2 Members of the Study Group

Mr J. Browne	Ireland	Mr H. Jansson	Sweden
Dr T.G. Carey	Canada	Mr K. Jørstad	Norway
Dr T. Cross	Ireland	Mr G. Nævdal	Norway
Dr W.S. Davidson	Canada	Dr T.R. Porter	Canada
Dr A. Ferguson	UK	Dr J.A. Ritter	Canada
Mr K. Goryczko	Poland	Dr A.B. Thompson	UK
Mr S. Gudjonsson	Iceland	Dr E. Verspoor	UK
M R. Guyomard	France	Professor W. Villwock	Germany
Dr L.P. Hansen	Norway	Professor N.P. Wilkins	Ireland
M Y. Harache	France	Mr A.F. Youngson	UK

1.3 Present at the Study Group Meeting

J. Browne	Ireland
W.S. Davidson	Canada
K. Friedland	USA
L.P. Hansen	Norway
H. Jansson	Sweden
K.E. Jørstad	Norway
E.C.E. Potter	UK
R. Porter	Canada
R.L. Saunders	Canada
E. Verspoor	UK
A.F. Youngson (Chairman)	UK

1.4 Approach to Terms of Reference

Having regard to its terms of reference the Study Group decided to approach its tasks in the following way.

a) By identifying the types of problems which may arise:

   i) assessing the evidence for genetic differentiation among wild Atlantic salmon populations, its extent and its geographical basis (Section 2);

   ii) identifying genetic differences which may exist between wild and farmed salmon populations in single localities caused by management of salmon in culture (Sections 3 and 4); and

   iii) identifying the ways in which the character of local stream populations of salmon might be expected to be altered by the spawning of escaped farmed fish among indigenous wild fish (Section 4).

b) By identifying the range of biochemical genetic techniques available for field or experimental work, their particular advantages and constraints on their use (Section 5).

c) By considering the design of experimental work to determine the consequences of the spawning of escaped farmed salmon, having regard to a) and b) above (Sections 6-8).

2 GENETIC VARIATION AMONG ATLANTIC SALMON POPULATIONS

2.1 Population Structure

Atlantic salmon are divided into a large number of more or less reproductively isolated populations or stocks. These can have either non-anadromous or anadromous life histories. Non-anadromous populations are found throughout most of the species range in eastern North America (Scott and Crossman, 1973) and also occur in many areas of Scandinavia (Berg, 1985). Between watersheds, the reproductive isolation of non-anadromous populations from each other and from anadromous populations is ensured by land barriers. Within watersheds it is facilitated by obstructions to movement such as waterfalls and by genetically and environmentally controlled behavioural factors. These include limited migration and movement as well as unknown factors preventing interbreeding where populations are sympatric. For example, even though anadromous and non-anadromous forms can interbreed (Hutchings and Myers, 1985), reproductively separate populations of the two forms can exist sympatrically within some river systems (Verspoor and Cole, 1989; Birt et al., in press).

Anadromous salmon are also divided into a large number of more or less reproductively isolated populations as a consequence of their homing to natal rivers to spawn. Most studies have found that more than 90% of Atlantic salmon return to their natal river system after their ocean migration (Huntsman, 1950; Hawkins et al., 1979; Went, 1969; Larsson, 1974). Huntsman's (1950) work also showed homing to tributaries within rivers. The strength of this homing within river systems is indicated by recent studies on the Girnock Burn in Scotland, a small 9 km tributary of the River Dee. Using coded wire microtags salmon hatched in the Girnock Burn were shown to make up a variable part of the adults spawning later in the stream but at least 90% of the 2SW females spawning in 1990 had left the stream previously as smolts (Hay et al., in prep.).

There are several assumptions in the comparisons of straying rates within a watercourse and the genetic structure between the populations. The observed straying frequencies (5-10%) are in agreement with the genetic structure observed, but must be maximum values. Studies on spawning success under controlled

conditions and measurements on reproductive success suggest that the combination of "strayer genes" into the population is much lower, possibly 1-2% (see also Section 2.3).

We are lacking empirical data on the effective straying frequency expressed as reproductive success. Such measurements are, however, necessary to evaluate the effects of the gene flow.

2.2 Evidence for Genetic Differentiation

The sub-division of Atlantic salmon by restricted patterns of interbreeding, geographically or temporally, may lead to genetically differentiated populations over time. This may occur through genetic drift, peculiarities in gene flow and natural selection for genetic types adapted to local environmental conditions. Genetic differentiation may occur with respect to either the nuclear or the mitochondrial genomes. The nuclear genome, the primary pathway of inheritance is represented by two copies, one from each parent, while the mitochondrial genome is derived exclusively from the female parent.

Genetic differentiation among Atlantic salmon populations could potentially take two forms. Differences could be with respect to the type and frequency of alleles present at individual genetic loci or they could be with respect to how the genetic loci are organised physically into chromosomes. These are the basic physical units of inheritance. Genetic differentiation has been assessed in two ways. One is through direct studies of individual loci and of the physical nature of chromosomes. The second is indirectly by assessing the heritability and population divergence of phenotypic traits.

2.2.1 Individual genetic loci

Nuclear genome

Visual polymorphisms: There are no known visual polymorphisms in Atlantic salmon determined by allelic variation at single genetic loci, such as that reported for spotting in the brown trout Salmo trutta (Skaala and Jørstad, 1987).

Protein polymorphisms: Genetic variation among populations has been examined at over 40 genetic loci coding for enzymatic proteins (Cross and Ward, 1980; Ståhl, 1987). More than 300 populations from across the species' range have now been assessed (Ståhl, 1987; Ståhl and Hindar, 1988; Verspoor, 1986, 1988a,b; Koljonen, 1989; Crozier and Moffett, 1989; Verspoor and Jordan, 1989; Jordan, 1990; Verspoor et al., in press). This has led to an extensive data base too detailed to review here but the following generalisations can be made:

a) The genetic variation within populations over time is generally less than differences among populations, even within river systems (Jordan, 1990; Verspoor et al., in press).

b) Significant genetic differences can exist between salmon populations in different tributaries within most moderate and large river systems (Ståhl, 1987; Ståhl and Hindar, 1988; Verspoor et al., in press).

c) Genetic differences increase with increasing geographic distance between populations (Ståhl, 1987; Verspoor, 1988a; Verspoor and Jordan, 1989; Jordan, 1990).

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d) Genetic differences are:

    i) 3-5 times greater between continents than within continents.

    ii) 1-2 times greater among regions than within regions.

    iii) 1-6 times greater among rivers within regions compared to among populations within rivers (Ståhl, 1987; Jordan, 1990).

    iv) sufficient to allow classification of the majority of individuals captured at West Greenland to continent of origin with a high degree of accuracy (Verspoor, 1988a; Verspoor and Reddin, in prep.).

Non-protein coding DNA: Molecular genetic methods are now being applied to the direct study of genetic loci using locus-specific nuclear DNA probes (see Section 5.2.6). Initial results have been achieved using probes which identify genetic loci coding for hypervariable repeat DNA sequences (Taggart and Ferguson, 1990a,b). These are the loci used to produce DNA "fingerprints". These loci show large numbers of alleles. Differences in allele frequencies between rivers within Northern Ireland appear to exist at the loci studied.

Ribosomal RNA genes have also been examined for genetic variation and appear to allow populations from Europe and North America to be distinguished (Cutler et al., in press). Recently attempts have been made to use this procedure to assess the continental composition of Atlantic salmon in the West Greenland fishery. To date the results are inconclusive and additional populations need to be included in the data base.

Mitochondrial genome

Restriction site polymorphisms: Restriction endonucleases which cut DNA at specific base sequences have been used to detect the presence or absence of restriction sites in mitochondrial DNA. These result in what are frequently referred to as restriction fragment length polymorphisms or RFLPs.

Population differences have been found with respect to fragment patterns produced by various enzymes. Differentiation, as for nuclear protein loci, appears to be greatest between continents (Bermingham, 1990; Birt et al., in press; McVeigh et al., in press). Some regional differences may exist within continents (Bermingham, 1990; Knox and Verspoor, in press). However, population studies to date are too limited so assess the extent of differentiation with any accuracy. Differences have also been detected within regions between rivers (Davidson, unpublished; Verspoor and Knox, unpublished) within rivers (Hovey et al., 1990) and between allopatric (Palva et al., 1989) and sympatric populations (Birt et al., in press) of anadromous and non-anadromous forms.

2.2.2 Chromosomal structure

Nuclear genome chromosome number and arm number

Studies of Atlantic salmon chromosomes are constrained by technical difficulties. Most studies suggest a difference in both chromosome number (2N) and arm number (NF) between European (2N=56-58, NF=74) and North American (2N=54-56, NF=72) (Hartley, 1987, 1988). However, Nygren et al. (1972) found no difference between salmon from the two continents and Barsiene (1981) found salmon with

both NF=72 and 74 in Russia. There is evidence that Spanish populations have higher frequencies of non-modal 2N numbers compared to populations in Scotland and Norway (Garcia-Vasquez et al., 1988, 1991).

Chromosome structure

Techniques which differentially stain DNA depending on its physical and chemical nature indicate that there may be continental differences in patterns of C bands and in the presence of quinacrine staining (Q) bands (Philips and Hartley, 1988). No differences between populations within regions have been found as yet (Hartley, 1988). The patterns of chromosome banding have been used in other species to detect polymorphisms for inversions of chromosome sections. G-banding, the general type of analysis employed in these studies, has not been observed in Atlantic salmon chromosomes. This means that we do not know whether or not salmon chromosomes are polymorphic in this regard.

The mitochondrial genome consists of a single, circular DNA molecule. No specific information exists on gene order variation among populations but given the conservative nature of mitochondrial genome in other species this seems unlikely.

2.2.3 Phenotypic variation with a genetic basis

Saunders (in press) has updated his review (Saunders, 1981) of phenotypic traits which appear to show heritable variation among stocks.

These are:

- egg size;

- survival to various life stages

- rate and pattern of growth

- body form

- precocious sexual maturation of male parr

- age of smolting;

- age and size at sexual maturity

- seasonal pattern of adult return from the sea

- resistance to disease

- resistance to low pH

Additionally, circumstantial evidence suggests that stock differentiation within respect to the following traits also has a genetic component:

- fecundity

- seaward migration

- migratory behaviour at sea

- multiple spawning

This list is limited to those traits on which studies have been done. These represent some of the more important traits know to show variation among populations. These traits provide only a glimpse into the full extent of the underlying genetic variation which controls phenotypic diversity. Most of the studies have been based on comparisons of river populations within regions. There are few studies of differences between populations within rivers and between regions or continents. Additionally, most variable phenotypic traits, if studied, would be expected to show a genetic component to that variation, though the genetic contribution may in many cases be small. Some or all of these traits may be subject to selection and lead to adaptive genetic differentiation among populations with respect to the loci involved.

2.3 Estimates of Genetic Exchange among Populations

Estimates can be made of the historical average amount of genetic exchange among populations from the observed genetic differentiation at neutral loci (Slatkin, 1985). The estimate is expressed as the average number of individuals among a population's successful breeders, which have been exchanged with other populations per generation. The estimate for exchanges among physically isolated non-anadromous populations in Newfoundland is 0.5 fish (Verspoor, in prep.). For exchange among populations within river systems the value varies from 3.8 to 22.5 fish (Jordan, 1990; Verspoor et al., in press). Values for 2.3 to 3.9 have been obtained for exchange between rivers within regions (Ståhl, 1981; Jordan, 1990; Verspoor, in prep.), of 3.5 and 2.1 for exchange among regions within continents and of 0.5 for exchange between continents (Jordan, 1990). These values may be less than actual straying rates as they relate only to straying which results in the incorporation of the strayed genes into the native gene pool.

It is not possible to translate these values into a proportion of the population exchanged without historical knowledge of the effective size of breeding populations. These are not known because individual spawning success (including male parr) has not been measured. However, it is reasonable to assume that tributary populations are likely to number at least several hundred fish in the case of those rivers for which between tributary estimates of exchange have been made. If so, then the proportion of breeders in these tributaries which are non-native is likely to be in the order of 5%. Among rivers, effective numbers exchanged are lower, population sizes are larger and genetically effective straying will be lower - probably less than 1%.

2.4 Evidence for Adaptive Genetic Differentiation

Our understanding of the adaptive importance of the genetic differentiation observed is limited. One clear example of genetic adaptation is the difference in resistance to the skin parasite Gyrodactylus salaris observed between Baltic and Norwegian salmon (Bakke et al., 1990). The difference allows Baltic salmon to survive in association with the parasite. However, Norwegian salmon have become extinct in many rivers where the parasite has been introduced.

Genetic variation at one enzymatic locus, MEP-2*, shows a consistent association with environmental temperature (Verspoor and Jordan, 1989; Verspoor et al., in press) which indicates an adaptive genetic response. It is not known whether this directly involves the locus or results from linkage with one or more other loci affected by selection. However, genetic variation at the locus is also as-

sociated with variation in maturation (Jordan et al., 1990) and growth performance (Jordan, 1990). There is also some circumstantial evidence for genetic differentiation among populations at the transferrin locus being the result of an adaptive response (Verspoor, 1986).

Genetic variation associated with many of the population differences in phenotypic traits discussed above (maturity, fecundity, homing and body morphology) are likely to be adaptively important. This is clear where traits such as resistance to disease and survivorship are concerned (eg Standal and Gjerde, 1987). However, convincing proof in the form of experimental studies is lacking for most traits. This is the result of the difficulties of performing selection studies under natural conditions. The only case where insight has been gained is the study on juvenile body morphology by Riddell and co-workers (Riddell and Leggett, 1981; Riddell et al., 1981) in which heritable variation in body shape and fin size were associated with water flow conditions. Although experimental demonstration of the differential adaptation of different genetic types was lacking, Claytor and MacCrimmon (in press) have shown a general association of water flow conditions with body morphology consistent with Riddell's prediction.

Hansen and Jonsson (1991) have demonstrated a clear genetic component to the seasonal return patterns of populations which are very likely to be adaptively relevant and further study may demonstrate this specifically.

The genetic basis of most performance characters is polygenic. Many adaptations may involve functional complexes and even structural assemblages of genes integrated as co-adapted gene complexes. It should be noted that the adaptive state of individuals or the adaptive capacity of populations may depend on maintaining the integrity of these units.

2.5 Summary

In spite of the large number of studies which have been performed our understanding of the genetic differences among Atlantic salmon populations is limited. It has been possible to assess only a part of the genetic variation in a small proportion of the genetic loci in the nuclear genome of the salmon. For these loci, almost exclusively coding for enzymatic proteins, the understanding of population differentiation is informative although Atlantic salmon appear to be generally less variable than the other salmonid species. How representative these loci are of genetic variation in the nuclear genome as a whole is not clear. It has been suggested that variation among the regulatory loci which control the expression of structural genes, is likely to be greater. Higher levels of variation also appear to be the case for the non-coding hypervariable DNA loci.

Genetic variation in mitochondrial DNA is expected to be greater than that in nuclear DNA coding for proteins (Moritz et al., 1987) because the mitochondrial genome lacks the endogenous capacity for repair present in the nuclear genome. The mitochondrial genome might therefore be expected to accumulate mutations more rapidly. However, population studies have so far been limited and we do not as yet have a clear picture of the relative differentiation of populations with respect to the two genomes.

Our understanding of the extent of genetic differentiation among Atlantic salmon can be summarised as follows:

a) Significant genetic differences exist among populations even within river systems.

b) Genetic differentiation among anadromous populations increases with increasing geographic distance between their native locations.

c) Genetic differentiation between continents is greatest. This is observed with respect to allele frequencies, the presence and absence of alleles, chromosome number and chromosome structure in the nuclear genome and with differences in the frequencies.

3 TRANSFER OF STOCKS

3.1 Introduction

Stocking of rivers has been carried out for a long time in all countries supporting salmon. In the past many transfers were made both between and within countries. On the whole these introductions were probably unsuccessful because the methods of stocking were unsatisfactory. In recent years, fewer fish have been moved for restocking rivers.

However, the development of cage-rearing has resulted in extensive movements of salmon between and within countries. Motivation for distant transfers of stock includes the expectation of faster growth or later maturity. Other transfers have reflected local shortages of eggs or smolts or the availability of cheaper smolts or eggs elsewhere.

Because of the relatively large genetic difference between North American, European Atlantic and Baltic salmon, most concern has been expressed regarding transfer of fish between these areas.

3.2 Scotland

The following data have been derived from government documentation of disease certification since 1984. Approximately 11.6 million ova have been imported to Scotland from Norway in repeated imports from multiple source farms and hatcheries, 2.8 million from Sweden from two source farms, 0.9 million from Finland in two imports from the same source and 30 thousand from Eire in a single import. Many farmed fish in Scotland have been derived from Norwegian source rivers, directly or through supplies of ova from Norwegian farms.

Transfers of ova within the UK are not documented centrally. It is possible that transfers of ova from within the UK have been made to farms in Scotland.

Within Scotland, transfer of ova from the eastern rivers to fish farms, which are almost exclusively located in western and northern marine locations, has been both common and widespread; most Scottish farmed fish of Scottish river origin have been derived from eastern Scottish rivers. The use of farmed strains based on the wild populations of western rivers is uncommon.

The mixing of farmed strains founded on different source populations has almost certainly been extensive. In general, the provenance of stock in Scottish fish farms is not fully documented and in many cases it is not known.

The exchange of strains among farms within Scotland is also largely undocumented.

In the past decade, farmed juveniles have been released deliberately into many rivers throughout Scotland, including eastern rivers, in attempts to enhance

adult returns. More recently, this practice has reduced because of an awareness of the possible adverse consequences of such stocking.

3.3 Ireland

Cross and Ni Challanain (in press) established the origins of lines of farmed salmon in Ireland as part of a study of the genetic constitution of farmed fish. Responses to a questionnaire covering 80% of Irish smolt production in 1989 showed that the five most common lines were of Scottish or Norwegian origin. Five additional lines, comprising a total of less than 10% of production, had been derived from either Irish or foreign sources.

3.4 Canada

The number of regional stock transfers for aquaculture has been minimal. The Saint John River stock is preferred in Bay of Fundy aquaculture. This stock has been transferred to Newfoundland where it is being tested as an aquaculture stock in comparison with local stocks. Saint John River fish have also been transferred to Nova Scotia where they are being assessed for aquaculture in that province.

3.5 England and Wales

Extensive stocking has been and still is undertaken in England and Wales; many eggs and juvenile salmon of Scottish origin have been introduced into English and Welsh rivers. The effects of these transfers are not known. Eggs from one land-locked salmon stock originating in Maine, USA have been introduced into Wales but the fish have not been released into rivers.

There is now no salmon farming in England and Wales. One salmon farm operated in Wales for a period in the 1980s rearing fish of Scottish origin; this unit has now ceased to operate. However, smolts of Norwegian and Scottish origin are reared in England to support the Scottish salmon farming industry.

3.6 Norway

Until 1987, smolts from Scotland, Iceland, Finland and Sweden (Baltic salmon) were imported to the country because of a lack of smolts in the aquaculture industry. In 1987, all imports of smolts to the country were banned. At present, about 70% of the eggs used in the industry originate from the Fish Farmers Breeding Station. This strain was originally a mixture of many Norwegian river stocks and has been selected for economically important characters for about 20 years.

3.7 Sweden

In Sweden, salmon farming is a small industry and uses only Swedish stocks.

3.8 USA

Atlantic salmon mariculture, concentrated in north eastern Maine, is based mainly on Penobscot (Maine) and Saint John (New Brunswick) River populations. In

the past, Scottish, Norwegian, Icelandic and Finnish salmon have been introduced to Maine. These fish are being or have been grown in sea cages.

4 GENETIC DIFFERENCES BETWEEN WILD AND CULTURED SALMON

Genetic differences between wild and cultured salmon in particular regions of localities can become established deliberately or inadvertently. They may comprise differences in performance characters or in neutral characters.

4.1 Sources of Difference

4.1.1 Stock differences

The most basic level of sources of difference has been considered in the previous sections of this report. Firstly, wild salmon populations are variable with respect to selectively neutral genetic characters and with respect to performance characters. Secondly, fish farmers have commonly chosen to use non-local wild populations to found farmed strains. Non-local wild populations have been used widely within countries and transfers of ova between countries, have also been common.

Transfers between localities have often reflected the availability of large numbers of ova from particular sources. However, in many cases the progeny of particular wild populations have been sought out because the overall character of the wild populations or some special attribute seemed especially consistent with the aims of culture. Usually, the basis of choices like these has been intuitive; decisions were made without any systematic knowledge of wild populations with respect to the desired traits. An alternative approach has been to obviate the necessity for making these choice by selecting wild source populations on the basis of a preliminary assessment of the performance in culture of salmon drawn from many wild populations. Farmed strains of salmon have been founded in Norway in this way.

4.1.2 Selective breeding

The second level of sources of difference is the application of the processes of selection in deliberate attempts to alter the character of founding stocks. Indeed, it is the express intention of most fish farming operations to improve (in the sense of making the average cultured fish a more valuable commodity) founding stocks for culture and to continue the process in each generation.

Some of the target traits for selection are almost certainly of adaptive relevance in the lives of wild fish. Selection can be practised for basic life-history traits such as age at smolting, growth and age at sexual maturity (Refstie et al., 1977; Gjedrem, 1978; Bailey et al., 1980; Gjerde, 1984; Bailey and Loudenslager, 1986). Production traits such as flesh colour and carcass weight can also be altered by selection (Gjerde and Gjedrem, 1984). It is less easy to envisage the possible adaptive significance of traits like these for wild populations. However, many of the performance and production traits being examined show partial inter-dependence and may also be correlated with other unrecognised traits of adaptive importance.

Major enterprises in Norway and Canada have adopted the techniques of individual and family selection in dedicated research units. Commercial production units almost invariably apply the less powerful technique of mass selection to the same ends. Evaluating the progress of selection schemes in salmon aquaculture

has been especially difficult in the absence of adequate control groups of fish (or in most cases, in the total absence of control) and because continual improvement of culture techniques has altered the environmental background in which genetic constitution is expressed.

In Norway, collection of eggs from 40 different river populations constituted the basis for test programmes (Gjedrem et al., 1988). Offspring from the strains were compared for different performance characters (mortality, growth rate, age at maturity, etc). Based on measurements of such characters, a farmed stock of salmon was constructed from the best performing river strains and families. The existing large scale breeding programme is organised by the Fish Farmers Organisations and carried out at the breeding stations at Kyrksæterøra and Sundalsøra. A number of multiplying stations are also incorporated in the breeding system and eggs from the organised breeding system constitute about 70-75% of the total market.

The origin of the present farmed strain was 40 river populations. The actual number of river populations in each of the four different year classes constructed was much lower. A detailed analysis of the contribution of the original stocks in the present farmed strain today has revealed that very few river populations (1-5) dominate the present farmed stock in Norway (Gjedrem et al., in press).

In Canada, the Salmon Genetics Research Programme (SGRP) is developing four strains for the New Brunswick mariculture industry in the Bay of Fundy. These strains are based on the Saint John River, New Brunswick mixture of stocks collected at the Mactaquac dam midway up the river. The SGRP is serving as the primary breeder supplying smolts to a number of marine growers. Selection for incidence of yearling smolts, marine growth and age at maturity is progressing with encouraging results. The Saint John River mixture of stocks produces grilse to multi-sea-winter salmon in a ratio of about 1:1 in nature; the incidence of grilse in strains developed from this stock mixture is much lower in the Bay of Fundy aquaculture conditions, possibly because low sea temperature affects sexual maturation.

The improvement in performance of the farmed strains is measured in several ways. As controls, offspring from wild fish are used in Norway and also an unselected line is used as comparison for the selected line in both Norway and Canada. In addition, in Norway milt is stored at low temperature and used for constructing control groups in later generations.

In both Norway and Canada the effects of domestication/selective breeding are demonstrated in the performance and behaviour of the fish under farming conditions. The results of selection so far have been improvements in growth rate and in response to handling, as well as a reduction in early maturation - in Norway at least.

4.1.3 Inadvertent effects

A third source of genetic difference between wild and cultured salmon arises when inadvertent change results from the conditions of culture themselves. Thus, passive selection may result when the probability of any individual's survival to stripping is dependent on some unrecognised genetic attribute or where the choice of broodstock is conditioned by some unrecognised genetic trait. Indeed, experience suggests that avoiding passive selection is difficult even when deliberate attempts are made to do so. Total mortality rates before sexual maturity are much lower in culture than in the wild and this relaxation and alter-

ation of selection may also be a factor in any genetic divergence of wild and cultured stock. Finally, human errors may lead to the groups of fish being mis-classified according to their genetic history.

4.2 Variable Genetic Characters

4.2.1 Performance characters

Differences in performance among wild populations of salmon have been covered in Section 2.2.3 above. The existence of local genetic adaptations in wild popu-lations which have a strong selection basis might be expected to reduce the re-productive success of farmed escapes and the survival of their progeny. However, where natural selection in streams occurs at lesser intensities, local adap-tations in stream populations may be disrupted more permanently. Some of the target traits for selection in culture are almost certainly of adaptive rel-evance in the lives of wild fish. Some of the others may be correlated with un-recognised traits of adaptive importance. It is possible to envisage how changes in the character of local stream populations of salmon might be altered by the presence of escaped farmed fish from strains which have been subject to delib-erate or inadvertent selection.

4.2.2 Neutral characters

Extensive comparisons of genetic differences between wild and farmed salmon stocks have been made by examining allele frequencies at variable protein loci. This variation is usually assumed to be selectively neutral in the sense that differences in genotype at single protein loci are unlikely to affect the out-come of fishes' lives. However, it can be inferred that any pressures which cause change in the distribution of variation at neutral loci are likely to act on other loci in a qualitatively similar manner.

In some studies, reduced genetic variability has been demonstrated in groups of farmed salmon. Thus, average heterozygosity at protein loci was lower in farmed salmon groups than in wild fish and this was attributed to bottle-necking caused by the use of low numbers of founding broodstock (Cross and King, 1983; Ståhl, 1983). The relationship between broodstock numbers and genetic variability was demonstrated specifically by Verspoor (1988b). Variability was not demonstrably reduced among farmed strains in culture in Scotland but differences in allele frequencies were shown to exist between wild Scottish fish and farmed fish (Youngson et al., in press). These were attributed in part, to the presence in farms of strains of salmon of Norwegian origin, differing both from wild Scottish fish and from farmed fish based on wild Scottish populations, because of regional differences in allele frequencies. However, differences were also evident in comparisons of farmed strains with the specific wild populations on which they had been founded. These were attributed largely to the effects of genetic drift.

Exceptionally in these comparisons, allele frequencies at the MEP-2* locus ap-peared to have shifted directionally to increase the frequency of the 125 allele in farmed strains in one year of study. This suggested that inadvertent, passive selection had occurred, perhaps because of performance differences among the MEP-2* genotypes; variation at the MEP-2* locus appears to violate the general assumption of neutrality for variable protein loci (Verspoor and Jordan, 1989; Jordan et al., 1990; Jordan, 1990). However the presence of a directional shift in MEP-2* allele frequencies could not be confirmed in a subsequent, independent test of the hypothesis (Youngson et al., in press).

With the possible exception of variation at the MEP-2* locus, changes in local allele frequencies caused by the spawning of escaped farmed fish may not have direct effects on the character of local wild populations - other than on allele frequencies themselves. However, regional, and particularly clinal, variation in the frequencies of neutral genetic characters may be associated with adaptive genetic variation; in wild salmon populations geographical and genetic distance are correlated across the species' range. Reduced genetic variability in farmed salmon and the spawning of escaped fish might be expected to reduce variability in wild populations on a local basis. The spawning of escaped fish which differ from indigenous fish through the effects of bottle-necking or genetic drift might be expected often to raise levels of genetic variation in stream populations. On a wide scale however, both these effects would be expected to be less marked, since bottle-necking and drift will affect allele frequencies at single variable loci in a random manner. As a result, the magnitude of any overall effects should diminish according to the genetic/geographical distance over which the founding stock was displaced, the number of independently bred escaped fish spawning at any locality, the cumulative number of years in which spawning takes place and the distances over which escaped fish stray before spawning.

4.2.3 The effects of domestication

An experiment was conducted in Norway to assess the interaction of domesticated and wild salmon and the success of domesticated salmon spawning in an artificial stream channel (B Jonsson, pers. comm.). Secondary sexual characteristics were poorly developed in the domesticated fish. They were observed to be unsuccessful in spawning with wild salmon. The domesticated males did not participate fully and none were observed to spawn. Some wild males mated with domesticated females but these did not dig proper redds; the redds were shallow and poorly covered.

These observations contrast with studies carried out both in Scotland and Canada. In Scotland, escaped fish entered the River Polla and spawned in large numbers six months after major accidental damage to a farm nearby. Spawning was demonstrated specifically in the case of females where single redds could be assigned to farmed or wild females according to whether the pigment canthaxanthin was present in the ova each redd contained (Webb et al., in press). However, it was shown by observation and radiotracking that farmed males and particularly farmed females differed from native wild fish in tending to spawn lower in the river. They also differed in tending to spawn later in the autumn, overcutting some of the redds made earlier by wild fish. Farmed and wild fish were observed to pair and to cross. It is intended to confirm this specifically by genetic analysis of the progeny of single redds and of the adults which were observed to spawn there. Part of the study is being repeated now, following the return of another group of escaped fish to the river.

In Canada, observations were made in the Port Daniel river on first generation farmed salmon intentionally released into the river. Farmed males were observed to spawn successfully with wild or famed females; farmed females spawned with wild or farmed males. Furthermore, farmed males were classed as more aggressive than wild males (M Le Gault, pers. comm.). It was also observed that the farmed salmon were not able to ascend the·river beyond a small waterfall which was not a barrier to the movement of wild salmon.

5 BIOCHEMICAL GENETIC TECHNIQUES

5.1 Background Considerations

5.1.1 Assumptions

The species Salmo salar is thought to consist of many stocks or populations that form distinct breeding units (see Section 2.1). It is assumed that these populations have been separated from one another, both spatially and temporally, sufficiently long enough that they have become fixed for different alleles in different populations. A combination of these fixed loci gives rise to an adaptive gene complex that has been selected as a result of the environmental and physical characteristics of a particular population's habitat (eg length of river, flow rate, average temperature, etc). These assumptions lead to the hypothesis or prediction that it should be possible to identify segments of the genome that will act, individually or in groups, as genetic markers for different levels of organisation within the species. These markers have been and continue to be the target of salmon geneticists. The null hypothesis that they do not exist cannot be proved but it should not be discounted.

5.1.2 Genetic markers

The loci involved in adaptive gene complexes are subject to positive selection. However, the majority of polymorphisms that are detectable by biochemical, cytogenetic or recombinant DNA techniques are considered neutral or subject primarily to purifying selection (i.e., the removal of deleterious alleles). Where there are exceptions, they are likely to be found in electrophoretic variants of proteins. These polymorphisms may be maintained by balancing selection as a result of yearly fluctuations of environmental factors such as temperature. Although it would be desirable to monitor those loci that are subject to environmental selection, this is not yet possible. We are, therefore, constrained by technology and history to those polymorphic loci that are easily detected. As a result, the alleles examined are subject to random drift rather than selection and, although their frequencies may vary, it is usual to find the majority of all possible alleles in a given population (Davidson et al., 1989). One potential means of measuring an impact on a population is to detect a significant change in these allele frequencies.

5.1.3 Practical considerations

When considering which genetic markers and techniques to use to monitor interactions between populations, it is important to bear in mind the practical problems that may arise. It is likely that fortuitous experiments (e.g., large escapes from commercial sea cages) will have to rely on detecting changes in allele frequencies. Background information concerning allele frequencies of the domesticated fish and the natural population to be monitored is essential. It can then be determined how many samples will be required to detect a significant change in any allele frequency. The cost per sample, including the initial capital cost of equipping a laboratory to carry out the procedure, must be estimated. The ease of doing the analysis and the reproducibility of the technique from laboratory to laboratory are also important considerations. In addition, one must decide if it is necessary or desirable to monitor both maternal and paternal lineages. These factors are not trivial points. If large sample sizes will be required to detect any differences in allele frequency one must also consider how the removal of these samples (if invasive methods are to be used) will affect the system being studied.

5.2 Methods

5.2.1 Allozymes

Allozymes, or protein electrophoretic variants, have been used most extensively to study Atlantic salmon populations. Although many loci have been examined relatively few are polymorphic (Ståhl, 1987; Verspoor, 1988a). In those which have been examined it is extremely rare to get fixed differences between different populations (Davidson et al., 1989). An investigation of additional loci may produce some more polymorphic loci as was the case in chinook salmon (Shacklee and Phelps, 1990). Some alleles may be subject to selection (Jordan et al., 1990) and this could confuse interpretation of results. The advantage of this procedure is the low cost, ease of the technique and the number of samples that can be processed per day.

5.2.2 Chromosomes

Karyotypic differences exist in Atlantic salmon as the result of Robertsonian fusions and fissions (Hartley, 1988). The chromosome number may vary but the arm number usually remains constant. There appear to be major differences in chromosome number between salmon populations from North America and Europe (see Section 2.1.2.2). However, sample sizes are small as are the number of populations studied. This is because it is rather an elaborate procedure and is unreliable. Good chromosome preparations are difficult to produce routinely and interpretative problems results from examining poor preparations. This procedure is unlikely to be used routinely to monitor population interactions.

5.2.3 Mitochondrial DNA - restriction enzymes

Three distinct mitochondrial genotypes have been detected using restriction endonucleases. These may be referred to as the Baltic type, the European type and the North American type (Bermingham, 1990). The European type has been detected in the northern range of Atlantic salmon in North America (Birt et al., in press; McVeigh et al., in press). It would be feasible to use the North American genotype in an experimental introduction into a European river however, as there are no reports of the North America genotype being detected in Europe. Restriction enzymes that have four base pair recognition sites will probably continue to detect rare genotypes in different populations (Palva et al., 1989; Hovey et al., 1990). These rare genotypes may occasionally be present at high enough frequencies to be used as genetic markers (Knox and Verspoor, in press). The procedures require a well equipped laboratory to isolate purified mitochondrial DNA if restriction enzymes that recognise four base pairs are to be used. The number of samples that can be processed is limited and the procedure is expensive.

5.2.4 Mitochondrial DNA - polymerase chain reaction

A new procedure involves amplifying a specific region of DNA using the polymerase chain reaction (Kocher et al., 1989). The region is defined by oligonucleotides that recognise specific sequences that flank the region to be amplified. The process relies on a heat-stable DNA polymerase and cycles of heating and cooling the sample. This technical innovation allows one to prepare microgram quantities of the specific region of interest from a crude preparation of DNA from a small amount of tissue (e.g., 100 mg of muscle or 50 l of blood). The amplified DNA may then have its nucleotide sequence determined by standard procedures. This method has been applied to the Atlantic salmon's cytochrome b

gene (McVeigh et al., in press). The nucleotide sequence is the most fundamental unit of genetic information. The results of analysing over 240 salmon from more than 20 populations from both sides of the Atlantic indicate that there is very little genetic variation in salmon compared to tuna (four species) (Bartlett and Davidson, 1991); Atlantic cod (Carr and Marshall, 1991); or capelin (Davidson and Birt, unpublished observations). Only three genotypes were detected. One corresponded to the European genotype detected by restriction endonucleases and two others comprised sub-sets of the North American genotype. The Baltic genotype is being analysed at present. Other regions of the genome (e.g., the ATPase 6 region) identify rainbow trout from different river systems (Beckenbach et al., 1990). This is not the case for Atlantic salmon (McVeigh and Davidson, unpublished results). The D-loop region is thought to be the most variable region in the mitochondrial genome and this segment is being studied but no results are available yet. This is a highly specialised procedure that requires a dedicated laboratory for efficient analysis. It is expensive and time-consuming but gives the greatest possible information. The procedure may be adapted to nuclear genes in addition to mitochondrial genes. A well set up laboratory could handle 60 samples a week routinely.

5.2.5 Minisatellite probes - fingerprinting

This procedure, developed by A Jeffries, makes use of polymorphisms that are the result of different numbers of tandem repeats of a nucleotide sequence, usually 13-16 base pairs long (VNTRs - variable number of tandem repeats). This method is used primarily to identify an individual (e.g., in a forensic setting) rather than to define populations. Work with salmonids indicates that Jeffries' probes hybridise to many bands on a southern blot (>40) (Taggart et al., 1990a). This makes the interpretation of banding patterns to difficult and so single-locus probes based on the Jeffries' probes are being developed (see below). DNA fingerprints can also be produced using the bacteriophage M13 as the probe (Fields et al., 1988). A more easily interpreted pattern is seen (usually 6-10 bands). In a small preliminary study involving benthic and pelagic populations of Arctic charr from Loch Rannoch, Hartley found that there were one or more bands that were common to fish from one population but they were absent from all charr from the other population. This procedure will be tested on Atlantic salmon populations in April 1991 but no results are available at the moment. This technique requires a basic molecular biology laboratory. Although expensive, many samples (eg 50) can be processed per day.

5.2.6 Minisatellite probes - single-locus probes

This procedure is a development of DNA fingerprinting. Instead of many bands, only two bands are detected (one strong band in a homozygote). Preliminary studies by Taggart and Ferguson (1990a,b) have shown that this procedure works in Atlantic salmon and that each locus has between five and seven alleles (even in a small sample from only four river systems). However, the alleles are distributed among rivers rather than confined to one particular river. Future studies with more populations are required to address this question and these are in progress. Like DNA fingerprinting above, this procedure can screen many individuals at several loci, all of which are highly polymorphic. This requires a good molecular biology laboratory and the cost is primarily in producing and characterising the probes. Single-locus probes may be the key to rigorous experimental studies (see Section 7).

5.2.7 Additional techniques

Recent development in other fields (eg forensic science, tissue typing, gene mapping) is having an impact on population genetics. The major histocompatibility complex (MHC) is one of the most polymorphic regions of the human genome. The products of the MHC genes are associated with disease resistance. In humans, these alleles are identified using specific oligonucleotides and the polymerase chain reaction. This gives rise to AmpFLPs (amplified fragment length polymorphisms). The corresponding region in salmon will be worth examining because it may yield additional polymorphic markers from genes of known function. Another approach that has worked well in scallops (E. Zouros, Marine Gene Probe Laboratory, Dalhousie University, pers. comm.) is to use randomly picked cDNA clones to search for RFLPs. Approximately one clone in three produced polymorphisms in scallops. A vitellogenin cDNA detects RFLPs in Atlantic salmon (Davidson, unpublished results). As above with the MHC loci, this produces polymorphic loci at genes which may be adaptively relevant. An additional class of polymorphisms has recently been developed using random oligonucleotides and the polymerase chain reaction (Williams et al., 1990). This has revealed many polymorphic loci in other systems but the nature of the mutations is totally unknown. A general philosophy is to be aware of developments in other systems and to apply them to the study of salmon populations.

5.3 Conclusions

The biochemical genetic techniques exist to construct genetically marked groups of fish for comparison in experimental work of the general type considered in Section 7. The same techniques can be used in opportunistic study (Section 8) in many of the multiplicity of possible protocols which can be envisaged.

Some of the more recent techniques have not yet been sufficiently developed to assess their likely usefulness (and their limitations) either in monitoring the interactions of escaped fish with wild fish or as a basis for experiment (e.g., karyotyping). None of the established techniques can be discounted in all circumstances. Some of them are well-documented but have equally well-defined limitations (e.g., allozyme variation). Some are particularly suited for use in local circumstances or to test specific hypotheses (e.g., restriction analysis of mitochondrial DNA). Some procedures are probably too expensive or time-consuming to be used on the large numbers of samples which many studies would generate but future technical developments may alter this balance (e.g., the use of the polymerase chain reaction).

Overall, the Working Group's assessment, on three grounds, is that the use of locus specific probes among the current techniques, is likely to prove most powerful in the medium term. Firstly, locus specific variation is almost certainly adaptively neutral. Secondly, those probes which have been examined reveal relatively high levels of variability, even among the small numbers of populations and individuals which have been studied so far. Finally, in the near future the use of the probes may become a routine procedure within the range of most laboratories. However, the techniques are not yet sufficiently developed for general use or yet widely available.

Technical development continues. Novel molecular techniques such as the polymerase chain reaction/direct nucleotide sequencing and the use of minisatellite probes are being applied to Atlantic salmon population genetics. Their potential for revealing population-specific markers is still hard to assess. It is likely however, that these answers will be known by the end of 1992. Whatever the results, these procedures require the skills of someone trained as a molecular biologist. If laboratories are interested in carrying out population genetic

studies on Atlantic salmon or in monitoring the impact of one population on another, then it is essential for the laboratories to consider whether they want to establish their own molecular biology laboratory or start collaborating with groups already established.

6 PREVIOUS STUDIES OF RELATIVE PERFORMANCE IN WILD AND FARMED SALMONIDS

Wild Atlantic salmon populations are diverse with respect to characters which may well prove to have a genetic basis. Widespread movements of farmed stock between locations have occurred. Farmed stocks have been subject to deliberate and systematic attempts to alter their genetic constitution. Inadvertent genetic effects can be shown to have occurred in farmed Atlantic salmon stocks. Many other salmonid species have been propagated in culture and have probably been subject to the same pressures. It might be expected that some genetic changes would affect the performance of farmed salmon relative to wild fish in a measurable way.

The interactive performance of farmed and wild Atlantic salmon competing in the same natural environment has not yet been examined. However, related experimental studies have been performed on Atlantic salmon and other salmonid species (Skaala et al., 1990; Hindar et al., in press, Table 1). In the current context, the most pertinent studies have been performed on oncorhynchids.

Bams (1976) compared adult returns of Oncorhynchus gorbuscha introduced to the Tosolum river in British Columbia from a donor stock with returns of crosses between the native and donor stocks. More crosses than pure donor stock returned as adults. Overall returns of crosses were comparable to those expected of native stock and this was attributed specifically to the male parental component of the cross. However, the accuracy with which crosses homed to the original tributary of release was impaired relative to that expected for native fish.

Reisenbichler and McIntyre (1977) examined growth and survival of Oncorhynchus mykiss stocked into natural streams or a hatchery pond, using an allele at a variable protein locus as a marker. In stream conditions survival of the progeny of wild fish was greater than that of the progeny of farmed fish or crosses between wild and farmed fish; the crosses grew largest. The progeny of farmed fish grew best and suffered least mortality in the hatchery pond.

Chilcote et al. (1986) reported that the average individual reproductive success of summer-run Oncorhynchus mykiss of hatchery origin spawning in streams was 70% lower, to the smolt stage, than that of native fish. Genetic variation at the AGP-1* locus was used as a genetic marker. The fast allele at this locus was rare among wild fish and its frequency was increased among hatchery-bred fish for subsequent release by crossing females with male parents of chosen genotype. The progeny of hatchery fish, which had been released at 14 months of age, were predominant in the study stream after spawning. The effects of lower individual success of hatchery-bred fish were out-weighed by their greater numbers at spawning.

In a sequel to this latter study, Leider et al. (1990) documented further reductions in the relative performance of the progeny of the natural spawning of wild steelheads and fish of cultured origin. The mean frequency of the progeny of cultured fish diminished from 85% at the egg stage to 42% as adults. Original reproductive success diminished from 0.8 to 0.1 for cultured fish relative to wild ones, between the sub-yearling and adult stages.

7 DESIGN OF EXPERIMENTAL STUDIES

Two general approaches to determining the ecological, behavioural and genetic effects of the spawning of escaped farmed fish on wild populations of Atlantic salmon can be envisaged. One of these approaches might be to perform opportunistic study (Section 8). The other is to construct experimental studies to test specific hypotheses on the relative performance of fish of farmed origin and native wild fish competing in a natural stream.

The most general form of such an experiment was considered previously by the study group (Appendix 1). An important consideration of a general study is that it shall not be confounded by any necessity to maintain the groups of fish to be compared separately, in culture. This would be necessary in any study making use of conventional physical marks which can be made on or retained by only relatively large juveniles. As an alternative, variable protein markers might be used as intrinsic marks of the progeny of adults of selected genotype. The proposed scheme was designed to control for the possible non-neutrality of allozyme markers but given the recent development of probes for hypervariable non-coding loci, it is possible to consider simplifying the scheme considerably. Multiple rather than single comparisons might be made in single rather than in duplicated stream sections. Variation at these non-coding loci might be used as genetic markers, in the assumed absence of effect or by testing for effects within any experiment.

The variables to be considered for any experiment intended to compare the performance of the progeny of wild and farmed fish are numerous, adding further complexity to experimentation. The variables can be identified as follows:

a) The year in which comparison is made.

b) The chosen site (including the presence of competing species).

c) The genetic character of its native salmon population.

d) The farmed stock (including its genetic distance from the native wild population, its time in culture and the level of genetic variability within the farmed group).

e) The relative densities in which the farmed and native fish compete.

f) The use of pure farmed stock or the progeny of crosses with native fish.

g) The interactive effects of a-f.

A number of performance variables might be measured and compared in any experiment ranging through juvenile mortality and growth, age at smolting, time of smolt migration, marine mortality and growth, age and time of adult return. However, survival rates, reproductive performance and location of spawning are of over-riding importance. They will determine the strength of any genetic effect in future generations in the population being studied. Straying will determine the spatial, geographical distribution of the effect among other populations.

Studies like these might well demonstrate that differences exist in the performance of the progeny of wild and farmed fish but the large number of potential variables, some almost certainly uncontrolled, will limit generalisation from single experiments. Moreover, interpretative difficulties will exist when differences are demonstrated in characters which bear an uncertain relation to those characters of wild populations which are considered of value. Many of the valued characters are subjective and qualitative.

The Study Group discussed the different ways in which genetic effects of escaped farmed fish interbreeding with wild stocks might be manifest. It was felt that the possible effects might occur at a number of biological levels, as follows:

a) Genotypic changes.

b) Phenotypic changes.

c) Changes in the quality of salmon produced.

d) Changes to quality of salmon produced (e.g., size, season of return, age at return, etc).

e) Changes in the present or future adaptive capacity of the population.

Thus effects might occur only at the genotypic level, or they might also extend in varying degrees to the level of the phenotype where selection operates. At this level effects may have implications for the quantity of salmon produced by affecting fitness or may lead to alteration of the character of the population. Ultimately, genetic changes may effect the long term adaptive capacity of the population.

Consideration can be given to the risk associated with these categories of change - but the risks cannot be defined quantitatively. The group recognised that decisions on the acceptability of any change is dependent on the social, cultural, scientific or economic value placed on the original genetic make-up of the population. These considerations are beyond the scope of the group's remit.

8 OPPORTUNISTIC STUDY

An alternative means of assessing the effects of the spawning of escapes on native salmon populations might be to adopt an opportunistic approach, exploiting situations which may arise unintentionally (e.g., Webb et al., in press). As a result of accidents in fish farming, escaped farmed fish are present in many natural streams in localities where sea cage rearing is carried out - sometimes in large numbers. Escaped fish are present in lesser numbers in many streams distant from cage rearing sites. The effectiveness of this approach is likely to be limited where baseline information is not available on the native population. Even in more favourable circumstances, associations between the spawning of escaped fish and subsequent change will be uncertain, given the high year-on-year variation, sometimes cyclical, which wild populations show for many of those characters which have been examined.

9 CONCLUSIONS

As a result of aquaculture, local and systematic genetic differences between wild and cultured fish probably exist. Wild Atlantic salmon populations vary widely with respect to a number of genetic characters which have been studied. Most of these are probably adaptively neutral. Population have also been shown to differ with respect to performance characters, some of which almost certainly have a genetic component. This area of research has not been adequately studied.

These differences will have resulted from stock movements and from selective and inadvertent breeding effects. The size and the scope of the differences are likely to increase in future years as a result of continued development of aquaculture.

Escapes from aquaculture occur and it must be assumed that they will continue to do so. Fish of farmed origin are widespread in north east Atlantic fisheries and in some localities they are frequent (Anon., 1990, 1991; Gausen and Moen, 1991; Okland et al., 1991). Indeed, escaped fish now appear to out-number native fish in some rivers in Norway and Scotland. Escaped farmed fish spawn in rivers (Lura and Seagrov, in press; Webb et al., in press).

If farmed fish are genetically different from local wild populations, genetic changes will occur when escaped farmed fish spawn. If the progeny survive to re-produce these changes will persist. The techniques exist which will make it possible to examine genetic change in a rigorous experiment and to examine the ecological and behavioural interactions of groups of salmon of mixed origin, competing at single locations.

Other less rigorous and less comprehensive experiments will still yield useful information more rapidly and at lower cost. These will expand the body of knowl-edge which already exists and provide a fuller basis for making appropriate man-agement decisions. It will never be possible to derive all the information necessary to make management decisions in full knowledge of the consequences. In view of this, management of both farmed and wild populations should pursue con-servative strategies.

Thus, the productivity of fisheries and their genetic diversity should be moni-tored according to quantitative parameters. Where possible, steps should be taken to ensure that both are maintained.

The Study Group noted that many of the potential interactions between farmed and wild fish identified in this report might be alleviated rapidly by the general use of triploid female salmon in aquaculture. Triploid females are effectively sterile and it is possible that many will not even enter fresh water. Unfortu-nately, achieving 100% triploidy rates by heat or pressure treatment of eggs - the usual method of treatment - is difficult. In future more complex manipu-lations of ploidy in broodstock may resolve this difficulty.

10 RECOMMENDATIONS

a) That research on the effects of escaped farmed fish on natural populations of Atlantic salmon (particularly relative reproductive success and gene intro-gression) should be encouraged in the context of more general studies of local adaptation in salmon populations.

b) That these studies should be undertaken cooperatively and integrated by the parties involved to maximise the information gained given the many variables involved and the likely costs of the research.

c) That the occurrence of escaped farmed fish should be exploited in unplanned experiments to explore the mechanisms which segregate natural populations.

d) That future research should aim to give direction to management, with a view to tempering any effects which escapes of salmon from culture may be shown to have on wild populations - when this is considered necessary.

e) That management decisions, designed to reduce the risk of genetic impacts by farmed fish, be based on the body of information which exists now, since scientific understanding has increased less rapidly than aquaculture has grown and this may continue to be the case.

f) That the use of sterile, triploid salmon in the aquaculture industry be en-
   couraged, as widely as possible, to reduce the genetic risks which escaped
   farmed fish may pose to wild salmon populations.

g) That the work of the Study Group on the Genetic Risks to Atlantic Salmon
   Stocks be suspended but that its status be reconsidered at the 1993 Statutory
   Meeting of ICES.

h) That, in the interim, any specific questions be directed to the North
   Atlantic Salmon Working Group, the Genetics Working Group, or the
   Introductions and Transfers Working Group, as appropriate.

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12 LIST OF WORKING PAPERS

Jørstad, K.E., Skaala, Ø., and Nævdal, G. Genetic interactions between formed and wild population. New information from a trout model study.

Saunders, R.L. and Porter, T.R. Canadian contribution to ICES Study Group on Genetic Risks to Atlantic Salmon Stocks.

APPENDIX 1

GENERIC EXPERIMENTAL DESIGN FOR DETERMINING
GENETIC, ECOLOGICAL AND BEHAVIOURAL PERFORMANCE IN NATIVE AND INTRODUCED SALMON

The relative performance of native wild salmon and introduced salmon or crosses between the two groups competing in a natural stream might be compared in the following experimental designs. Ideally, performance ought to be compared in all its aspects from hatch until spawning, finally comparing reproductive success in terms of hatched progeny.

Any study will be compromised by any necessity to rear juveniles in tanks to the stage where the different groups can be marked by physical means. The alternative approach is to mark the groups at the outset with a genetic marker by crossing adults of known genotype.

If the neutrality of the effects of the genetic markers on performance is assumed, multiple comparisons may be made in single stream systems.

If neutrality cannot be assumed a more complex experimental design can be envisaged as follows, but it requires access to paired stream sites which can be controlled, at least temporarily, to prevent natural spawning.

Group	Stream 1			Stream 2		
	1	2	3	4	5	6
Genotype	AA	BB	AB	AA	BB	AB
Source	native	farmed or hybrid	native, farmed or hybrid	farmed or hybrid	native	native, farmed or hybrid

For any performance character it will be possible to assess the stream effect by comparing group 3 with group 6. The source and genotype effects can also be assessed. Further, source-genotype interactions can be investigated for the homozygote conditions.

The results of any experiment of these types will be site specific.